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Modelling predicts positive and negative interactions between three Australian tropical tree species in monoculture and binary mixture

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Abstract

Computer modelling promises to be an important tool for analysing and predicting interactions between trees within mixed species forest plantations. This study explored the use of an individual-based mechanistic model as a predictive tool for designing mixed species plantations of Australian tropical trees. The 'spatially explicit individually based-forest simulator' (SeXI-FS) modelling system was used to describe the spatial interaction of individual tree crowns within a binary mixed-species experiment. The three-dimensional model was developed and verified with field data from three forest tree species grown in tropical Australia. The model predicted the interactions within monocultures and binary mixtures of *Flindersia brayleyana*, *Eucalyptus pellita* and *Elaeocarpus grandis*, accounting for an average of 42% of the growth variation exhibited by species in different treatments. The model requires only structural dimensions and shade tolerance as species parameters. By modelling interactions in existing tree mixtures, the model predicted both increases and reductions in the growth of mixtures (up to ±50% of stem volume at 7 years) compared to monocultures. This modelling approach may be useful for designing mixed tree plantations.

Keywords: Crown competition; Forest model; Growth model; Growth reduction; Individual-based; Light interception; Mixed species; Shade tolerance; Tree competition; Tree interactions; SeXI-FS

1. Introduction

Concerns over the environmental impacts associated with large-scale monoculture forest tree plantations have lead to interest in the commercial application of mixed species plantations. Mixed species tree plantations have shown promise for mitigating the problems of monoculture stands including the depletion of nutrients, depletion of soil organic matter, soil erosion, and low biodiversity (Bauhus et al., 2004; Lamb et al., 2005). Apart from improved sustainability, mixed species plantations may provide the added benefits of product diversification, improved risk management and improved tree form (Forrester et al., 2004, 2006). Despite increased international interest in mixed species plantations in the last decade (Chen et al., 2003; Nichols et al., 2006), field experiments attempting to identify potential complementary pairs of species for commercial plantations have yielded only a few descriptive insights, drawn from a very limited number of species combinations (Binkley et al., 2003). However, considering the large number of potential tree species to choose from, long rotation times, and diverse environmental conditions, field experiments may not represent the most feasible approach for predicting stand dynamics and yield in potential species combinations. Coates et al. (2003) stated that prediction of stand dynamics and yield in mixed species stands cannot be easily accomplished with traditional field experiments. Design decisions made from the small amount of empirical evidence from few available trial mixture plantations are inherently weak, as stand development and productivity in mixtures is site specific (Coates et al., 2003).

Computer modelling promises to be a useful method for both explaining the stand dynamics in existing plantations and for predicting the dynamics in new plantations. Models of plant interaction are categorized as being either empirical, providing

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only a description of the outcome of competition, or process-based, offering a representation of the physiological processes underlying plant growth (Park et al., 2003). Empirical models are useful for making predictions within the range of data used to parameterise them but are not suitable for extrapolation (Freckleton and Watkinson, 2001). In mechanistic models that are based on the behaviour of individual trees, single trees form the basic units of a forest differing from each other in size and responding to local environmental conditions, such process-based models are based on ‘‘focal tree–neighbour trees’’ interactions (Liu and Ashton, 1995). Process-based models track species-specific demographic behavior and have become a major tool for simulating forest dynamics (Dye et al., 2004). In contrast to empirical models, process-based models have the ability to make predictions outside of the range of data used in their parameterisation, making them the models of choice for designing tree species mixtures.

