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Overcoming ecological barriers to tropical lower montane forest succession on anthropogenic grasslands: Synthesis and future prospects

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ABSTRACT

Understanding the ecological mechanisms that constrain forest succession in tropical degraded anthropogenic grasslands is a prerequisite for the design of techniques for restoring biodiversity and ecosystem processes. In this context, succession on post-agricultural lands may be arrested by a variety of site-specific biotic and abiotic factors. Here we synthesise our research on the effects of five biotic factors (seed dispersal, development of a soil seed bank, seedling emergence, herbivory, competition) and five abiotic factors (fire, microclimatic conditions, soil nutrients, water availability, disturbance) as constraints to forest succession on degraded anthropogenic grasslands in a tropical lower montane forest landscape in Sri Lanka. The aim of this research was to deduce ecologically and socially acceptable restoration techniques to accelerate forest recovery. Colonisation of grasslands by trees is constrained by limited seed dispersal from adjacent remnant forest patches and their incorporation into grassland soil seed banks. For the few tree seeds that are dispersed into grasslands, a combination of vertebrate herbivory and annual dry season fires reduces the likelihood that they emerge as seedlings. Removal of the grass canopy by clipping or tilling increases the emergence of woody plant seedlings close to the boundaries of forest patches, but has no effect beyond 20 m into the established grassland. Our research shows that isolation of seedling root systems from those of competing grasses increases the growth and survival of tree seedlings transplanted directly into grassland swards, while above-ground competition and exclusion of vertebrate herbivores has no effects on seedling growth and survival. These experiments identified that the early-successional species *Macaranga indica* Wight and *Symplocos cochinchinensis* (Lour.) S. Moore are potential candidates for use in reforestation programmes on abandoned grasslands. We propose a strategy for a model forest restoration programme based on the creation of vegetation islands using early-successional native tree species, the application of a tilling treatment around remnant forest patches, creation of fire breaks around vegetation islands, and the protection of isolated individual trees and tree patches within established grasslands. We highlight the importance of further research on the ecology and biology of seed dispersers and seed predators, and expansion of knowledge on the regeneration traits of native tree species, for future refinements of this restoration strategy.

1. Introduction

Large areas of the world's tropical forests have been cleared and degraded, which has led to a consequent loss of species diversity and ecosystem services (Parrotta et al., 1997; Lamb, 1998; Chapman and Chapman, 1999; Hooper et al., 2002; Foley et al., 2007). Deforestation and land degradation may push ecosystems over an ecological threshold, beyond which recovery is slow or impossible, and once abandoned these modified ecosystems may remain as they are or degrade further (Lamb, 1994a; Hooper et al., 2005; Gibbs et al., 2010; Holl and Aide, 2012; Hosonuma et al., 2012; Shoo and Catterall, 2013). Although abandoned areas in the tropics have been largely neglected in the past, when reforested they may provide valuable goods and services to humans such as provision of products of importance to local people, protection of watersheds, formation of buffer zones for mature forests and conservation of species diversity (Brown and Lugo, 1990; Aide et al., 1995; Wijdeven and Kuzee, 2000).

In Sri Lanka, natural forests have shrunk to half their size over the last three decades, due to large-scale conversion of forests to plantation agriculture, shifting cultivation, increasing population

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pressure, encroachment, unemployment and poverty (Vivekanandan, 1988; Wickramagamage, 1990; Baldwin, 1991). As a result of these human pressures, Sri Lanka was left with a dense forest cover of only 24% by 1994 (Food and Agriculture Organization, 2010). Many of the upper montane (>1500 m a.s.l.) and lower montane (900–1500 m a.s.l.) forests that protect the water catchments of the major rivers in Sri Lanka, and support high biodiversity, were cleared during the colonial era (1815–1948) for the cultivation of cash crops such as coffee and tea. Almost 30% of land under tea cultivation is marginal or uneconomic and nearly 26,600 ha of tea plantations were abandoned between 1956 and the 1980s (Fernando, 1998; Anandacoomaraswamy, 1999). Many abandoned tea plantations subsequently become converted into grasslands dominated by the native grass *Cymbopogon nardus* L. Rendle, although land use change is complex and in some parts of Sri Lanka tea production by small-scale farmers is expanding (Lindström et al., 2012). At the study sites for this research, grasslands are burnt during the dry season to maintain favourable grazing grounds for domestic cattle and buffaloes, to permit hunting, and to protect villagers against snakes and other wild animals (Ariyadasa, 2002; A.M.T.A.G., personnel communications with local villagers). These grasslands appear to resist natural succession and may remain in a degraded state for several decades, despite being surrounded by remnant forest patches. The aim of our research was to determine the factors that inhibit forest recovery on these anthropogenic grasslands within the buffer zone of part of the Central Highlands World Heritage Site supporting high conservation value lower and upper montane tropical forests.

