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Does soil variation between rainforest, pasture and different reforestation pathways affect the early growth of rainforest pioneer species?

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ABSTRACT

Rainforest deforestation and subsequent reforestation not only alter above-ground vegetation, but also lead to significant changes in the physical and chemical characteristics of soil and in biochemical cycles, which in turn are likely to influence the growth of rainforest plants. However, little research has directly linked soil condition to seedling growth under different forms of rainforest restoration.

This study compared the early growth of three rainforest pioneer species (*Alphitonia excelsa*, *Guioa semiglauca*, *Omalanthus nutans*) among soils collected from three different reforestation pathways, and from reference sites in remnant rainforest and pasture in subtropical eastern Australia. The types of reforestation were tree-planting for ecological restoration purposes, autogenic regrowth dominated by the non-native tree species camphor laurel (*Cinnamomum camphora*), and management of this regrowth to encourage native regeneration. Growth was measured in a shade-house, using soil from five sites in each site-type and three replicate plants of each species. Fifteen physical and biochemical properties were also measured in soil from each site; five of which were related to carbon and eight to nitrogen-dynamics.

Two-factor ANOVA of the exponential growth coefficients of seedling height and diameter showed that there was no interaction between tree species and site-type, but there were significant main effects of both these factors. Seedling growth rates did not differ between pasture and rainforest soils, but were around 25% lower in soils from camphor-dominated regrowth sites than in soils from treated camphor and replanted sites. Seedling growth rates were correlated with two independently-varying soil properties: soil pH and plant-available nitrate-nitrogen, whose inclusion as covariates in the ANOVA largely removed the significant site-type effect. These results indicate that reforestation pathways can affect seedling growth by altering the physical and biochemical properties of soil. However, the absolute magnitude of this effect was not large.

1. Introduction

Large areas of rainforest have been cleared throughout the world, mainly for the establishment of pastures and agricultural land (Aide et al., 1995; ITTO, 2002). Re-establishment of forests in these highly degraded landscapes is important to protect the land against erosion, to create habitat for wildlife and to restore biodiversity (Sun et al., 1995; Lamb et al., 2005). There are several different pathways by which forest might be restored on cleared land. A common pathway is spontaneous forest regrowth, which occurs when trees and shrubs that are present in the soil seed bank or that are dispersed to sites from external sources, establish after cessation of grazing or cultivation (Aide et al., 1995; Kanowski et al., 2003; Catterall et al., 2008). These initial colonisers, which may be native or non-native species, act as pioneers and often facilitate the growth of a variety of other species (Erskine et al., 2007). In cases where non-native species initially dominate the regrowth, managed suppression of these species, once recolonisation by other species has commenced, may be used to accelerate the development of a native tree community (Kanowski et al., 2008a). An alternative pathway which implies a high level of human intervention is ecological restoration planting, in which a diverse range of native tree seedlings is densely planted in order to overcome potentially limiting factors such as depleted soil seed banks and competition from pasture grasses (Erskine et al., 2007).

In all reforestation pathways, pioneer tree species play an important role in the dynamics and development of forest cover (Connell and Slatyer, 1977; Brown and Lugo, 1990; Aide et al., 1995; Erskine et al., 2007). Rainforest pioneer species typically produce many small seeds that are widely dispersed by

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frugivores or by wind (Hopkins and Graham, 1984; Garwood, 1989; Vazquez-Yanes and Orozco-Segovia, 1993; Dalling et al., 1997) and are fast-growing, which enables them to compete with grasses and weeds, thereby creating conditions which may favour the recruitment of other rainforest species that are slower growing but shade tolerant (Erskine et al., 2007). The growth of tree seedlings, especially in their early stages, can be strongly affected by soil properties (Nussbaum et al., 1995; Burslem, 1996; Gunatilleke et al., 1996; Woodward, 1996). This is particularly the case for pioneer species as a consequence of their small seeds and rapid growth habits (Chapin et al., 1986). In particular, changes in nitrogen (Tilman, 1986) and phosphorus availability (Vitousek and Matson, 1984; Ewel, 1986) are known to influence the growth of some pioneer species.

Deforestation can significantly alter soil physical and chemical properties and biochemical cycles in rainforest landscapes, although different studies have reached varying conclusions about the extent to which reforestation re-establishes the full range of soil properties (Bashkin and Binkley, 1998; Rhoades et al., 2000; Rasiah et al., 2004; Silver et al., 2005; Zheng et al., 2005; Maloney et al., 2008; Paul et al., 2010). Nevertheless, there is a general consensus that reforestation can successfully restore many aspects of the nitrogen cycle, including nitrogen (N) stocks, nitrogen mineralisation, nitrate concentrations, and nitrification rates (Lamb, 1980; Robertson and Vitousek, 1981; Robertson, 1984; Vitousek et al., 1989; Rasiah et al., 2004; Scowcroft et al., 2004; Paul et al., 2010). Such changes could be expected to influence the growth of rainforest plants. However, little research has directly linked soil conditions to seedling growth under different forms of rainforest restoration.

