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Seed and microsite limitations of large-seeded, zoochorous trees in tropical forest restoration plantations in northern Thailand

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ABSTRACT

On deforested or degraded land, planting mixtures of native forest tree species facilitates establishment of incoming tree seedling species (species recruitment) by rapidly re-establishing canopy cover. However, delayed colonization of plantations by large-seeded, zoochorous (LSZ) tree species can affect the species composition, structure, and function of the developing forest. The objective of this study was to investigate whether microsites limit establishment (germination and early seedling survival) of LSZ tree species in three 13-year-old, seasonally dry, tropical forest restoration plantations in northern Thailand. We conducted a seed sowing experiment that combined five LSZ tree species with four microsite treatments in a split-plot design. All five tree species were previously absent from the understory of the plantations, despite seed sources being present in nearby natural forest. The four treatments simulated potential microsites that naturally-dispersed seeds may encounter. They included seed deposition on the surface of soil and on leaf litter, as well as seed burial beneath soil and beneath leaf litter. We fenced the experimental areas to prevent seed predation and focus on the environmental effects of microsites on the different stages of seedling establishment. Following seed sowing, we measured germination and seedling survival, mean height, and stem diameter over 26 months. The microsites treatments did not significantly affect germination and seedling survival, providing strong evidence that establishment of the tested species was not limited by the applied microsite environments. Furthermore, although there were significant differences in germination and survival among species, relatively high overall germination (37%) and 26-month seedling survival (58.5%), irrespective of microsite treatment, suggested that environmental conditions in the 13-year-old plantations generally met the requirements for germination and early seedling establishment. Microsite treatments also did not correlate with seedling height or stem diameter at 20 months, suggesting that initial germination microsites have no effect on seedling growth and robustness. Taken together, the results of this investigation support the hypothesis that seedlings of LSZ tree species are slow to colonize tropical forest restoration plantations because of seed limitations resulting from inadequate seed dispersal or low seed availability. The successful establishment of LSZ seedlings from sown seeds in this experiment suggests that direct seeding beneath the canopy of restoration plantations may be an effective way to offset seed dispersal limitations in restoration plantations. Furthermore, the absence of microsite treatment effects suggests broadcast sowing of seeds may be a simple way to recolonize closed-canopy restoration plantations with LSZ tree species.

1. Introduction

Tropical forest restoration using mixed-species plantings of indigenous trees can rapidly re-establish tree canopy cover on deforested and degraded lands (de Souza and Batista, 2004, Lamb, 2011, Elliott et al., 2013). These canopies facilitate recolonization of the site by additional, non-planted tree species (species recruitment), by shading out herbaceous weeds, improving soil conditions, ameliorating the understory microclimate, and attracting seed-dispersing wildlife (Lamb, 2011, Goosem and Tucker, 2012). In forest restoration sites that exist close to natural forest, such species recruitment may occur rapidly, increasing tree species richness by accelerating diversification of understory regeneration (Sinhaseni, 2008, Lamb, 2011, Bertacchi et al., 2016). Still most tropical forest restoration plantations are relatively young (< 25 years), thus little is known yet about the long-term recovery of their tree species composition. In some older, naturally regenerating, secondary tropical forests, however, tree species composition remains distinct from that of primary forests even many decades

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after canopy closure (Aide et al., 2000, Chazdon, 2003, Brearley et al., 2004, Chua et al., 2013). This suggests that there may be limits to the ability of natural recruitment to recreate the original tree species composition in recovering forest ecosystems. These limits may be particularly strong for large-seeded, zoochorous (animal-dispersed) tree species (LSZ) as they are often among the last to return to secondary forests (Aide et al., 2000, Chazdon, 2003, Brearley et al., 2004, Chua et al., 2013).

Reduced or delayed recruitment of LSZ trees may have consequences, both for regeneration of these species and for the composition, structure, and ecological functioning of the developing forests. LSZ species are often long-lived, shade-tolerant, late-successional species that are able to regenerate in the forest understory (Leishman et al., 2000). Such trees tend to have higher wood density and higher rates of CO_2 fixation than smaller-seeded species and are larger at maturity (Osuri and Sankaran, 2016). Consequently, their absence from forests may alter not only forest composition, but also forest structure and function. In addition, the failure of some LSZ tree species to regenerate may increase their risk of regional extirpation or even extinction (Brodie et al., 2009, Wotton and Kelly, 2011, Caughlin et al., 2014).

The seeds of most late-successional LSZ species are recalcitrant, that is, they are able to germinate rapidly after shedding but lose viability quickly, particularly if they are exposed to desiccation (Pritchard et al., 2004, Daws et al., 2006). Rapid germination may allow LSZ species to avoid seed predation and, because they allocate relatively few resources to physical defense, to be more efficient at seed resource provisioning than orthodox (i.e. desiccation tolerant) seeds (Daws et al., 2005). The low longevity of recalcitrant seeds, however, generally precludes their accumulation in the soil seed bank (Vazquez-Yanes and Orozco-Segovia, 1996). Therefore in order for LSZ species to recolonize the restoration plantings, they must rely on frugivores to disperse their seeds soon after seed maturation. Yet large seeds are less likely to be dispersed than small seeds because the number of frugivorous species that are capable of dispersing a seed generally decreases with increasing seed size (Kitamura et al., 2002, Corlett, 2017). In addition, hunting and habitat loss have reduced populations of large frugivores throughout the tropics and extirpated them from large stretches of their original distributions, further decreasing the likelihood that large seeds will be dispersed (Wright et al., 2007). For these reasons, seed limitation resulting from poor dispersal is a frequently cited reason for the delayed return of LSZ tree species in regenerating forests (Lamb, 2011, Chazdon, 2014, Reid et al., 2015).