A range of biotic and abiotic factors and interactions among them have been identified as barriers to tree seedling establishment in post-agricultural lands, although their relative importance may vary greatly among study sites. Research in other tropical regions has shown that forest recovery on degraded lands may be limited by low seed availability (Uhl et al., 1981, 1988; Nepstad et al., 1991, 1996; Holl, 1999; Wijdeven and Kuzee, 2000; Zimmerman et al., 2000), seed and seedling predation or herbivory (Nepstad et al., 1991; Cohen et al., 1995; Holl and Quiros-Nietzen, 1999; Holl et al., 2000), and low emergence and high mortality of tree seedlings (Nepstad et al., 1996), harsh microhabitat conditions (Uhl et al., 1988; Nepstad et al., 1996), fire (Lamb, 1994a; Hoffmann, 1996; Zhuang, 1997; Eva and Lambin, 2000; Hooper et al., 2005), low soil nutrient and water availability (Uhl et al., 1981, 1987; Corlett, 1991; Hoffmann, 1996; Nepstad et al., 1996; Zhuang, 1997; Holl, 1999; Hooper et al., 2005) and competition with pasture grasses (Chapman and Chapman, 1999; Slocum, 2000; Hooper et al., 2005). In many studies these factors have been examined in isolation, which is a constraint when factors have non-additive interactions or synergistic effects on the likelihood of tree seedling recruitment (Gunaratne et al., 2010).

Although anthropogenic disturbance is generally responsible for the low rate of tree invasion into tropical grasslands, cessation of this disturbance does not readily lead to rapid forest recovery (Hau and Corlett, 2003). Controlling fire regimes, direct seeding and tree planting have been used worldwide to promote regeneration on degraded lands (Hooper et al., 2002; Lwanga, 2003; Florentine and Westbrooke, 2004). In the tropics, many degraded sites have been replanted with timber tree species from a small number of genera, such as *Pinus*, *Acacia* or *Eucalyptus* (Lamb, 1994a; Wishnie et al., 2007). These trees are unlikely to catalyse rapid regeneration of native forest trees because they are not attractive to local seed dispersal agents, except as perches and/or lookout posts. Although exotic tree species may act as nurse plants that facilitate the growth of native species beneath them with time (Bandaratilake, 1988; Kuusipalo et al., 1995), efforts to reforest abandoned post-agricultural lands with native species have received much more attention in recent years (Butterfield, 1995; Loik and Holl, 1999; Holl et al., 2000; Elliott et al., 2003; Hau and Corlett, 2003; Wishnie et al., 2007; Griscom et al., 2005; Lamb et al., 2005; Griscom and Ashton, 2011; Hall et al., 2011a). Many degraded lands in Sri Lanka have been reforested with *Pinus* spp., but indigenous species from Sri Lanka could well merit more attention (Wood, 1988; Ashton et al., 1997, 1998).

In spite of the rapidly growing areas of abandoned degraded lands in tropical Asia, the role of these biotic and abiotic factors in arresting succession on degraded grasslands in the region remains poorly understood. The Western Ghats of India combined with Sri Lanka have been classified as one of the top ten hotspots for the number of likely extinctions of both plants and terrestrial vertebrates due to habitat loss (Brooks et al., 2002). Moreover, as emphasised by Primark and Corlett (2005) "despite the obvious similarities in tropical rain forests due to their location around the equator, the policies, tactics, and techniques that work in one region may prove ineffective or even disastrous in another" thus the task we are faced with is not "saving the rain forests", but "saving the many rain forests". Therefore, it is essential to develop a thorough understanding of the factors that constrain forest regrowth in post-agricultural abandoned lands in South Asia in order to reduce further fragmentation of remnant forests and to increase the goods and ecological services provided by them.

In this paper we synthesise evidence derived from research on a range of barriers to establishment of woody plant species on degraded anthropogenic grasslands growing in a tropical lower montane environment in Sri Lanka, and propose practical techniques for forest restoration based on overcoming those barriers (Skinner, 2004; Gunaratne, 2007; Gunaratne et al., 2010, 2011; Taylor, 2011; Mogollones-Barrera, 2013). At our study sites, seedlings of forest trees are very rare in man-made grasslands even decades after they have been abandoned after agricultural use. The main objective of this research was to determine the mechanisms that constrain secondary succession on these degraded human-induced grasslands, and to rank the factors in terms of their relative importance.

2. Methods

2.1. Study site

The findings summarized in this paper stemmed from research conducted from December 2003 to the present at c. 1000 m a.s.l. on the eastern slopes of the Knuckles Forest Reserve (KFR, Appendix A). The KFR was declared as part of the Central Highlands World Heritage Site in 2010 by UNESCO (World Heritage Committee, 2012). The mean annual rainfall on the eastern slopes of the KFR is 4512 mm, and minimum and maximum temperatures are 18° and 26 °C, respectively. There is a dry period from July to September when mean monthly rainfall declines to 60–100 mm. Strong winds during the dry season exacerbate the low rainfall during this period.

The study was conducted in a landscape comprising fragments of lower montane tropical forest embedded in a matrix of human-induced grasslands originating from former tea plantations that have been subsequently abandoned (for further details on site history see Gunaratne et al., 2010, 2011). By 2003 most of the grasslands in the KFR were dominated by the grass *C. nardus* (L.) Rendle, which grows to a height of 0.5–1.0 m and is subject to repeated annual dry season fires (all authors, personal observations). Some herbs and shrubs (mostly Melastomataceae and Rubiaceae), and a few fire-tolerant tree species, survive as scattered individuals in the grass matrix. Surprisingly, seedlings of primary or secondary tree species are rare, even though these areas are surrounded by remnant forest patches (Skinner, 2004). Moreover forest patches

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