

When sex is not enough: ecological correlates of resprouting capacity in congeneric tropical forest shrubs

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Abstract In moist tropical forests resprouting may be an important component of life history, contributing to asexual reproduction through the clonal spread of individuals derived from shoot fragments. However, in contrast to other ecosystems where resprouting is common, the ecological correlates of resprouting capacity in tropical forests remain largely unexplored. In this study we characterized shade tolerance, resprouting capacity and sexual reproductive success of eight co-occurring *Piper* species from lowland forests of Panama. In field experiments we found that shade-tolerant *Piper* species had a higher capacity to regenerate from excised or pinned stem fragments than light-demanding species in both gap and understory light conditions. In contrast, shade-tolerant species had lower recruitment probabilities from seeds, as a consequence of lower initial seed viability, and lower seedling emergence rates. All *Piper* species needed gap conditions for successful seedling establishment. Of 8,000 seeds sown in the understory only 0.2% emerged. In gaps, seed germination of light-demanding species was between 10 and 50%, whereas for shade-tolerant species it was 0.5–9.8%. We propose that the capacity to reproduce asexually from

resprouts could be adaptive for shade-tolerant species that are constantly exposed to damage from falling litter in the understory. Resprouting may allow *Piper* populations to persist and spread despite the high rate of pre-dispersal seed predation and low seed emergence rates. Across *Piper* species, we detected a trade-off between resprouting capacity and the annual viable seed production per plant but not with annual seed mass produced per plant. This suggests that species differences in sexual reproductive success may not necessarily result from differential resource allocation. Instead we suggest that low sexual reproductive success in the understory may in part reflect reduced genetic diversity in populations undergoing clonal growth, resulting in self-fertilization and in-breeding depression.

Keywords Asexual reproduction · Life history · *Piper* · Seed germination · Shade tolerance

Introduction

For most plant species, abundance and distribution are strongly influenced by the low probability that seeds survive and develop into established seedlings (Grubb 1977; Swaine et al. 1997; Dalling and Hubbell 2002; Svenning and Wright 2005). The recognition of this limitation, and the inference that variation in early life history characteristics might explain the coexistence of numerous species, has motivated much research on the regeneration ecology of plants (Grubb 1977; Denslow 1987; Garwood 1989). Consequently, the intrinsic and extrinsic factors influencing seed dispersal, seed germination, and seedling establishment success have been studied in detail. In contrast, surprisingly little is known about the traits that influence the frequency of an

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alternative asexual recruitment pathway via resprouting (Bond and Midgley 2001). The term “resprouting” is usually used to refer to vegetative growth of rooted plants after loss of biomass (Bellingham and Sparrow 2000), and may also include vegetative growth from plant fragments (Klimešová and Klimeš 2003). Here we consider resprouting of broken plant parts to be a form of asexual reproduction, since newly detached plant fragments can be dispersed and recruit in the population as “new” individuals.

Important determinants of the relative frequency of resprouting at the community level are thought to be disturbance frequency and site productivity (Clark 1991; Bellingham and Sparrow 2000). According to the Bellingham and Sparrow model, resprouting is favored over seed production at sites with intermediate disturbance and low to intermediate productivity, whereas seed production is favored in productive sites and when disturbance is either moderate and rare or severe and frequent (but see Klimešová and Klimeš 2003). Given that successful resprouting depends on stored resources (Sagers 1993; Bond and Midgley 2003) diverted from seed production (Chapin et al. 1990), a trade-off between the ability to resprout (asexual reproduction) and seed production is expected (Iwasa and Kubo 1997; Bond and Midgley 2001). Ample literature on fire-prone ecosystems has explored this tradeoff and had found that, in general, a dichotomy exists where nonresprouters produce more seeds and show greater seedling growth and survival than congeneric resprouters growing in the same site (reviewed by Bond and Midgley 2003), and that a general shift at the community level in allocation to resprouting versus seedling regeneration occurs across disturbance gradients (Clarke and Dorji 2008). A similar trade-off has been suggested for hurricane-prone forests (Bellingham et al. 1994); however, this trade-off has not been explored in tropical forests that lack frequent large disturbances. The generality of the resprouting—seed regeneration trade-off, also known as the persistence—recruitment tradeoff, needs further tests in a wide range of species and ecosystems.

In tropical forests levels of disturbance and productivity vary among micro-sites. Forest understories are low-productivity environments relative to forest gaps and clearings because of low light availability. Furthermore, plants growing in the understory are exposed to higher rates of mechanical damage than plants in gaps (Aide 1987; Gartner 1989; Clark and Clark 1991; Guariguata 1998; Paciorek et al. 2000) resulting from litterfall from the canopy overstory. Therefore, in the context of Bellingham and Sparrow’s (2000) model, shade-tolerant species that complete their life cycle in the understory should have a higher resprouting capacity but lower sexual success than light-demanding species. In support of this view, Putz and Brokaw (1989) found that light-demanding species tend to

have fewer trees of resprout origin than shade-tolerant species, and Zimmerman et al. (1994) found a strong positive correlation between shade tolerance and frequency of resprouting rates in response to hurricane damage. Nonetheless, Paciorek et al. (2000) did not find a simple relationship between the relative shade tolerance of a species and its annual resprouting rate for trees in the 50-ha forest dynamics plot on Barro Colorado Island (BCI), Panama. Because these studies rely on observations of naturally occurring resprouting success, it is difficult to evaluate whether high resprouting success in shade-tolerant species is simply the result of a higher rate of damage by falling debris in the understory compared to gaps (Uhl et al. 1988; Aide 1987; Gartner 1989; Clark and Clark 1991; Guariguata 1998; Paciorek et al. 2000), or if it reflects a greater ability of shade-tolerant species to resprout when damaged. Moreover, these studies have not been accompanied by seed production data, preventing an evaluation of this aspect of the persistence—recruitment trade-off in tropical forests.

Resprouting from fragments and bent shoots is a common means of asexual reproduction in a variety of tropical plant species (Gartner 1989; Kinsman 1990; Greig 1993b; Sagers 1993); however, the ecological correlates of this mode of reproduction have rarely been explored. In this study we examined whether light requirement and a reproductive resource allocation trade-off can account for species differences in asexual reproductive success among eight species of *Piper* shrubs in the semi-deciduous tropical forest on BCI. *Piper* spp. are known to reproduce asexually by fragmentation and layering (Greig 1993b), and exhibit a broad range of life histories ranging from light-demanding species to strongly shade-tolerant species. Using *Piper* as a model system we addressed the following four main questions:

1. Are there functional traits that separate the eight *Piper* species according to their shade tolerance?
2. Are there differences in resprouting capacity among species and shade-tolerant groups?
3. Are there differences in seed production and seed germination among species and shade-tolerance groups?
4. Do differences in sexual versus asexual reproductive capacity provide evidence for trade-offs that influence recruitment success in this species-rich genus?

