

Simulating the evolution of optimal rooting strategies in shallow soils and extreme climates

Michael Renton and Pieter Poot

*School of Plant Biology and Centre for Climate Change Forest and Woodland Health,
University of Western Australia, Crawley, WA 6009, Australia*

**correspondence: michael.renton@uwa.edu.au*

Highlights: Functional-structural models of root development combined with evolutionary optimisation algorithms can provide insights into why plant species develop different strategies in different environments and conditions.

Keywords: evolutionary algorithm, ecological optimisation, resource acquisition, rooting strategies

INTRODUCTION

Through evolution, plants develop strategies to acquire the limited resources they need to survive, grow and reproduce, such as light, water and nutrients. These strategies would be expected to be adapted to the particular environment a plant experiences, with extreme conditions potentially leading to highly specific strategies. An example of such extreme conditions is that faced by perennial plants that grow in shallow soil in seasonally dry climates such as on rocky hills and ridges in the Mediterranean climate of southwest Australia; these plants usually germinate during the wet winter but then face a long summer drought in shallow soils that have very limited capacity to hold and provide water (e.g. Mishio 1992, Groom and Lamont et al. 1995).

There is evidence that water held within the underlying bedrock can be essential for meeting the transpiration demands of shrubs and trees during the dry season (e.g. Rose et al. 2003, Querejeta et al. 2007). Previous research has shown that species specialized for shallow soils in SW Australia have particular root morphologies that appear to have evolved to improve their chance of finding fissures in the underlying rock that can provide access to such water; the shallow soil endemics tended to differ from related species from deeper soils by investing a larger portion of their biomass in roots, and distributing their roots faster and more evenly through the soil (Poot et al 2012, Poot and Lambers 2003a&b, Poot et al 2008, Poot and Lambers 2008). These results provide a possible explanation for the narrow endemism of many shallow-soil endemics because their root system traits seem to be adaptive in their own shallow-soil habitat in terms of obtaining access to fissures and water in the underlying rock, but are likely to be maladaptive in deeper soils. Indeed, it has been argued that the restricted range of shallow-soil endemics may be due to the high degree of root structure specialization required to survive in these extreme conditions, together with the fact that these adaptations are relatively costly and are likely to provide relatively fewer benefits in deeper soil environments (Poot et al 2012).

Dynamic functional-structural models of plant growth (FSPMs) can potentially be used to predict the costs and benefits of different growth strategies in terms of resources gained and used, and how these costs and benefits vary according to differences in the temporal and spatial patterns in the availability of the resources. This can in turn provide insight into why different species develop and use different growth strategies in different environments and conditions. A computational model was developed to represent root development within a single growing season within a Mediterranean climate where rainfall is relatively plentiful for a period of the year and negligible for the remainder of the year (Renton et al 2012). The model is able to represent a wide range of relevant rooting strategies in a relatively simple and thus computationally efficient way. This allows computational evolutionary optimization algorithms (Fogel 1994) to be applied to the model, which in turn allows us to explore how ecological strategies evolve to best exploit available resources, and how this evolution of ecological strategies may vary with different patterns of resource availability.

TARSIERS

Our Tool for Analysis of Root Structures Incorporating Evolution of Rooting Strategies (TARSIERS) illustrates the potential of the approach of linking an FSPM with a computational evolutionary optimization algorithm. This tool is based on a computational FSPM that aims to capture the important processes involved

in root growth and development and water acquisition in a range of situations where water is the key limiting resource. The model was motivated by the southwest Australian shallow-soil case studies referred to above, but was constructed with the intention to be flexible enough to address questions about optimal rooting strategies in other conditions and species as well. The overall dynamics of the model are summarized and some different aspects of the model illustrated in Fig. 1, and details are available in Renton et al (2012). In brief, the model is based on a set of parameters that define various characteristics of the rainfall, soil, water uptake and biomass (known as Fixed Parameters, since they are assumed to be fixed for a particular environment), and another set of parameters that controls how the root structure develops over time (known as the Strategy Parameters, since they define the plant's growth strategy). The model employs a daily time step to simulate how the roots of a single plant grows through the soil after germinating at the start of the wet rainy season, and continues the simulation through this wet period until the start of a dry period. To keep the FSPM relatively computationally simple, we only represented the primary and secondary roots (we assume that these are the most important in defining the overall architecture of the root system and its access to water, both during the initial wet period and the subsequent drought period).

