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Co-occurring tree species show contrasting sensitivity to ENSO-related droughts in planted dipterocarp forests

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ABSTRACT

This study explores the diversity in sensitivity to drought of moist tropical forest tree species. Yearly tree growth records collected over a ten-year period in two one-hectare 70-year-old damar agroforest plots in Sumatra are analysed. These agroforests are mixed tree plantations, dominated by *Shorea javanica* K. & V., a dipterocarp tree cultivated and tapped for its commercially valuable resin (damar). Many indigenous fruit tree species grow in these agroforests, as well as timber tree species originating from the nearby natural forest. During the census period the multi-species stands were subjected to three El Nino Southern Oscillation (ENSO)-related droughts (1994, 1997 and 2002). At the tree community level, these droughts were associated with a marked decrease in radial stem growth. Multilevel modelling was used to explore the relative contribution of species, tree size and individual tree characteristics to the observed response to drought.

All tree species appeared to be sensitive to drought but the amplitude of the response varied significantly across species. Predicted species mean decrease in stem radial growth rate on drought years (i.e. years with 6 months with less than 50 mm/month rainfall) ranged from less than 5% to more than 80%. Shared species were ranked consistently between plots indicating that the results were robust. Stem diameter significantly affected tree sensitivity to drought in two species only, but in opposite ways: in *S. javanica*, larger trees appeared to be less sensitive while the opposite was true for *Lansium domesticum*, an abundant fruit tree. Individual tree sensitivity to drought contributed significantly albeit to a small extent to the overall response to drought. This individual tree effect did not show any pattern of spatial correlation and hence could not be related to topographic features. It is likely to reflect the individual's unique history and genotype.

1. Introduction

Mixed species forest stands are expected to show a more stable production overtime than monospecific stands because of competitive interactions between species in the community (the "covariance" effect) as well as statistical averaging (the "portfolio" effect) as functional diversity will increases with the number of species and while the likelihood that all species are sensitive to a given ecological stress will diminish (Lehman and Tilman, 2000). Knowledge of species' autecology can provide guidance as to which species may be assembled in what proportion to stabilize production in a particular ecological context (Noordwijk et al., 1994). One major uncertainty faced by foresters worldwide is the impact that global climatic change will have on tree growth in the coming decades. In the subtropics, decreases in the amount of precipitation are likely (IPCC, 2007) and while models do not generally agree on the change in precipitation that will occur in many tropical regions (IPCC, 2007) the precipitation patterns will probably be affected significantly in many tropical areas.

It is well established that trees in tropical seasonal climates do not grow at a constant rate but are affected by seasonal climatic variations (Borchert, 1994, 1998). Most species produce growth rings that are annual (Brienen and Zuidema, 2005; Schongart et al., 2006). Annual tree ring width has been shown to be related either to total rainfall (Schongart et al., 2006), or to within year rainfall distribution (Worbes, 1999; Enquist and Leffler, 2001; Brienen and Zuidema, 2005).

Although trees in tropical moist forests benefit from a more stable climatic environment, most trees that grow to an adult size are likely to face sub-optimal water supply at one time or another

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during their life cycle (Engelbrecht et al., 2007). In fact, even in aseasonal wet tropical climates where annual rainfall exceeds annual potential evaporation, mild seasonal droughts are common and exceptional drought spells do occur (Walsh and Newbery, 1999). Whether the impact is positive or negative at the tree community level seems to depend on the intensity of the drought. For instance, in a lowland forest in central Panama, it was found that tree growth was enhanced during moderate El Nino events but reduced when severe drought coincided with El Nino event (Wright and Calderon, 2006). Drought may affect species differently in terms of both tree survival and tree growth.

In case of a long dry spell the whole population of trees is likely to suffer water limitations, but individual trees may be more or less susceptible either due to species specific physiological adaptation or because of particular attributes at the time of the drought such as vigor, size, crown exposure or access to permanent water source. In a lowland moist rain forest in Borneo, for instance, annual growth rates of small trees declined significantly from a period of low drought intensity to a period of high drought intensity, while larger trees seemed unaffected (Newbery and Lingenfelder, 2004). Concordant pattern of inter-annual fluctuations were recorded across species and size classes in a lowland rain forest in Costa-Rica indicating impact of climate on growth. However, in this case annual growth pattern did not correlate with rainfall pattern (Clark and Clark, 1994) but with the daily minimum temperature annual mean (Clark et al., 2003).