Materials and methods

Study site and study species

This study was conducted in the tropical semi-deciduous forest of the Barro Colorado Nature Monument (BCNM),

a 5,600-ha forested area which includes BCI in Gatun Lake and the adjacent peninsulas on the mainland. Most field experiments were conducted on BCI, while the experiments in gaps were conducted on the Buena Vista Peninsula, about 1 km north of BCI. BCNM is located in Panama (9°10'N, 79°51'W) and is described in detail elsewhere (Leigh 1999). Annual rainfall on BCI averages 2,600 mm, with a pronounced dry season between January and April.

The genus *Piper* is represented by 22 species on BCI (Croat 1978), including both light-demanding and shade-tolerant species. Here we focused on eight common species. Five species are usually found growing in the understory, *Piper dariesensis* C.DC., *Piper cordulatum* C.DC., *Piper aequale* Vahl, *Piper grande* Vahl., and *Piper schiedeana* Steud.; and three species are usually found in gaps and clearings *Piper dilatatum* L.C. Rich, *Piper marginatum* Jacq. and *Piper peltatum* L. (personal observation).

Characterization of species' shade tolerance

To characterize shade tolerance we used a suite of leaf functional traits: leaf life span, specific leaf area (SLA), leaf N and C content, and C assimilation rate, all of which are known to vary with species' habitat preferences (Reich et al. 1992, 1999; Ackerly and Reich 1999). Light-demanding species exhibit short leaf life span, high SLA, high N concentration and C assimilation rates, whereas shade-tolerant species present the opposite suite of characters. All measurements were taken for 25 reproductive-sized plants of each species, whereas leaf longevity data were obtained from a subset of 10–15 individuals per species. Given that habitat type influences trait values we searched for individuals of all species in all light environments. Most light-demanding species were found and sampled in clearings and gaps, and all shade-tolerant species were found and sampled in the understory. The distance between plants ranged from 50 to 1,000 m.

Light environment

Total photosynthetically active photon flux density (PPFD; mol m⁻² day⁻¹) was estimated from hemispherical photographs as a measure of the light environment of each plant. Relative measures of light availability among sites taken with hemispherical photographs correlate well with direct measurements made with quantum sensors (Engelbrecht and Herz 2001). Photos were taken directly above each plant with a Nikon Coolpix 950 equipped with a fisheye lens. Photos were taken on overcast days or early and late in the day. The images were analyzed using the software program Gap Light Analyzer (version 2; Frazer et al. 2000).

Leaf gas exchange, structure (SLA) and chemistry (%N and %C)

During December 2004 and January 2005 measurements of C assimilation were made with a portable gas exchange system (LI-6400; Li-Cor, Lincoln, Neb.). Measurements were taken between 0800 and 1100 hours on one newly matured leaf per individual at 400 μmol mol⁻¹ CO₂, under saturating light (1,400 μmol m⁻² s⁻¹ PPFD) using the red-blue light source LED attachment of the Li-6400. Leaf temperature was maintained at 30°C. For plants in the understory, leaves were previously induced in a stepwise fashion at PPFD levels of 400, 600, 800 and 1,000 μmol m⁻² s⁻¹ before maximum photosynthesis (A_{\max}) was measured. For light-demanding species, A_{\max} increased until 1,400 μmol, and for shade-tolerant species photosynthesis saturated earlier (around 300–500 μmol) but no inhibition was observed at higher light levels. Leaves were then removed. After the leaf area was measured, leaves were dried for 1 week at 65°C and weighed to calculate SLA (cm² g⁻¹). Percent total leaf N (%N) and C (%C) were then determined using a CHN analyzer-elemental combustion system (ECS 4010; Costech Analytical Technologies, Valencia, Calif.).

Leaf longevity

Starting in January 2000, newly expanding leaves from all individuals were tagged using colored wires. Leaves from the same cohort were all coded with the same color. Every month, for 1 year, new leaves were labeled. Monthly surveys of leaf loss were conducted for 3 years to record the number of leaves still present from each cohort. Complete records for 3 years were only possible in 10–15 plants of the original 25 plants. Mean leaf life span for each individual was calculated as $\frac{\sum T_{iF} - T_{iL}}{N}$, where T_{iF} is the time when the i th leaf was recorded fallen, T_{iL} is the time when that same leaf was first labeled, and N is the total number of leaves labeled on the plant.

A principal component analysis (PCA), using leaf trait and light environment data was computed. Comparisons of leaf traits among species were performed with a one-way ANOVA. Differences among species were evaluated with Tukey's studentized range test. Data were tested for normality and homogeneity and transformed as necessary.

Interspecific variation in resprouting ability

Three experiments were conducted to determine whether species differ in the ability to regenerate asexually. In each experiment we assessed the ability to resprout from fragmented shoots; resprouting ability can be equated here with

asexual reproductive ability as resprouts yield new individual plants (ramets). Resprouting events were recorded as successful when new leaves were observed emerging from the fragment.

Survival of cuttings in the green house

The ability to resprout from fragments under well-watered, herbivore-free conditions was measured in the green house under two light treatments. A high light treatment received 40% of full sunlight at midday, and a low light treatment received 2% of full sunlight. Each light treatment was replicated on three benches. On each bench, we placed six large trays (80 × 40 cm) filled with forest soil and with two cuttings of each species, for a total of 12 cuttings per species per bench. Survival of individual cuttings was assumed to be independent and the proportion of the 12 cuttings surviving on each bench was the response variable used in the analysis. Cuttings were taken from the low-mid portion of branches and consisted of a stem fragment with at least two nodes. All cuttings were approximately the same size (12–15 cm long) to control for potential differences in survival and growth related to resource availability in the fragment. Cuttings were obtained from at least ten plants per species and were randomly assigned to treatments. Cuttings were inserted in the soil so that the lower node was completely covered. Cuttings were watered every other day. The experiment began in February 2003; six months later the number of surviving cuttings was recorded.

A mixed model ANOVA was carried out to compare species differences in cutting survival under different light environments. The main fixed effects were light treatment and shade tolerance with species nested within shade tolerance.

Survival of cuttings in the field

A second experiment, established at the beginning of the wet season in June 2003, compared survival of fragments across the range of habitats in which *Piper* species are usually found (gaps, understory slopes and understory plateaus). Fragments were transplanted into four 7 × 8-m artificially created gaps in secondary forest on the Buena Vista Peninsula, on BCNM, and into four similar-sized experimental blocks in the understory of BCI. Understory blocks contained two adjacent plots, one located on a ridge-top plateau and one on a slope 30–50 m below the plateau. The plots were spread over the north-east part of BCI. All slope plots had a similar slope (28–30°). In each plot, 25 cuttings of each species were randomly assigned to separate 1-m × 1-m subplots laid out 0.5 m apart. All cuttings were approximately the same length (mean = 15 cm, with at

least two nodes). Cuttings of a given species were obtained from at least ten plants. Cuttings from all plants were pooled and then randomly assigned to plots. Each cutting was inserted in the soil so that the lower node was completely covered, and approximately 3–4 cm deep. Cuttings were planted 15 cm apart from each other. During the study there were no signs of above-ground competition (no crown overlap); however, we cannot discount root competition. Cutting survival was followed for 3 years.

