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Effects of allelopathy and competition for water and nutrients on survival and growth of tree species in *Eucalyptus urophylla* plantations

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ABSTRACT

Allelopathy and resource competition are considered to be two primary mechanisms responsible for loss of biodiversity in plantations of *Eucalyptus* species. However, these two processes are usually studied separately, and they have been rarely tested on native woody species. In this study, we used a bioassay to assess sensitivities of twenty broad-leaved tree species on roots, stem growth and seed germination to leaf aqueous extracts of *Eucalyptus urophylla* S.T. Blake and categorized them into two types: inhibited and uninhibited (including stimulated and unaffected). To compare the relative importance of allelopathy and resource competition, we planted these two species groups into the *E. urophylla* plantation separately and treated with three gradients of irrigation-nutrients. The results showed that the allelopathic effects of aqueous extract of *E. urophylla* were species-specific and could be inhibitory, neutral or stimulatory. Compared to the inhibited species, the uninhibited species grew faster and survived better after they were planted in an *E. urophylla* plantation for approximately 10 years, suggesting that allelopathy from *E. urophylla* is an important restraining factor on native woody communities. Individuals from both species groups grew faster following higher resource treatment at the early but not the late stage of growth. Saplings did not vary in their survival rates across resource gradients. This indicates that resource competition between *E. urophylla* and native woody species has only a limited role in reducing the diversity of native species in an *E. urophylla* plantation. We conclude that allelopathy is more important than resource competition in mediating the reduction in plant biodiversity in *E. urophylla* plantations. Our study suggests that mixing certain types of species (e.g. *Helicia cochinchinensis*, *Pterospermum lanceaefolium*, *Cinnamomum burmanni*, *Machilus chinensis*, *Acmena acuminatissima* and *Castanopsis chinensis*) in *E. urophylla* plantations can mitigate against plant diversity loss.

1. Introduction

Large scale plantations have been established by fast-growing tree species with the aim of producing timber for products such as paper, solid wood and firewood (Evans, 2009). Forestry plantations are typically characterised by densely planted monocultures of non-native trees. As a result, some native species have become endangered, and beneficial ecosystem services provided by native forests are diminishing (Foroughbakhch et al., 2001; Sangha and Jalota 2005).

Eucalyptus, which belongs to Myrtaceae and native to Australia and South East Asia, is one of the fastest-growing and highest-yielding tree genera in tropical and subtropical areas (Zhao et al., 2007). *Eucalyptus* have been introduced into more than 120 countries, and they comprise one-third of the world's total plantation area (Wu et al., 2015). There were 4.4 million ha of *Eucalyptus* plantation established in south China by the end of 2014 (Ou and Wang, 2015). However, the planting of *Eucalyptus* is still a controversial issue. Criticism is mainly focused on the serious ecological problems caused by continuous planting of *Eucalyptus* in monoculture, such as soil degradation, increasing invasiveness and loss of understory biodiversity (Huang et al., 2007; Tang et al., 2013; Jin et al., 2015; Williams 2015). Studies have documented altered community composition (e.g. vegetation and soil microbial communities) in *Eucalyptus* plantations compared to other vegetated habitats (Proença et al., 2010; Calviño-Cancela et al., 2012; Wu et al., 2013). Reduction in biodiversity in *Eucalyptus* plantations is therefore a crucial issue for the long-term sustainability of native ecosystems (Tererai et al., 2013).

Resource competition is an important mechanism which accounts for the adverse impact of *Eucalyptus* on native vegetation (Forsyth et al., 2004; Tererai et al., 2013). *Eucalyptus* plantations are often established on nutrient-poor bare ground, and because they are strongly competitive for soil nutrients and water, they may outcompete native species (Michelsen et al., 1996; Robinson et al., 2006; Neyland et al., 2009).