While pure stands of trees have been modelled extensively and successfully for decades using both empirical and process-based models, relatively few models have been developed for mixed species plantations and forests (Bartelink, 2000; Kimmins et al., 1999; Coates et al., 2003; Canham et al., 2004). The vast variety of possible species mixtures and environmental conditions emphasises the need for developing approaches that include processes and causalities in order to be able to generalise relationships (Bartelink, 2000). Several forest models (FORECAST, SORTIE, COMMIX) have been presented for whole forest ecosystems and forest succession that combine process-based modelling and much additional information on environmental variables, tree autecology, tree physiology, and forest succession (Kimmins et al., 1999; Coates et al., 2003; Bartelink, 2000). Over 100 parameters are required for calibration of FORECAST (Kimmins et al., 1999) including nutrient uptake efficiencies and biomass allocations, and over 26 species-specific variables are required in COMMIX (Bartelink, 2000) including specific leaf areas, leaf angle distribution and coefficients for tree biomass partitioning. Thus, these models have limitations for application in even-aged mixed tropical plantations due to the limited information available on most tropical trees species and the large amount of environmental and tree-specific input data required.

In contrast to mechanistic models based on extensive parameterisation, growth reduction models capture the growth of a broad range of species using a few simplified assumptions regarding plant growth and easily derived species-specific parameter values (Park et al., 2001; Coates et al., 2003). Dimensional growth of forest tree species is determined in growth reduction models by estimating a tree's maximum growth potential, and, through modifier functions, estimating an individual tree's reduced growth potential (Reed et al., 2003). Growth modifier functions are usually developed to represent the proportional impact of one or more limiting, or sub-optimal, environmental factors. Growth reduction models have provided useful approximations for the growth interactions in both monocultures and binary mixtures plantations (Canham et al., 2004; Park et al., 2001) and require parameters that are comparatively easily acquired.

The growth reduction approach forms the basis of the process-based modelling system *SeXI-FS* (spatially explicit individually based-forest simulator, Vincent and Harja, 2004) chosen for our study. Our aim is to determine whether a relatively simple individual-based mechanistic model can describe the interactive processes that determine the relative success of forest trees in a mixed-species experiment. Design of future mixed species plantations are discussed with respect to species-specific growth rates, structural development and photosynthetic responses to light. We anticipated that this modelling approach has applications for understanding relatively unknown tropical forest species with potential for plantations.

2. Materials and methods

2.1. Mixed species plantation

The experiment (Experiment 785 Atherton) was designed and established in 1997 on private land with funding from the Rainforest Cooperative Research Centre, the Queensland Department of Primary Industries and Rural Industries Research and Development Corporation, and is described in detail in Nhan (2001). The site is located near the town of Babinda, on the humid tropical coast of north Queensland, Australia (17°8′S, 145°58′E, altitude 25 m, average annual rainfall 4050 mm, mean minimum and maximum temperatures of 20 and 30 °C). The soil is a red podsolic. The site was previously planted with sugarcane and has a west-south-west aspect. Three Australian forest tree species were planted, *Flindersia brayleyana* F. Muell, *Elaeocarpus grandis* F. Muell and *Eucalyptus pellita* F. Muell. Treatments consisted of monocultures or binary mixtures of the species with three replicates for each treatment. Tree seedlings were planted using a replacement design with the same tree density in the monoculture and the mixture. Mixtures contained alternate rows of each species. Plots contained 8 rows of 14 trees with an initial 2 m of between-row and within-row spacing. The high establishment stocking was chosen to encourage early canopy closure and rapid onset of competition. The experiment was thinned 26 months after planting by removing every tree in every second row at a 45° angle to the planting line, halving overall density (4 m between-row and in-row spacing) but ensuring that similar inter-species competitive relationships were maintained (Nhan, 2001).

Tree height, girth (diameter at breast height, dbh at 1.3 m), crown width and depth were measured at ages 14, 26, 38, and 84 months after planting. Crown diameters and depths were measured 14, 26, and 96 months after planting (Nhan, 2001). To determine crown porosity, digital photos of the crowns of three individuals of each species were taken perpendicular to the ground next to the trunk of the tree 96 months after planting.

2.2. Model

The functions defining a tree species in the model used here are:

- stem diameter at breast height (*dbh*) as a function of tree age (*t*);