To test for species differences in cutting survival, the proportion of the 25 cuttings surviving in each sub-plot was compared using a nonparametric equivalent of ANOVA (Kruskal and Wallis 1952). Separate analyses were conducted for gap and understory sites. In the understory, slopes and plateaus were compared, and because survival was similar in these two habitats, data were pooled to compare species differences using the data from the eight plots (four plateaus and four slopes). In gaps, comparisons of cutting survival were only made for shade-tolerant species as none of the cuttings of light-demanding species survived.

Layering experiment: rooting and establishment success of pinned down branches

A third experiment was designed to simulate layering, where shoots grow from the nodes of prostrate trunks or branches pinned to the ground by fallen objects. Two branches of the same length on the same plant were experimentally pinned down using metal wires. To evaluate the relative importance of being rooted (access to soil water and to stored resources in the root), one branch was left connected to the plant while the second branch was cut and disconnected from the plant.

Layering treatments were replicated on 25 plants of each of eight species located in the understory along six BCI trails, and in the BCI laboratory clearing. The experiment began at the beginning of the wet season (April 2003), and resprouting success (i.e., presence of new roots and leaves) was recorded 7 months later. The effects of species and treatment (connected or disconnected) on shoot survival were analyzed using log-linear contingency analysis. Differences between treatments for each species were determined using a Fisher's exact test; data for understory and clearing species were also pooled to determine whether shade tolerance was associated with layering ability.

Interspecific variation in sexual reproduction

Seed germination

Mature *Piper* infructescences from 16 to 43 similar-sized plants per species were collected along six trails on BCI

and from gaps and clearings. Seeds from these infructescences were used to measure initial seed viability. Seeds were cleaned from the fruit and surface sterilized with a 10% bleach solution. Initial seed viability was tested by germinating 50 seeds from each plant on 1% agar in Petri dishes in a growth chamber for 7 weeks, after which no additional germination occurred. The proportion of seeds germinating was logit transformed and species differences tested using one-way ANOVA.

To assess whether species differed in emergence success across environmental conditions, seeds were planted in the same understory slope, plateau and gap plots as used to assess cutting survival. Seeds used in this experiment were from the same infructescences used to assess initial viability. To evaluate the effect of post-dispersal seed predators on seedling emergence success, a subset of seeds of the same species were sown inside 20-cm-tall plastic cylinders that were half buried in the soil and coated with Tanglefoot (Tanglefoot, Grand Rapids, Mich.), a sticky barrier to crawling insects. The effectiveness of the enclosures in preventing access to ants was first tested by baiting enclosures with tuna fish. No crawling insects were observed inside the enclosure. In each plot two sets of 50 unprotected seeds and 50 protected seeds from each species were sown for a total of 200 seeds per species per plot (200×4 plots = 800 seeds per habitat type \times 3 habitats = 2,400 seeds total). Seedling emergence was censused every 2 weeks for 24 weeks. In the gap plots, differences in seedling emergence success among species and treatments (protected vs. unprotected) were compared using analysis of deviance. Seedling emergence success observed in the field experiments was adjusted for differences in growth chamber seed viability by dividing the proportion of seeds emerging in the field by the mean proportion of seeds germinating in the growth chamber. Litter cover was removed from all plots before the start of the experiments and removed every 2 weeks.

For understory plots no statistical analysis was possible to test for species differences in emergence success in the field because of very low emergence. For gaps, we assumed a negative binomial error distribution in the generalized linear model using PROC GENMOD because the dependent variable, number of emerged seedlings, was not normally distributed and the variance increased with the mean.

Fecundity characteristics

To estimate annual seed production, the total number of mature infructescences produced per plant per year and seeds produced per infructescence were counted on those

plants used to follow leaf life span. As not all of those plants were fruiting during the collection year, fruits were also collected from an additional set of plants from which no PPF measurements were taken. The species' seed mass was estimated by weighing 30 seeds from each individual on a precision balance. Annual seed mass production was estimated by multiplying the annual seed number by the seed mass. Although seeds can be produced asexually in some tropical shrubs and trees via apomixis (Osunkoya and Swanborough 2001; Ng et al. 2004), enclosure and hand-pollination experiments demonstrate that seeds of the species in this study are sexually produced (E. Lasso, unpublished data), as has been shown for other *Piper* species (Figueiredo and Sazima 2000). Therefore a measure of "annual sexual reproductive potential" for each species was calculated by multiplying the number of infructescences produced per plant per year by the number of viable seeds produced per infructescence based on growth-chamber seed germination trials.

Differences among species in the number of infructescences per plant, the number of seeds per infructescence, annual seed output per plant, seed mass, and the annual sexual reproductive potential were analyzed by a one-way ANOVA and evaluated with a Tukey's studentized range test. Data were log transformed before the analysis. Multivariate comparisons of fecundity data were made using PCA.

Relationship between asexual reproductive ability and annual sexual reproductive potential

To determine how a species' annual sexual reproductive potential is related to its asexual reproductive ability, an asexual reproductive ability index (ARAI) was calculated for each species. The ARAI was calculated by averaging the proportion of cuttings surviving across the field and green house experiments previously described. Because species differ in their size at reproduction, plant size could potentially affect the amount of resources available to allocate to seed production. Therefore, species' annual sexual reproductive potential and annual seed mass was scaled to the average plant height of each species obtained from 15 reproductive individuals.

Two Pearson correlation analyses were performed using log-transformed ARAI data. The first analysis correlated species' mean annual sexual reproductive potential with ARAI. The second analysis correlated mean annual seed mass produced per plant with ARAI.

All statistical analyses in this study were performed with SAS version 9.1, and the PCA were computed using the software PC-ORD (McCune and Mefford 1997).

Results

Characterization of species' shade tolerance

PCA, using functional traits, and data on the light environments occupied by plants, showed a clear grouping of species according to shade tolerance (Fig. 1). Species usually found in gaps and clearings exhibited short leaf life span, high SLA, high N concentration and C assimilation rates, whereas species usually found growing in the understory presented the opposite suite of characters (Table 1).

The PCA analysis showed that shade tolerance was well described by the two first axes. Collectively, they explained 72.6% of the variance in the data (Fig. 1). Variables correlated with PCA-1 were: respiration ($r = -0.79$), leaf longevity ($r = -0.55$), %C ($r = 0.84$), %N ($r = 0.86$), A_{max} ($r = 0.86$). Variables correlated with PCA-2 were: PPF (D) ($r = -0.86$), leaf longevity ($r = -0.47$) and SLA ($r = 0.26$). The first principal component (PCA-1), representing 60.8% of the total variance, clearly separated a group of shade-tolerant species from light-demanding species (Fig. 1). Light-demanding species with positive PCA-1 axis scores had higher values of C and N concentrations, and photosynthetic capacity (A_{max}). Shade-tolerant species with negative PCA-1 axis scores had greater respiration rates and leaf longevity. PCA-2 explained 11.8% of the variation among species. All shade-tolerant species were grouped together along this axis, whereas light-demanding species were scattered along this axis, with greater axis scores for *P. dilatatum*, probably due to its occurrence in sites with lower total PPF (Table 1).