Allelopathic effect is another important factor that has been blamed

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for the reduction of plant biodiversity in *Eucalyptus* plantations (May and Ash, 1990; Michelsen et al., 1996; Fang et al., 2009). Allelopathic effects have been studied extensively (Sasikumar et al., 2002; Bajwa and Nazi, 2005; El-Khawas and Shehata, 2005). In general, allelochemicals are released into the environment by volatilization, leaching, decomposition and excretion (Blum, 2011). Phenolic acids and volatile terpenes have been extracted from the leaves, bark and roots of *Eucalyptus* (Santos et al., 2013; Zhang et al., 2014) and their phytotoxic effects on seed germination and early seedling growth after being accumulated in soil by leaf leaching, plant residues decomposition and root exudation have been examined (Florentine and Fox, 2003; Ahmed et al., 2008; He et al., 2014). Leachate of *Eucalyptus* foliage, which contains a variety of oils and resins, exerts an direct/indirect allelopathic effect on neighboring species (e.g. plant roots and seeds, or soil microbes), thus reducing the abundance and richness of understory species (Ziaebrahimi et al., 2007; Ruwanza et al., 2015). However, other researchers do not agree with this (Silva et al., 1995; Yirdaw and Luukkanen, 2003; Zhang et al., 2016). They argued that supporting evidence for inhibitory effects of *Eucalyptus* were derived mainly from indoor experiments which focused on germination and root growth of sensitive weeds and crops (El-Khawas and Shehata, 2005; Carvalho et al., 2015), and there are few studies concerning the allelopathic effects of *Eucalyptus* on tree species in the field. Indeed, *Eucalyptus* can have a "catalytic effect" or "nurse effect" on the regeneration of natural forest biodiversity in degraded lands (Loumeto and Huttel, 1997; Feyera et al., 2002). On the other hand, a variety of factors, including environmental conditions (Yirdaw and Luukkanen, 2003), concentration of allelochemicals (Inderjit and Duke, 2003), and soil substrate (Parepa and Bossdorf, 2016) contribute to the variation in allelopathy. More field-based studies are needed to evaluate allelopathy under natural conditions.

Increasing species diversity could enable a plant community to use a site's resources more effectively (Petchey and Gaston, 2002; Kelty, 2006; Forrester et al., 2010; Li et al., 2014). Considering to the sustainable development of artificial forest, Chinese government is considering ways to reconstruct *Eucalyptus* plantation monocultures in an effort to reduce their possible negative ecological effects (Sun et al., 2017). Mixed plantations of *Eucalyptus* and native species have been proposed to maximize productivity and enhance ecological services of forest plantations (Turnbull, 1999; Forrester et al., 2005; Erskine et al., 2006; Wu et al., 2015). Many studies have reported that allelopathy is species-specific (Fang et al., 2009; Kim and Lee, 2011; Meiners et al., 2012) and the selection of species for reconstruction of *Eucalyptus* monocultures remains an issue (Tesfaye et al., 2015; Sun et al., 2017). In order to improve forest management, allelopathy and resource competition should be taken into consideration during species selection.

The substrate (e.g. soil nutrients) can influence the production of allelochemicals by the donor species (Einhellig, 1996), and allelochemicals can interfere with nutrient acquisition in the target plant by negatively influencing mycorrhizal symbiosis (Stinson et al., 2006). Resource competition and allelopathy may operate simultaneously and/or sequentially, influencing community structure and vegetation dynamics (Inderjit and del Moral, 1997), but the exact nature and mechanisms of the interactions are poorly understood.

In this study, we investigated the allelopathy and resource competition on woody species in *E. urophylla* plantations. First, we conducted a bioassay to test allelopathic effects of leaf aqueous extract of *E. urophylla* on root, stem growth and seed germination of twenty broad-leaves woody species. Based on their sensitivities to the aqueous extracts, they were divided into two types (i.e. inhibited or uninhibited). And then, to assess the relative importance of allelopathy and resource competition, we planted the two groups of saplings into the *E. urophylla* plantation separately and treated with three gradients of irrigation-nutrients and determined the seedling survival and basal growth of those twenty species.

