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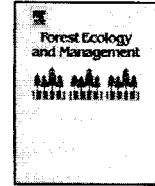
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Direct seeding of late-successional trees to restore tropical montane forest

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ABSTRACT

Natural regeneration of large-seeded, late-successional trees in fragmented tropical landscapes can be strongly limited by a lack of seed dispersal resulting in the need for more intensive restoration approaches, such as enrichment planting, to include these species in future forests. Direct seeding may be an alternative low-cost approach to planting nursery-raised tree seedlings, but there is minimal information on its efficacy or when in the successional process this technique will be most successful. We tested directly seeding five native tree species into habitats representing passive and active restoration approaches: (1) recently abandoned pasture; (2) naturally establishing, young secondary forests; and (3) young, mixed-species (fast-growing N-fixers and commercially valuable species) tree plantations established to facilitate montane forest recovery in southern Costa Rica. We monitored germination, survival, growth, and above- and below-ground biomass over a 2-year period. Germination in pastures, secondary forests, and tree plantations was similar (~43%). Seedling survival after one and two years was significantly higher under tree plantations (91% year 1, 75% year 2) compared to secondary forests (76, 44%) or pastures (74, 41%). Moreover, seedlings had greater total biomass and lower root:shoot ratios in the plantations, suggesting higher nutrient availability in that treatment. Costs for direct seeding were 10- to 30-fold less per 100 seedlings after 2-year compared to nursery-raised seedlings planted at the same sites; however, there are important trade-offs to the two restoration approaches. Planting nursery-raised seedling is a more effective but higher cost approach for rapidly establishing canopy cover and restoring large areas whereas direct seeding is a more efficient way to enrich an existing system. We particularly recommend using direct seeding as a complementary measure to the more intensive restoration approach of planting fast-growing and N-fixing trees.

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1. Introduction

Natural regeneration of late-successional trees in fragmented and degraded landscapes can be strongly limited by a lack of seed dispersal into successional habitats (e.g. Duncan and Chapman, 1999; Holl, 1999; Rodrigues Da Silva and Matos, 2006; Wijdeven and Kuzee, 2000); this limitation is particularly acute for larger-seeded animal-dispersed trees. Studies across a range of locations in the tropics show that movement of larger seeds beyond the edges of forest fragments is rare (Cole, 2009; del Castillo and Rios, 2008; Dosch et al., 2007; Duncan and Chapman, 1999; Holl, 1999; Ingle, 2003) and establishment of these species in natural regeneration

is limited even after many decades of succession (Aide et al., 2000; Finegan, 1996). The lack of natural recruitment of these species has led to concerns over their persistence in fragmented and degraded landscapes, and more aggressive restoration efforts such as enrichment planting have been suggested as a necessary step to augment severely dispersal-limited species in future forests (e.g. Dosch et al., 2007; Martinez-Garza and Howe, 2003; Zimmerman et al., 2000).

The predominant method used to restore degraded tropical lands is to plant nursery-raised tree seedlings (Chazdon, 2008; Lamb et al., 2005). Although this can be an effective technique for quickly establishing forest cover (Holl et al., 2010; Montagnini, 2001; Wishnie et al., 2007), there are drawbacks that make this method less useful for the restoration of most mature-forest species. First, the selection of species available from nurseries is often limited to trees that have commercial or agricultural value, and for which propagation techniques are known (Sautu et al., 2006). Second, studies of the seed biology of mature-forest trees suggest that a majority of larger-seeded species are recalcitrant (sensitive to desiccation and temperature, and germinate rapidly; Daws et al., 2005; Sautu et al., 2006; Vazquez-Yanes and

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