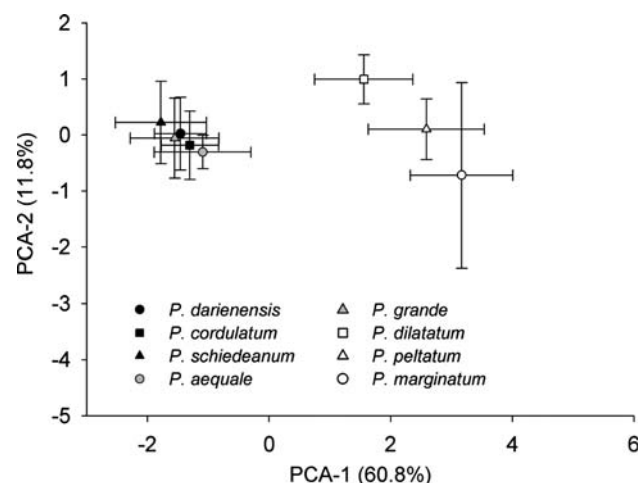


Fig. 1 Principal component analysis of eight *Piper* species using leaf trait and light environment data (see Table 1). Open symbols are for species found in clearings and gaps; black and gray symbols are for species from the understory. Both axes cumulatively explain 72.6% of the variance in the data. PCA Principal component axis

Because PCA analysis did not support a gradient of shade tolerance in this study, species were classified in two groups: light-demanding species, *P. dilatatum*, *P. marginatum* and *P. peltatum*, and shade-tolerant species, *P. darienensis*, *P. cordulatum*, *P. aequale*, *P. grande* and *P. schiedeanum*. Light data from the canopy photos alone did not help to distinguish *P. dilatatum* from shade-tolerant species. However, *P. dilatatum*'s physiological traits clearly separated it from shade-tolerant species (Table 1).

Interspecific variation in resprouting ability

Asexual regeneration success, inferred from survival of cuttings in the green house, differed among species (species effect: $F = 9.3$; $df = 6$; $P < 0.0001$), and according to shade tolerance, depending on the light conditions to which the cuttings were exposed (habitat * light interaction: $F = 16.7$; $df = 1$ (48); $P < 0.0003$). Shade-tolerant species survived better in low light conditions (46% survival in low vs. 39% in high), whereas light-demanding species survived better in high light conditions (40% in low vs. 72% in high; Fig. 2a).

In the field, cutting survival in the understory was not different between slope and plateau conditions (plateau = 13.4% and slope = 13.6%) (Kruskal–Wallis $\chi^2 = 0.66$; $df = 1$; $P = 0.41$; Fig. 2b). Overall, all species had similar cutting survival in the understory, ranging between 1.5 and 3%, with the exception of *P. darienensis* that had 59% cuttings alive at the end of the third year (Kruskal–Wallis $\chi^2 = 23.6$; $df = 4$; $P < 0.0001$; Fig. 2b).

Species differed in the survival of their cuttings planted in gaps (Kruskal–Wallis $\chi^2 = 9.8$; $df = 4$; $P < 0.04$). Mean survival was higher for *P. darienensis* and *P. cordulatum*, i.e., 36% and 41%, respectively. Mean survival of the other shade-tolerant species ranged between 6%–14% (Fig. 2b). None of the cuttings of light-demanding species survived the entire 3 years.

Species also differed in resprouting success when branches were pinned down ($G = 74.7$, $df = 6$, $P < 0.0001$), and in the effect of a branch connection on resprouting success ($G = 12.3$, $df = 1$, $P = 0.0004$). Species differences were due to the low survival of two light-demanding species, *P. marginatum* and *P. peltatum*. *P. marginatum* did not resprout in any of the treatments and *P. peltatum* had only 8% survival after 7 months when disconnected and 28% when connected (Fig. 2c). Shade-tolerant species' survival of connected branches ranged from 60% to 100%, whereas survival of disconnected branches ranged from 36% to 100%. Only two species had significantly different survival between connected and disconnected branches: *P. grande* (connected, 88% vs. disconnected, 48%; Fisher's exact test, $P = 0.033$) and *P. dilatatum* (connected, 77% vs. disconnected, 36%; Fisher's

Table 1 Physiological, structural and chemical traits used to characterize species' shade tolerance [photosynthetic photon flux density (Total PPF_D; mol m⁻² day⁻¹), specific leaf area (SLA; cm² g⁻¹),maximum assimilation (A_{max} ; μmol cm⁻² s⁻¹), dark respiration (R_d ; μmol cm⁻² s⁻¹), and leaf longevity (days)]

Species/trait	Total PPF _D	%N	%C	SLA	A_{max}	R_d	Leaf longevity
Shade tolerant							
<i>Piper darienensis</i>	3.25 a	2.13 a	38.13 a	197.9 a	4.21 a	-0.25 a	677.9 a
<i>Piper cordulatum</i>	3.44 a	2.09 a	39.29 a	168.5 b	5.28 a	-0.29 a	588.1 a
<i>Piper schiedeianum</i>	3.16 a	2.17 a	34.95 b	209.1 a	4.45 a	-0.20 a	860.6 a
<i>Piper aequale</i>	3.47 a	2.36 a	39.33 a	278.8 c	4.57 a	-0.26 a	634.1 a
<i>Piper grande</i>	3.43 a	2.14 a	37.24 a	228.4 a	4.15 a	-0.20 a	760.3 a
Light demanding							
<i>Piper dilatatum</i>	3.69 a	3.23 b	41.62 c	455.5 d	8.76 b	-0.90 b	140.7 b
<i>Piper peltatum</i>	6.49 b	3.09 b	44.05 d	479.1 d	12.96 c	-0.97 b	125.1 b
<i>Piper marginatum</i>	8.20 b	4.13 c	45.02 d	393.4 d	13.11 c	-0.89 b	100.7 b

Means with different letters differ significantly (one-way ANOVA; $P < 0.05$)

exact test, $P = 0.009$; Fig. 2c). When species were pooled according to their shade tolerance, shade-tolerant species as a group had higher survival (74%) than the group of light-demanding species (23%; $\chi^2 = 84.0$; $P < 0.0001$; Fig. 2c).

Interspecific variation in sexual reproduction

Seed germination and establishment success

Light-demanding species had significantly higher seed viability (mean = 85.2% germination) than shade-tolerant species (mean = 34.6%; $F = 102.4$; $df = 1$; $P < 0.0001$; Fig. 3), when measured in a growth chamber. In contrast, seedling emergence success in the field was very low. Results suggest that gap conditions are necessary for seedling establishment for all *Piper* species. The few seeds that successfully germinated and established were in gaps, while seeds failed to emerge when sown in the understory, with the exception of a small number of *P. aequale*. Of the 8,000 seeds sown in the understory, only 16 (0.2%) emerged, all from *P. aequale*. No further analysis was possible for the understory.