2. Materials and methods

2.1. Site description

Experiments were carried out at Shuilian Moutain Forest Park, Dongguan city, Guangdong province, China (113°42′ E, 22°58′ N). The climate of the region is subtropical monsoon and a rainy season from April to September. The mean annual temperature is 23.2 °C and mean annual precipitation is 1780 mm. The soils are latosol developed on granite with a pH of 3.8.

Shuilian Mountain Forest Park has an extensive practice of *E. urophylla* plantations, which have been established in 1992 and protected from any artificial disturbance after initial establishment. *E. urophylla* trees dominate the canopy with about 15–20 m high and the density of 10 individuals/100 m^2. The average basal diameter of the trees is about 22 cm. A few native tree species distribute sporadically in the plantations, such as *Diospyros morrisiana*, *Rhus sylvestris*, *Sapium discolor*, *Aporosa chinensis* and *Adinandra millettii*. The shrub species cover is about 60%. Moreover, vertical stratification of shrub and herbaceous plants is not obvious, and the understory is dominated by shrub species such as *Psychotria rubra, Ilex asprella* and *Adina pilulifera* and herbaceous species such as *Scleria levia*, *Microstegium vagans* and *Neyraudia reynaudiana*.

2.2. Plant species

Initially, we collected fifty-six broad-leaved tree species for the glasshouse experiment (Table S1). We collected seeds of fity-four native species from late 2005 to early 2006 from Heishiding Nature Reserve and Dinghushan Nature Reserve; both reserves are located in Southern China within 200 km radius of the studied plantations. Two species (*Leucaena leucocephala* and *Albizia lebbeck*) were introduced nitrogen (N)-fixing species and they were selected to improve soil fertility (Chen et al., 1999; Forrester et al., 2006; Hoogmoed et al., 2014). Some species, such as *Castanopsis fissa*, *Erythrophleum fordii*; *Michelia maclurei* and *C. burmanni*, were used to reconstruct the *E. urophylla* plantation (Wang et al., 2002; Yi et al., 2004). Many other species like *Liquidambar formosana* (Hamamelidaceae), *Delonix regia* (Leguminosae) and *C. camphora* (Lauraceae) were used to establish public ecological forests or scenic forest (Wang et al., 2002; Huang et al., 2006). *Schima superba* and *M. maclurei* were confirmed to be excellent choices for establishment of firebreak forest (Xue et al., 2005).

2.3. Experimental design

2.3.1. Experiment 1: Assessing the sensitivities of native species to allelopathic effects of E. urophylla

Previous studies have shown that leaf leaching is the main allelopathic pathways of *Eucalyptus*. *E. urophylla* leaves contain a higher diversity and higher quantities of phenolics and terpenoids than roots (Turk and Tawaha, 2003). To get closer to the natural conditions, we assessed allelopathy of *E. urophylla* with water as extraction solvent (Vyvyan, 2002; Lorenzo et al., 2013).

Before testing, we cleaned the seeds and sterilized them by soaking in 0.5% $KMnO_4$ solution for 20–30 min, then rinsed in tap water three times (Fang et al., 2009). To prepare aqueous extracts of *E. urophylla*, we collected the leaves on different individuals by an aleatory sampling from the *E. urophylla* plantation at Shuilian Moutain Forest Park in autumn 2005. We chose the intact and healthy leaves, and then cleaned and cut them into pieces (1–2 cm). The stock solution of foliar extracts was prepared by soaking 100 g (fresh weight) in 1000 mL of deionized water for 24 h in darkness, and then filtered to make a stock solution (1:1) (Malik, 2004; Fernandez et al., 2016). Diluted solutions (1:7 and 1:10) were prepared from the stock solution with water. Aqueous extracts were stored at 4 °C until used.

The three filtrates (1:1, 1:7 and 1:10) were treated as the aqueous