Overall the studies reviewed above suggest that rainfall and tree growth (annual and monthly) are well correlated in a seasonal climate but not necessarily so in tropical moist forest, where solar radiation might be more limiting than rainfall. Other studies which report tropical moist forest species differential performance in response to drought are either restricted to seedling stage (Veenedaal et al., 1996; Engelbrecht and Kursar, 2003) or only discuss changes in demographic rates (Condit et al., 1995; Potts, 2003). Hence there is a lack of evidence that species react specifically and consistently to inter-annual variation in rainfall pattern in aseasonal climate. This is particularly the case for Asian species. It may be surmised that in aseasonal climate where frequency and predictability of drought events is low, the selective pressure has not yielded significant functional diversity in the response to dry spells.

We explore this functional diversity here by analysing species growth response to occasional droughts in a South-West Sumatra dipterocarp planted forest. South-West Sumatra benefits from a humid aseasonal climate, but water limiting situations arise during dry spells which have occurred repeatedly in the last decades despite the lack of a regular dry season.

We first examine the effect of drought episodes at the community level. We then model individual tree response considering effects of taxonomic grouping, stem diameter and their interaction, and individual tree level characteristics. From this analysis we produce a preliminary ranking in terms of sensitivity to drought of 15 Asian tropical tree species.

2. Materials and methods

2.1. Permanent sample plots characteristics

The permanent sample plots were located in the West Lampung district, Southern Sumatra in Indonesia. Land in the study area is defined as moderately dissected rolling marine terraces, acid tuffs and fine felsic sedimentary rocks with slopes ranging from 8 to 15% (National Coordination Agency for Surveys and Mapping, 1989).

Average annual rainfall at the location of the study is 3500 mm, showing a peak in October/November with about 400 mm/month and a minimum in June/July with about 200 mm/month. Variation between years is important and in the decade covered by this monitoring period, there have been three years characterized by unusually severe dry seasons (1994, 1997 and 2002). Simultaneous droughts were reported as having occurred elsewhere in the region. They affected the whole of Sumatra and Western Indonesia and they coincided with ENSO events (Wang et al., 2004; McPhaden et al., 2006). At the scale of Sumatra, the 1997–1998 drought is remembered by all for its haze transnational problem; it was both the strongest drought and the strongest ENSO event as measured by the Nino 3.4 SST index (Field et al., 2004; Wang et al., 2004). The 1994–1995 drought is also remembered for its haze transnational problem, even though it was both a milder drought and a milder ENSO event (Field et al., 2004; Wang et al., 2004). The 2002–2003 ENSO event was similar in magnitude to the 1994–1995 episode, but was associated to much less haze (Field et al., 2004; Wang et al., 2004).

Previous pronounced droughts also occurred in 1972, 1982 and 1991 (data from Krui rainfall monitoring station).

In 1993, two one-hectare plots were demarcated in mature damar agroforests. All stems >5 cm diameter at breast height (dbh) were recorded and mapped to the nearest *m*. These agroforests are 70-year-old (or older) mixed tree plantations, managed by local farmers through a mix of natural regeneration and gap planting (Michon and de Foresta, 1997). They are dominated by *Shorea javanica* K. & V., a dipterocarp tree cultivated and tapped for its commercially valuable damar resin (de Foresta and Boer, 2000). Many indigenous fruit tree species grow in these agroforests, as well as pioneer tree species and timber tree species originating from the nearby natural forest. Main differences between plots are summarized in Table 1 and diameter distributions are shown in Fig. 1. The Gunung Kemala plot has higher basal area, higher stem number and higher species richness. Additional information on plot characteristics can be found in Vincent et al. (2002). Rainfall data was recorded in Krui, the major city in the area, located 3 km from the closest sample plot ("Pahmungan") and 7 km from the furthest sample plot ("Gunung Kemala").

2.2. Tree growth monitoring

Mortality, recruitment and tree growth were monitored once a year during a 10-year period (i.e. until March 2003). Girth measurements were made using a flexible meter tape. Position of

Table 1
Main biophysical characteristics of the two permanent sample plots of damar agroforest. Data on stand structure are given for year 1993 and 2003 (stems $\geq$ 5 cm dbh). Gunung Kemala site is at about 300 m above sea level; Pahmungan site is at about 50 m above sea level. The two sites are located about 7 km apart.

Clay–sand (%)	Year	Basal area (B.A., m^2/ha)	Density (stems/ha)	Number of species	*S. javanica* density	*S. javanica* B.A. (%)
Gunung Kemala						
54–15	1993	42.39	442	49	244	91.4
	2003	43.33	775	97	196	79.9
Pahmungan						
60–12	1993	25.25	402	46	197	64
	2003	26.57	487	50	196	60.2