In gaps, after adjusting field emergence success in the gap plot for differences in seed viability measured in the growth chamber, we found a significant effect of species on emergence of seeds in the protected treatment ($\chi^2 = 20.4$; $df = 6$, 216; $P = 0.0023$). Emergence was still rather low, but the highest germination of seeds was observed for the three light-demanding species, *P. marginatum* (47.3 ± SE = 18.9%), *P. peltatum* (20.3 ± 11.7%), and *P. dilatatum* (10.5 ± 4.3%), followed by the two shade-tolerant species, *P. grande* (9.8 ± 4.6%) and *P. aequale* (9.4 ± 3.3%). Three understory species had very low emergence: *P. schiedeianum* (1.3 ± 1.3), *P. darienensis* (0.56 ± 0.5%) and *P. cordulatum* with no emerging

seedlings (Fig. 3). Seedling emergence was highly variable. Therefore, post-dispersal predation effects were not significant (protection treatment effect; $\chi^2 = 0.43$; $df = 1$, 216; $P = 0.51$); however, emergence tended to be higher when protected than when unprotected for light-demanding species (Fig. 3).

Fecundity characteristics

Species differed significantly in all fecundity characteristics (Table 2), with more than 2 orders of magnitude variation in seed production per plant per year. The understory species produced fewer infructescences per plant ($F = 31.8$; $df = 1$; $P < 0.0001$), fewer seeds per infructescence ($F = 113.1$; $df = 1$; $P < 0.0001$), and per plant per year ($F = 43.6$; $df = 1$; $P < 0.0001$), had lower germination ($F = 100.3$; $df = 1$; $P < 0.0001$) and consequently lower annual sexual reproductive potential ($F = 84.5$; $df = 1$; $P < 0.0001$) than light-demanding species. Shade-tolerant species also produced larger seeds than light-demanding species ($F = 4277$; $df = 1$; $P < 0.0001$; Table 2).

PCA performed on the fecundity variables listed in Table 2 showed that the first two components described 74.8% of the variation in fecundity characteristics. The first principal component (PCA-1), representing 55.1% of the total variance, describes a seed size-number trade-off (Fig. 4). Species with more positive PCA-1 axis scores were those with large seeds and those with more negative scores produced more seeds per plant per year. The second principal component, representing 19.7% of the variation in fecundity traits, appeared to separate species by shade tolerance with more positive PCA-2 scores for light-demanding species (Fig. 4) due to higher seed germination and number of fruit per plant. PCA indicated that

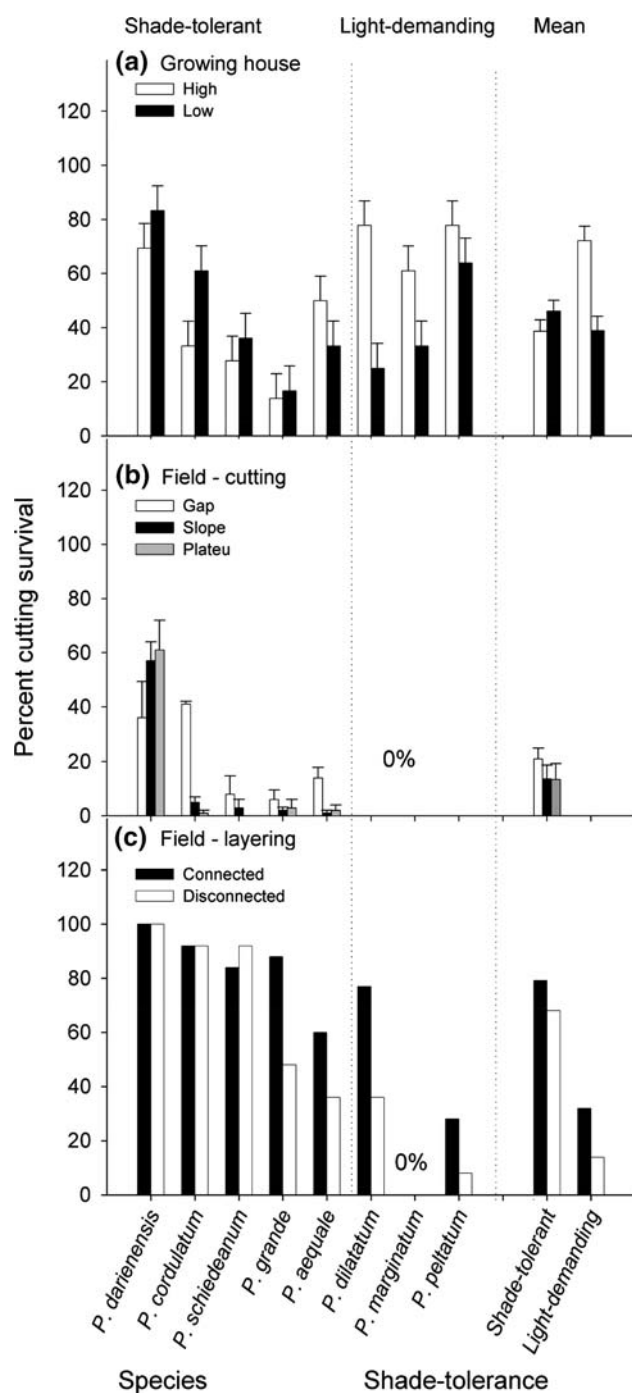


Fig. 2 Comparison of asexual reproductive ability of *Piper* species with different shade tolerances. **a** Plants grown in greenhouse under high light and low light regimes. **b** Plant grown in different field conditions (slopes, plateau and gap). **c** Percent survival in the field, after 7 months, of bent and pinned-down branches that were connected and disconnected from the plant

P. schiedeanum has a combination of reproductive traits that distinguishes it from other *Piper* species. Low PCA-1 and PCA-2 scores for this species reflect small seed mass and high seed number per infructescence.

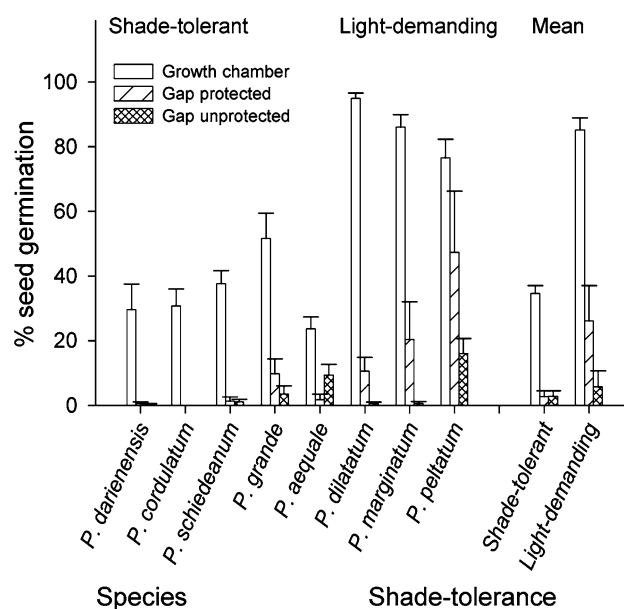


Fig. 3 Seed germination in growth chamber and two gap conditions

Relationship between asexual reproductive ability and the annual sexual reproductive potential

Shade-tolerant species showed large variation in sexual reproductive potential compared to light-demanding species (Fig. 5a). Asexual reproduction ability index (ARAI) was negatively correlated with annual sexual reproductive potential (Pearson correlation = -0.75; $P = 0.034$; Fig. 5a), but not with annual seed mass (Pearson correlation = 0.36; $P = 0.38$; Fig. 5b). A similar result was obtained when the analysis was repeated without scaling for plant size; log seed production plant⁻¹ year⁻¹ was negatively correlated with ARAI (Pearson correlation = -0.75; $P = 0.035$) and log seed mass plant⁻¹ year⁻¹ was not correlated with ARAI (Pearson correlation = 0.19; $P = 0.65$).