The present study examines how changes to soil properties associated with deforestation and reforestation affect the early growth of rainforest pioneer trees in subtropical Australia. Previous research in this region described the effects of deforestation and reforestation on the properties of soil (Paul et al., 2010). In this study we measured the growth of greenhouse-raised seedlings of three rainforest pioneer species using the same soils, collected from replicate sites in pasture, rainforest and three reforestation pathways (tree-planting for ecological restoration, regrowth dominated by a non-native tree species, and similar regrowth treated to promote the growth of native tree seedlings). We test the effect of site-type on seedling growth rates, investigate the association between seedling growth and the physical and biochemical properties of the soils, and consider whether the observed seedling growth variation is consistent, with expectations based on previously established relationships between seedling growth and soil factors.

2. Methods

2.1. Study region

This study was carried out in the 'Big Scrub' region in eastern subtropical Australia, 28°40′–29 S; 153°10′–153°30′ E. The region was once extensively covered by lowland subtropical rainforest over an area of 75,000 hectares (Floyd, 1990). Geologically, the region is defined by a basaltic plateau on the southern slopes of the Mt Warning shield volcano, 100–150 m above sea level, formed from basaltic flows and associated sediments(Lott and Duggin, 1993). The major soil type is a fertile, red, well-structured, acid and porous soil with a high clay content (Lymburner et al., 2006). Mean daily temperatures range from 13 °C to 26 °C and annual rainfall averages around 1300–2300 mm (varying spatially), with wetter months generally between November and May (Bureau of Meteorology, 2009).

In the mid-late 19th century, the rainforest cover was largely cleared for the development of pasture and agricultural land (Floyd, 1990). The most common land-cover types at the beginning of the 21st century were actively grazed pastures, macadamia plantations, and spontaneous regrowth, with <1% of the area supporting mature remnant rainforest (Neilan et al., 2006), classified as complex notophyll vine forest (Floyd, 1990).

Reforestation of former rainforest areas in the study region has mainly occurred through three different pathways. First, the non-native tree species camphor laurel (*Cinnamomum camphora*) dominates regrowth on abandoned land. Camphor laurel regrowth (henceforth referred to as "camphor-dominated regrowth") covered around 25% of the Big Scrub region at the time of this study (Neilan et al., 2006). Within this regrowth, the seedlings of a diverse array of native rainforest trees also occur, as a result of dispersal by frugivorous birds (Neilan et al., 2006; Kanowski et al., 2008b). Second, some stands of camphor-dominated regrowth have been treated to accelerate the development of secondary rainforest by strategically poisoning mature camphor trees and seedlings with herbicide, liberating a dense growth of rainforest seedlings (Kanowski and Catterall, 2007; Kanowski et al., 2008b). Third, many small areas of land across the region have been reforested with ecological restoration plantings, comprised of a high density and diversity of native rainforest tree seedlings (Erskine et al., 2007). Within 3–5 years, such plantings can form a closed canopy which shades out grasses and weeds and attracts seed-dispersing frugivores (Catterall et al., 2008).

2.2. Experimental design

The experimental design consisted of five site-types (pasture, camphor-dominated regrowth, treated camphor regrowth, ecological restoration planting, and rainforest) with five replicate sites in each site-type. The sites were interspersed across a large part of the Big Scrub region; spanning 25 km from east to west and 30 km from north to south.

The minimum distance between replicate sites was 5 km. All sites were located on soils developed from basalt, at elevations between 100 and 150 m, and the pre-clearing forest-type would have been similar (Floyd, 1990). All reforested sites were cleared in the late 19th/early 20th century, managed for dairy farming until the 1960s, then retired from agricultural use or used only for very low intensity grazing. Detailed characteristics of all five site-types are as follows.

Pasture sites (PA) were characterised by a dense cover of short grass and were actively grazed by cattle or horses. Discussions with landholders revealed that fertilisation with lime ($CaCO_3$) and superphosphate ($Ca(H_2PO_4)_2$) had been a common practise of pasture management.

Camphor-dominated sites (CD) contained regrowth 20–40 years old (determined from interviews with landholders), in which camphor laurel was the dominant canopy tree (70–90% of the canopy) and the canopy was closed (above 70%), with an average height of 25 m. At most sites, the understorey of camphor stands was dominated by a dense growth of exotic shrubs, although a diverse array of native rainforest trees were usually present as seedlings (Neilan et al., 2006; Kanowski et al., 2008b).

Treated camphor sites (TC) had previously consisted of 15–30 years old camphor regrowth. At the time of sampling, these sites were in their third to sixth year following treatment by glyphosate poisoning of the mature and seedling camphor trees. They had a closed canopy approximately 10–15 m high, dominated by rainforest species, including pioneers and later successional species. For descriptions of such sites see Kanowski et al. (2008a).

Ecological restoration plantings (ER) were 12–20 years old, with canopy cover of 60–85%, and the trees comprising a diverse range