Forest Ecology and Management 359 (2016) 1–10

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Tree fern competition reduces indigenous forest tree seedling growth within exotic *Pinus radiata* plantations

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ARTICLE INFO

Article history:
Received 25 June 2015
Received in revised form 22 September 2015
Accepted 23 September 2015

Keywords:
Fern filtering
Forest restoration
Non-harvest plantation
Pinus radiata
Tree fern

ABSTRACT

Tree ferns are recognized as "keystone" species for their role in casting deep shade on forest floor environments, acting as a differential ecological filter on forest regeneration processes. Tree fern dominance is a feature of New Zealand's central North Island exotic *Pinus radiata* (Pinaceae) plantations, particularly beyond 20 years following plantation establishment. In circumstances where plantation forests are managed for restoration of indigenous forest species, rather than timber harvest, an understanding of the competitive role of dense tree fern stands on forest regeneration processes in these "non-harvest" plantations is necessary.

We investigated the competitive effect of tree fern (Cyatheaceae and Dicksoniaceae) cover on seedling growth rates of two mature forest tree species, *Podocarpus totara* (Podocarpaceae) and *Pittosporum eugenioides* (Pittosporaceae), over two austral summers in five 36–92-year *P. radiata* plantations. We experimentally manipulated tree fern canopies in order to contrast heavy versus light shading. Tree fern removal significantly increased the growth rate of both *P. totara* and *P. eugenioides*, and the growth rate of the shorter-lived, faster-growing, light demanding *P. eugenioides* was greater than that of *P. totara* with tree fern removal. Damage to the seedlings by mammalian animal browsers when tree ferns were removed was greater than that occurring under tree fern cover. This damage diminished the effect of tree fern removal on seedling growth rates for *P. totara*, but not for the faster growing *P. eugenioides*.

The physical clearance of tree fern stands and then the establishment of fast growing, locally representative, indigenous canopy tree species of low palatability, along with protection from animal browse, are suggested restoration strategies. Our results are consistent with existing literature in showing that where tree ferns are a dominant feature of plantation understories, deep shade is likely to reduce canopy species seedling growth rates, reducing the potential for forest regeneration.

1. Introduction

The interception of light by dense understorey vegetation can have a profound effect on forest regeneration processes, and ultimately the rate and trajectory of forest successions (Bazzaz and Pickett, 1980; George and Bazzaz, 1999; Royo and Carson, 2006). Steep gradients of declining photosynthetically active radiation near the forest floor shape the structure and composition of the seedling bank, which directly influences the competitive and reproductive dynamics of forest regeneration (George and Bazzaz, 1999). Through competitive processes, tree fern dominated forest understories have been found to exert an ecological filtering effect ("fern filtering") on tree regeneration processes (Bystriakova et al., 2011; Coomes et al., 2005). In particular, given the deep shade cast by tree ferns' near horizontally-arched megaphyll fronds, tree ferns are increasingly recognized as "keystone species" (cf. Paine, 1969) due to their disproportionally large influence on forest floor regeneration processes (Gaxiola et al., 2008; Coomes et al., 2005; Newton and Healey, 1989).

As a result of their prolific spore production, tree ferns have the ability to rapidly colonize disturbed areas (Conant, 1976), and in some species such as *Dicksonia squarrosa* (Dicksoniaceae) also through clonal growth (spreading rhizomes). Following volcanic disturbance on recent substrates of the Hawaiian Islands, tree ferns (*Cibotium* spp.) often vigorously invade the nutrient-enriched soils, forming a dense canopy cover and casting heavy shade (Drake and Mueller-Dombois, 1993; Mueller-Dombois, 2000). Tree ferns of the genus *Cyathea* also form dense stands on landslide substrates in

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http://dx.doi.org/10.1016/j.foreco.2015.09.036
0378-1127/

Puerto Rico, arresting woody successions for decades (Walker et al., 2010). In New Zealand's indigenous, temperate, podocarp–broadleaved forest, tall tree ferns intercept about half of the incoming radiation and reduce the ability of conifers to escape the competitive effects of the faster growing angiosperms (Coomes et al., 2005). In a similar vein, Carswell et al. (2007) found that conifers (Podocarpaceae) were not likely to occur in areas with high amounts of tree fern cover, and Gaxiola et al. (2008) manipulated tree fern stands, finding that frond removal significantly increased the height growth rate of seedlings (podocarp and angiosperm) planted on the forest floor.