Discussion

Do species differ in sexual reproduction and resprouting capacity according to shade tolerance?

Our results show large differences in resprouting ability, seed production and sexual reproductive potential between shade-tolerant and light-demanding species. Annual seed production was greater in light-demanding than shade-tolerant species. Additionally, light-demanding species had higher viability of seeds resulting in an annual sexual reproductive potential several orders of magnitude greater than for shade-tolerant species. Within the shade-tolerant group of species a dichotomy also became evident as a

Table 2 Summary of fecundity characteristics of eight species of *Piper* from Barro Colorado Island, Panama (mean \pm 1 SE)

	Infructescences/ plant	Seeds/ infructescence	Seed plant ⁻¹ year ⁻¹	% Viable seeds ^a	Seed weight (mg)	Annual sexual reproductive potential
Shade tolerant						
<i>P. darienensis</i>	3.7 \pm 0.9 a (15)	51 \pm 150 a (15)	177 \pm 43 a (15)	29.6 \pm 6.0 a (21)	5.73 \pm 0.1 a (10)	52 \pm 13 a
<i>P. cordulatum</i>	7.9 \pm 1.5 a (21)	123 \pm 127 b (21)	940 \pm 176 b (21)	30.7 \pm 4.2 a (43)	2.76 \pm 0.1 b (16)	250 \pm 55 b
<i>P. schiedeanaum</i>	10.4 \pm 1.5 ab (12)	3,878 \pm 168 e (12)	38,835 \pm 7,783 c (12)	37.6 \pm 6.1 a (20)	0.03 \pm 1e ⁻³ c (34)	14,602 \pm 2,926 d
<i>P. aequale</i>	6.4 \pm 1.4 a (15)	1,345 \pm 150 d (15)	8,606 \pm 1,931 d (15)	23.6 \pm 5.3 a (27)	0.04 \pm 4e ⁻³ c (18)	2,031 \pm 456 c
<i>P. grande</i>	4.7 \pm 1.2 a (16)	825 \pm 145 cd (16)	3,777 \pm 870 e (16)	51.6 \pm 6.2 ab (20)	0.09 \pm 2e ⁻³ c (26)	1,949 \pm 449 c
Mean	6.3 \pm 0.7 a	1,244 \pm 66.5 a	8,573 \pm 1,916 a	34.6 \pm 2.6 a	1.07 \pm 0.19 a	3,196 \pm 741 a
Median	4	712	1,695	23.3	0.08	538
Light demanding						
<i>P. dilatatum</i>	13.3 \pm 1.7 b (22)	1,108 \pm 124 d (22)	14,432 \pm 2,122 f (22)	94.9 \pm 6.3 b (19)	0.14 \pm 3e ⁻³ c (49)	13,710 \pm 2,017 d
<i>P. peltatum</i>	6.5 \pm 0.9 ab (17)	1,320 \pm 141 d (17)	8,960 \pm 1,686 d (17)	86.0 \pm 6.9 b (16)	0.03 \pm 7e ⁻⁴ c (19)	7,706 \pm 1,450 d
<i>P. marginatum</i>	16.7 \pm 1.7 b (26)	830 \pm 114 cd (26)	14,513 \pm 2,086 f (26)	74.6 \pm 6.0 b (21)	0.12 \pm 7e ⁻³ c (22)	10,885 \pm 1,562 d
Mean	12.9 \pm 1.0 b	1,086 \pm 73.3 b	13,033 \pm 1,206 b	85.2 \pm 3.7 b	0.11 \pm 5e ⁻³ b	11,010 \pm 1,026 b
Median	10	1,003	9,645	93.3	0.13	8,208

Sample sizes are in parentheses

Means with different letters differ significantly (mixed model ANOVA; $P < 0.0001$)

^a Data from seed germination trials in the growth chamber

result of a trade-off in the size and number of seeds produced. Three of the species, *P. aequale*, *P. schiedeanaum* and *P. grande*, produced seeds of similar size to those of the light-demanding group, whereas *P. cordulatum* and *P. darienensis* produced fewer seeds that were several orders of magnitude larger (Table 2). In contrast, the ability to resprout, and therefore to reproduce asexually was lowest in light-demanding species, intermediate for the small-seeded shade-tolerant species, and highest for the large-seeded shade-tolerant species. As a result, annual sexual reproductive potential was negatively correlated with asexual reproductive ability.

Differences in sexual versus asexual reproductive capacity in *Piper* are consistent with the model of Bellingham and Sparrow (2000), which predicts that resprouting is favored over seed production at sites with intermediate disturbance and low productivity. Plants growing in the understory, exposed to continuous mechanical damage from falling litter (Aide 1987; Gartner 1989; Clark and Clark 1991; Guariguata 1998; Paciorek et al. 2000) and chronic light limitation showed stronger resprouting capacity but lower sexual success than light-demanding species living in a more productive, less disturbed habitat. Although previous studies have already suggested the existence of a positive correlation between shade tolerance and frequency of resprouting in tropical forests (Putz and Brokaw 1989; Zimmerman et al. 1994), these studies were limited to observations of naturally occurring resprouting success. Observed differences in

resprouting rate may therefore have arisen from either a higher rate of damage in the understory, or from a greater ability of shade-tolerant species to resprout when damaged. In this study, our field experiments show that high resprouting success in shade-tolerant species reflects a greater ability of shade-tolerant species to resprout when damaged. Our results contrast with the findings of Dietze and Clark (2008) in temperate forest that indicate that species' variation in resprouting is not related to shade tolerance. However, in temperate forests all species have to store reserves to overwinter regardless of their shade tolerance. Given that successful resprouting most likely depends on stored resources (Kobe 1997), differences in resprouting ability may be smaller in temperate than in tropical forests.

Why have only shade-tolerant species evolved the capacity to regenerate asexually from fragments?