Simply increasing the number of LSZ seeds in the understory, however, may not guarantee their recruitment in restoration forests. Seedling establishment (seed germination followed by survival and growth of the seedling) in all forests may also be limited by the availability of establishment microsites with suitable biotic and abiotic conditions in the understory (Putz, 1983, Molofsky and Augspurger, 1992, Dalling and Hubbell, 2002). Such microsites are defined by features of the forest floor that may be on a scale of no more than a few centimeters, yet they often determine the abundance, survival, and early growth of plants (Harper, 1977, Whittaker and Levin, 1977). On forest restoration plantations, the importance of microsites for seedling establishment may be even greater than in naturally occurring forest, since the initial conditions of land requiring active restoration are often poor (e.g. soil compaction, low levels of soil organic matter and low soil water retention) due to long-term, intensive, agricultural activity, such as repeated weeding and burning (Chazdon, 2003, Lamb, 2011).

The seeds of LSZ species that are naturally dispersed into restoration forests are likely to lodge in microsites that are defined by the seed's location with respect to soil and leaf litter. For example, seeds that fall onto leaf litter or exposed soil may lodge where they have landed or they may work their way below litter or be buried beneath leaves or soil by seed-caching animals. Where seeds end up may determine their exposure to potential threats and affect their ability seeds to access resources such as light, water, and soil. Seeds resting on bare soil may benefit from good seed-soil hydraulic conductivity and favorable aeration (Makana and Thomas, 2005), but exposed seeds on both soil and leaf litter may also be at increased risk of seed predation and desiccation (Doust et al., 2006). Furthermore, seeds lodged on the surface of leaf litter may be blocked from reaching the mineral soil (Molofsky and Augspurger, 1992). By contrast, seeds that have worked their way below leaf litter or have been buried beneath leaves or soil may have access to soil and be shielded from predation and desiccation (Cintra, 1997, Dupuy and Chazdon, 2008), but may also be forced to expend greater amounts of energy to grow above the substrate. This expenditure may reduce the robustness of seedlings that manage to emerge (Molofsky and Augspurger, 1992, Peterson and Facelli, 1992).

Microsites that shield recalcitrant seeds from desiccation may be particularly important in seasonally dry tropical forests (SDTFs). In aseasonal tropical rainforests, microsite variations in light availability rather than moisture are the primary limiting environmental factor affecting seedling survival (Augspurger, 1984, Brown, 1996, Schnitzer and Carson, 2001). SDTFs are distinct from aseasonal tropical forest because they grow where there is at least one prolonged season ($\geq$4 months) of severe to absolute drought (Dirzo et al., 2011). Thus in these forests moisture may be as or more limiting than light in SDTF (Vieira and Scariot, 2006, Poorter and Markesteijn, 2008, Ferreira et al., 2015). To maximize the availability of moisture for seedling establishment, many zoochorous SDTF tree species fruit at the beginning of the rainy season (Elliott et al., 1994, Daws et al., 2005), but the high year-to-year variability in timing and quantity of rainfall that is characteristic for this forest type may still leave seeds and seedlings vulnerable to mortality due to desiccation (Blain and Kellman, 1991, McLaren and McDonald, 2003, Vieira and Scariot, 2006).

In order to optimize the return of LSZ tree species to restored tropical forests, we need to understand the role that limiting factors play in their recruitment; but, to the best of our knowledge, the relative importance of seed and microsite limitations in a restoration forest setting has never been explicitly tested. We conducted a seed sowing experiment in13-year-old SDTF restoration plantations in northern Thailand to determine the degree to which recruitment of five LSZ tree species may be limited by seed availability and microsite conditions. Seedlings of the species used in this investigation had not recruited into plantations, despite the presence of mature individuals in the nearby natural forest. The experiment also investigated how initial microsite conditions might differentially affect the stages of seedling establishment, i.e. seed germination and early seedling survival and growth. Here we present the results of the two-year seed sowing experiment, explore the effects of the dry season on seedling survival, and suggest management practices that may assist in overcoming barriers that may prevent LSZ tree species recruitment in tropical forest restoration plantations.

2. Study site

Field work was conducted on three 0.16 ha experimental forest restoration plots along or immediately below the ridge of a watershed (1207–1310 m above mean sea level) in the upper Mae Sa Valley, Northern Thailand, approximately 2 km north of the village of Ban Mae Sa Mai (18°52′N, 98°51′E). Average annual precipitation at the nearest weather station to the plots was 2095 mm (Kog-Ma Watershed Research Station) (Elliott et al., 2003), with nearly all rain falling during the six-month wet season that extends from May to October. During the dry season (from November to April) precipitation averages less than 100 mm per month (Elliott et al., 2003).

The area was originally covered with seasonally dry evergreen forest (EGF) comprised of more than 250 tree species (~75% of which are evergreen) many of which are unique to this forest type (Maxwell and Elliott, 2001). However, much of the original EGF has been cleared for cultivation, tourism developments, and infrastructure. The forest in the study sites was cleared for cabbage cultivation about 20 years prior to restoration plantings. In 1996 local villagers decided to abandoned