Tree fern dominated understories also potentially develop within plantation forests (Allen et al., 1995; Harrington and Ewel, 1997; Ogden et al., 1997). While in commercial plantations held under a clear-fell harvest regime the extent of indigenous regeneration within the forest understorey can be limited, in some situations plantation owners want to retain their plantation to provide a nurse environment for the restoration of indigenous forest species (Carnus et al., 2006; Lamb et al., 2005; Lamb, 1998; Parrotta, 1992). In these situations the highly competitive understorey layers that are formed by tree ferns can limit the establishment of woody species (Nuttle et al., 2014; De la Cretaz and Kelty, 2002). Therefore, when tree fern dominated understories develop within these "non-harvest" plantations, forest and restoration managers require an understanding of the competitive role tree ferns have in the plantations' regeneration dynamics and how this might be manipulated to accelerate forest regeneration.

As of 2014, it was estimated that 7% (1.75 million ha) of New Zealand's land cover was occupied by plantation forests, the majority being located in the North Island (1.23 million ha), with a particular concentration of plantation forest in the central North Island (587,104 ha) (Ministry of Primary Industries [MPI], 2014). Ninety percent of New Zealand's plantation cover comprises *Pinus radiata*, with the remaining area comprising Douglas-fir (6%), Eucalypt (1%), and other softwood and hardwood species (3%) (MPI, 2014). Over the first two decades following plantation establishment, the understories of central North Island exotic *P. radiata* plantations often become colonized by tree fern species (Cyatheaceae and Dicksoniaceae), which increase in dominance over subsequent decades (Ogden et al., 1997). In plantation forests close to our study area, *P. radiata* stands >30 years old achieved a total basal area comprising 10–30% tree ferns and tree fern stem densities totaled 2000–2500 stems ha^{-1} (Ogden et al., 1997). Cyatheaceae and Dicksoniaceae tree fern species differ in their life history traits regarding growth rate and shade tolerance (Bystriakova et al., 2011). Within central North Island *P. radiata* plantations, the relative abundance among tree fern species changes as understorey illumination is altered over time by stand development (Ogden et al., 1997). Following plantation establishment, *Dicksonia* species appear during the first decade, whereas *Cyathea* species are gradually added during the second decade, and become more abundant with time. *Dicksonia squarrosa*, which is New Zealand's most common tree fern (Bystriakova et al., 2011), is known to dominate the tree fern community (Ogden et al., 1997). It is the only New Zealand tree fern species to reproduce via aerial buds (Large and Braggins, 2004), thereby taking on a multi-stemmed form and is also rhizomatous; forming potentially large, interconnected colonial stands (Brownsey and Smith-Dodsworth, 2000).

As the restoration potential of plantations is likely to be limited when the recruitment of future canopy tree species on the site is constrained by very dense understories (Nuttle et al., 2014; Royo and Carson, 2006; De la Cretaz and Kelty, 2002), we suggest dense stands of tree fern cover (Fig. 1) may limit recruitment of indigenous canopy tree species within these central North Island exotic *P. radiata* forests, thereby limiting their potential biodiversity value.

Fig. 1. Example of tree fern dominated forest understorey composition within mature *Pinus radiata* plantation forest, central North Island, New Zealand.

Here, we examine the shading effect of dense tree fern stands on the growth of seedlings of two indigenous forest canopy species, *Podocarpus totara* (Podocarpaceae) and *Pittosporum eugenioides* (Pittosporaceae), planted within exotic *P. radiata* plantations. We have experimentally manipulated the tree fern canopy in order to contrast heavy versus light shading of seedlings by tree ferns. We predict that the heavy shade cast by tree ferns will reduce the growth rate of these two indigenous forest canopy species, and we expect the species' contrasting life history traits to provide insights into the effect of heavy tree fern shade on an indigenous forest succession from exotic *P. radiata* plantations in New Zealand. *Podocarpus totara* is a long-lived (800–900 years; Hinds and Reid, 1957), albeit relatively light-demanding conifer (Ebbett and Ogden, 1998), which is generally avoided in the diet of introduced ungulates. However, ungulate browse does occur (Forsyth et al., 2002), and young *P. totara* shoots can be preferentially browsed when nutrient concentrations are seasonally elevated. *Pittosporum eugenioides* is a shorter lived angiosperm that exhibits faster growth rates (Williams and Buxton, 1989), is generally avoided in the diet of introduced ungulates (Forsyth et al., 2002), and is a species usually found in the early stages of New Zealand's indigenous forest successions. Therefore, we predict that under the heavy shade cast by tree fern stands under the *P. radiata* canopy—the longer-lived conifer *P. totara* will be less competitive than the faster-growing, more light-demanding angiosperm *P. eugenioides*.