We propose three non-mutually exclusive hypotheses to account for habitat differences in resprouting capacity. The first hypothesis arises from the observation that plants in the understory are exposed to higher probabilities of damage from falling litter (Aide 1987; Clark and Clark 1991) than species in gaps and clearings. Thus, the capacity to resprout and reproduce asexually may be adaptive in tolerating this physical damage. Plants in other ecosystems where disturbance from fire, flooding, drought or landslides damages above-ground biomass also commonly resprout (reviewed by Bond and Midgley 2001). The second

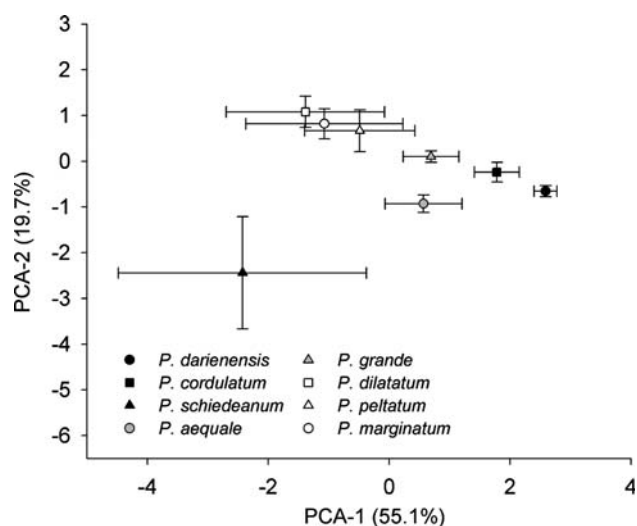


Fig. 4 Principal component analysis using fecundity characteristics of eight species of *Piper* from Barro Colorado Island, Panama (see Table 2). White symbols are for light-demanding species and black and gray symbols are for shade-tolerant species. Both axes cumulatively explain 74.8% of the variance in the data. Variables correlated with PCA-1 were: sexual reproductive potential ($r = -0.93$), seed plant⁻¹ year⁻¹ ($r = -0.91$), seed mass ($r = 0.63$). Variables correlated with PCA-2 were: seeds/infructescence ($r = -0.57$) and % viable seeds ($r = 0.74$)

possibility is that differences in resprouting capacity among shade-tolerant groups result from habitat differences in humidity and evapotranspiration. Relative humidity is lower and direct irradiance is higher in gaps than in the understory (Ashton 1992; Brown 1993), which may impede the growth of fragments with undeveloped root systems. Results of the green house experiment support this hypothesis as cuttings of light-demanding species were able to resprout and survive only when continuously watered. The observation that the number of resprouter species increases in more humid tropical forests (Everham and Brokaw 1996) is also consistent with this hypothesis. Finally, resprouting may have evolved in environments where opportunities for sexual reproduction are low. Low sexual success in the understory is the consequence of several factors. First, seed predation rates in *Piper* are higher for shade-tolerant than light-demanding species. In lowland tropical forest in Costa Rica, up to 76% of seeds are lost to pre-dispersal seed predators, contrasting with 12% for light-demanding species (Greig 1993a). Even though we did not quantify seed predation on BCI, we did observe Hemiptera species feeding on *Piper* infructescences, found empty seeds in some of the infructescences, and low seed viability overall. Second, light limitation in the understory limits the amount of resources available for reproduction; this resource pool is further diminished by the need for additional allocation to plant defense beyond that required in gaps (Coley and Barone 1996). Combined,

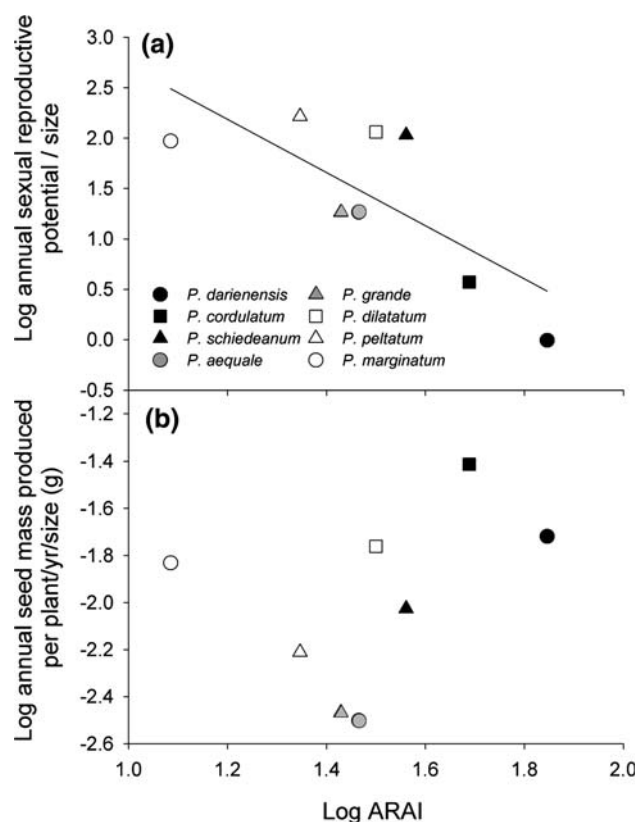


Fig. 5 Relationship between asexual reproductive ability of each species (ARAI) and **a** annual sexual reproductive potential scaled by plant size (Pearson correlation = -0.745 ; $P = 0.034$) and **b** annual seed mass produced per plant scaled by plant size (Pearson correlation = 0.36 ; $P = 0.378$). Each point represents a mean value for the species

these factors may make asexual reproduction critical to population persistence in the understory.

What mechanisms favor the capacity to resprout, and are they related to shade tolerance?

The mechanisms favoring a species' capacity to resprout are not well understood, but they are likely to be related to the potential to store resources in vegetative organs (reviewed by Bond and Midgley 2003). In the fire-prone shrublands of Australia and South Africa, resprouters have root starch concentrations 4–35 times higher than those of nonresprouters (Pate et al. 1990; Bell 1996; Bell and Ojeda 1999). Furthermore, root reserves decrease when plants resprout after burn events (Bowen and Pate 1993). Intra-specific comparisons of allocation to starch by seedlings of resprouter and nonresprouter variants have shown that resprouters accumulate a larger amount of starch in roots than nonresprouters and that this allocation difference is likely determined genetically (Verdaguer and Ojeda 2002). Studies done in temperate forest have also shown that

species frequently resprouting had abundant carbohydrate reserves in their roots, whereas species that rarely resprout have low reserves (Sakai et al. 1997). To our knowledge there are no studies explicitly comparing C allocation in resprouter and nonresprouter species in tropical systems, but some studies have reported a strong link between carbohydrate storage and light requirements, where storage is higher in shade-tolerant than in light-demanding species (Kobe 1997; Poorter and Kitajima 2007). Differences in C allocation may therefore provide the basis for habitat differences in resprouting ability, and is a consequence of the shade-tolerant syndrome (Kobe 1997; Poorter and Kitajima 2007), where higher carbohydrate reserves increase species survivorship in low-light environments.

The causes of the sexual/asexual trade-offs: resource allocation versus mating among clones

In *Piper*, seed production and asexual reproduction via resprouting are two processes competing for plant resources. Marquis et al. (1997) showed that *Piper* species from the understory need to accumulate carbohydrates to start seed production; only a small portion of current photosynthate is used in any reproductive event (Marquis et al. 1997). Therefore, if shade-tolerant species are subjected to more frequent and recurrent disturbance in the understory, and are forced to use carbohydrate reserves in resprouting more often than light-demanding species, a trade-off linked to species' habitat preference is expected between the two regeneration modes (Iwasa and Kubo 1997; Chapin et al. 1990). Our results, based on eight *Piper* species, along with Greig's (1993b) results from a different set of 30 *Piper* species at the La Selva Biological Station in Costa Rica provide evidence for the trade-off between sexual and asexual reproduction in this genus. Greig (1993b) found that shade-tolerant species regenerated primarily by vegetative means, especially from fragments or bent fragmented shoots (layering), and seldom from seeds, while shade-intolerant species appeared to reproduce primarily from seeds and rarely resprouted.

