Experimental and model evidence for complementary resource use in mixed-species rainforest tree plantations

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There is a growing scientific interest in tree plantations of high-value native rainforest timbers, planted as mixtures, in subtropical and tropical Australia. These plantations can provide ecological benefits, such as improved nutrient cycling and restoration of biodiversity, which cannot be provided by monoculture plantations. In addition, there is evidence that mixed-species plantations are more productive than monocultures if species interact in a complementary fashion. Most designs of rainforest tree mixtures are based on the concept that pairings of fast growing and light demanding species are less productive than pairings of species with different shade tolerances, although there is minimal data to support this assumption. We examined the dominant paradigm that mixtures of two fast growing species (*Grevillea robusta* and *Elaeocarpus angustifolius*) compete for site resources, while mixtures of shade tolerant (*Castanospermum australe*) and shade intolerant (*G. robusta* or *E. angustifolius*) species are complementary. Ecophysiological characteristics of young trees grown in a mixed-species plantation in subtropical Queensland were studied to determine interactions between species for nutrients. Plant characteristics were also entered into a physiologically based canopy model (MAESTRA, an updated version of MAESTRO[1,2]) to test hypotheses of interactions between species for light. MAESTRA uses plant functional attributes (such as leaf biochemistry) and structural variables to simulate radiation absorption and photosynthesis by individual plants in a stand. Essentially, a forest is represented as a three-dimensional array of tree crowns with a defined canopy shape and leaf distribution. Each crown is given an x and y co-ordinate, height, trunk space, canopy radius and one-sided leaf area. Radiation interception, photosynthesis and stomatal conductance are calculated for a target crown which is divided into 72 subvolumes (6 horizontal layers separated into 12 gridpoints). Interception of both beam and diffuse radiation for each subvolume is calculated and used to drive leaf models of photosynthesis[3] and stomatal conductance[4].

Contrary to predictions, there was experimental evidence for complementary interactions between the fast-growing species in terms of nutrient uptake, nutrient use efficiency and nutrient cycling. *E. angustifolius* had maximum demand for soil nutrients (79 g nitrogen (N) and 7 g phosphorus (P) tree^{-1}) during summer, efficient internal recycling of N (56% resorption from senescing leaves), produced a large amount of nutrient rich litter and had low P use efficiency at the leaf (70 μmol CO_2 (g P)$^{-1}$ s^{-1}) and whole plant level (3118 g biomass (g leaf P)$^{-1}$ y^{-1}). In contrast, *G. robusta* had high nutrient use efficiency for both N (7 μmol CO_2 (g N)$^{-1}$ s^{-1} and 198 g biomass (g leaf N)$^{-1}$ y^{-1}) and P (194 μmol CO_2 (g P)$^{-1}$ s^{-1} and 5600 g biomass (g leaf P)$^{-1}$ y^{-1}), maximum demand for soil nutrients (239 g N tree^{-1} and 9 g P tree^{-1}) in spring and produced litter low in nutrients.

MAESTRA simulations were performed for each species planted as a monoculture and results re-interpreted for a mixed species scenario. *E. angustifolius* monoculture simulations reduced rates of canopy photosynthesis by 70% compared to a single tree scenario. *G. robusta* maintained the highest rates of gross and net photosynthesis (5.4 mol CO_2 tree^{-1} d^{-1}) of the three species, while *C. australe* suffered comparatively little reduction in photosynthetic rates (19%), in a monoculture design compared to isolated trees. Initial model simulations tend to support the original hypothesis that mixtures of two light-demanding species (*E. angustifolius* and *G. robusta*) may not be as productive as combinations of shade tolerant (*C. australe*) and shade intolerant species.

However, in its present form, the MAESTRA model results have limited applicability for mixed-species plantations because they only simulate a single species stand scenario. Currently, the MAESTRA model is being modified to allow neighbouring trees to have a different canopy architecture and foliage distribution compared to the target tree. The combination of computer models and empirical data offer a new approach for analyzing stand dynamics in mixed-species plantations as well as establishing testable hypotheses that could be applied to a large-scale experimental system of replicated mixture and monoculture plots.

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