Results from *Piper* provide support for the emerging generalization from different ecosystems that plants that resprout are poor recruiters, whereas nonresprouters recruit more readily from seed (Keeley 1977; Bellingham et al. 1994; Bond and Van Wilgen 1996; Kruger et al. 1997). However, our finding that resprouting ability is negatively correlated with seed production but not with seed biomass indicates that this trade-off does not necessarily hinge on how resources are allocated. Cruz and Moreno (2001), who used seed mass production rather than number of seeds produced as a measure of reproductive effort, also found no evidence of a trade-off between seed mass production and resprouting success. Lower sexual success of resprouters,

either as a result of lower seed production or lower seed quality, could represent an indirect consequence on mating of resprouting or clonal spread (Charpentier 2002). Species that frequently resprout and spread asexually will have more genetically identical individuals in a population with a concomitant increase in self-pollination (Handel 1985; Eckert 2000), pollen waste and/or inbreeding depression (Muirhead and Lande 1997) potentially resulting in lower sexual recruitment success. There is a chicken or egg causality dilemma in understanding the causes of the sexual/asexual trade-off; did shade-tolerant species evolve the capacity to reproduce asexually to counteract their low sexual success or is the current lower sexual success observed a consequence of the abundance of clones in the population resulting from resprouting fragments?

Ecological differentiation of *Piper* species: including resprouting as a life history trait

Piper is a pan-tropical genus containing over 1,000 species (Burger 1971) and is often a dominant element in the understory of tropical forests. How do these ecologically similar species coexist? Our findings on the seed germination experiments suggest that all *Piper* species, regardless of their shade tolerance, require gap conditions to recruit. They all have photoblastic small-seeds ($\ll 1$ mg) (Vázquez-Yanes 1974; Vázquez-Yanes and Smith 1982; Orozco-Segovia and Vázquez-Yanes 1989; Daws et al. 2002) that fail to emerge when sown in the understory, even when surface litter is removed. Dependence on gaps for initial establishment has been shown for other very small-seeded shade-tolerant species (Ellison et al. 1993; Dalling et al. 2001) indicating that small seededness by itself may lead to a light requirement for establishment. Our results support a growing recognition that classifications of species into only two main functional groups, pioneer (light-demanding) and non-pioneer (shade-tolerant), based on their light requirements for seed germination and seedling establishment requirements are misleading (Swaine and Whitmore 1988; Ellison et al. 1993; Dalling et al. 2001; Wright et al. 2003). We have shown that leaf functional traits and data on the light environments occupied by plants grouped species according to shade tolerance (Fig. 1), but failed to further differentiate among shade-tolerant species. In contrast, reproductive traits provide the basis for greater species differentiation within the shade-tolerant group based on seed mass and seed number per infructescence (Fig. 4). Resprouting capacity has been recommended as a key plant functional trait to be measured worldwide (Cornelissen et al. 2003). Here we show it provides an additional axis of differentiation for species functional groups. The inclusion of resprouting capacity (the persistence niche) as a life history attribute together

with sexual traits (the regeneration niche) could prove useful in explaining vegetation dynamics and coexistence of similar species in tropical forests.

By including resprouting capacity as a life history attribute we can tentatively classify *Piper* species in this study according to three life history strategies:

1. Pioneer species that live exclusively in gaps, and are exposed to relatively low levels of litterfall damage, use resources in rapid growth to maturity and high reproductive output (high seed production). This group includes *P. marginatum*, *P. peltatum* and *P. dilatatum*. We include *P. dilatatum* in this group because, even though it can also persist under shaded conditions, it does not reproduce in the understory and because it shares all physiological and reproductive characteristics with the species in this group (see PCA in Fig. 1 and Fig. 4).
2. A cryptic gap-dependent group that includes species tolerant of understory light conditions as juveniles and adults. They can reach maturity and reproduce in understory conditions and have a high seed production, which presumably allows them to colonize gaps. Their capacity to reproduce asexually is intermediate, which allows them to persist to some degree after a disturbance. This group includes *P. schiedeana*, *P. aequale* and *P. grande*.
3. A shade-tolerant group that includes species with low seed output, and consequently a reduced potential to colonize gaps in comparison to other species. However, they have higher capacity to resprout and spread asexually, a strategy that allows them to persist and spread in the understory once they have established successfully. This group includes *P. darienensis* and *P. cordulatum*. This conceptual model we propose for understory *Piper* recruitment (and perhaps other small-seeded understory shrub species) involves occasional successful sexual recruitment in canopy and litter-free gaps followed by population expansion through asexual reproduction. Identification of clones using molecular markers in understory populations will be the next step to corroborate this hypothesis.

Implications of asexual reproduction

The capacity to resprout has mostly been studied in the context of understanding vegetation dynamics after disturbance in fire-prone communities, such as the shrublands characteristic of Mediterranean climates (Keeley et al. 2006). In these ecosystems, resprouting capacity is broadly accepted as a fundamental trait that can be used to classify species into functional groups (Keeley et al. 2006). However, resprouting in many ecosystems refers strictly to new

shoot production from below-ground tissue that survives the fire. Resprouting from excised plant fragments is unlikely to occur after a fire, and so is not necessarily linked to asexual reproduction and asexual spread, as is the case in forest systems where branch and tree falls are the most common form of disturbance. When a tree or branch falls, plants are often snapped and fragments are created. Species with the capacity to resprout from these fragments may persist in the site and increase their numbers, thus affecting vegetation dynamics and the demographic process.

The role of resprouting in gap regeneration is potentially large but remains poorly understood. The presence of species able to regenerate from fragmented individuals (a “fragment bank”) could potentially override the effect of the seed bank present in the area. For some species, cuttings have shown higher or similar survival than seedlings and higher growth rate than saplings (Sarukhán and Harper 1973; Khan et al. 1986; Dietze and Clark 2008) and they may have an advantage over seedlings in early growth and survival, at least over small seeds with limited resources. In temperate forests, recruitment from resprouting represents 26–87% of early gap regeneration (Dietze and Clark 2008). In the tropics, although similar types of estimates are missing, observations indicate that resprouting species may suppress species turnover after disturbance and gap formation (Linhart et al. 1987; Schnitzer et al. 2000), and that some gaps are not dominated by light-demanding species (Hubbell et al. 1999; Brokaw and Busing 2000), suggesting that resprouting could also be an important factor driving gap dynamics in tropical forests.

While we have shown that asexual reproduction is possible in a variety of congeneric species and is generally associated with limited sexual success, the prevalence of asexual reproduction in nature, and its contribution to vegetation dynamics remain unknown. The identification of clones and quantification of clonal frequency will therefore be key to understanding the recruitment, genetic structure and population demography of understory plants.

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