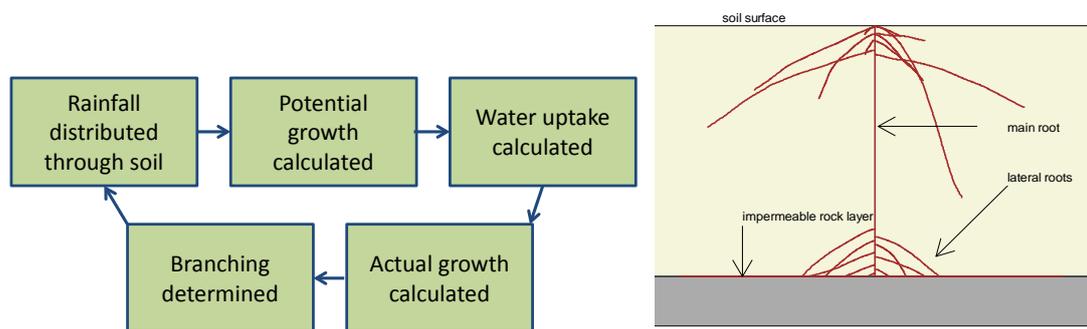


Fig. 1. Summary of dynamics of the FSPM at each time step (left) and illustration of FSPM components (right)

The full TARSIIERS links the FSPM with an evolutionary optimisation algorithm that simulates the evolution of a plant population over time. An individual genotype is defined by a set of values for the Strategy Parameters, and a population is a number of such sets. The Fixed Parameters are defined to represent the conditions of interest (soil of a certain depth and water holding capacity, rainfall frequency and amount, frequency of fissures within the underlying rock etc) and a relative fitness is defined; for example, this could be zero if the plant has failed to access a wet fissure in the underlying rock to sustain it through the summer, and the biomass of the plant achieved by the start of the drought period if it has succeeded in finding a fissure. An initial population is then constructed and the evolution of that population is then simulated across a number of generations. For each generation, the FSPM is run separately for each individual in the current population and the resulting relative fitness of the individual is recorded. A new population is then constructed for the next generation. For each individual in the new population, a mother and father are randomly selected from the previous population based on a multinomial random distribution, where the weightings for each individual are its recorded relative fitness. The values for the Strategy Parameters defining the genotype of the new individual are the means of the corresponding values for the parents, plus a specified amount of random variation. When the new population has been defined, it is set to be the current population and the process continues until a fixed number of generations have been simulated.

RESULTS AND DISCUSSION

TARSIIERS is able to successfully simulate the evolution of rooting strategies in particular conditions. The mean values of the Strategy Parameters change over the generations as more successful or 'fit' individuals in each generation have a higher probability of contributing to the next generation. The addition of random variation introduces novelty that allows new growth strategies to be explored (Fig 2). Moreover, different trajectories of evolution can be observed in different conditions, and the match between these trajectories and the conditions they are adapted for make ecological sense (Fig 2).

The FSPM in TARSIIERS is relatively simple compared to more detailed existing root FSPMs (eg. Lynch et al 1997, Bidel et al 2000, Dunbabin et al 2002), which makes it computationally feasible to link it with an evolutionary optimisation algorithm. Nonetheless, it includes enough detail and parameters to enable a wide range of developmental strategies to be explored. We plan to use TARSIIERS to investigate how the rooting strategy evolves in different ways as a number of environmental assumptions are varied, including soil

depth, soil type, frequency of fissures in the underlying rock, wet season duration, frequency and amount of rainfall during the wet season, and spatial heterogeneity in soil characteristics. We also plan to extend the tool to account for competition between plants, soil nutrients, and phenotypic plasticity.

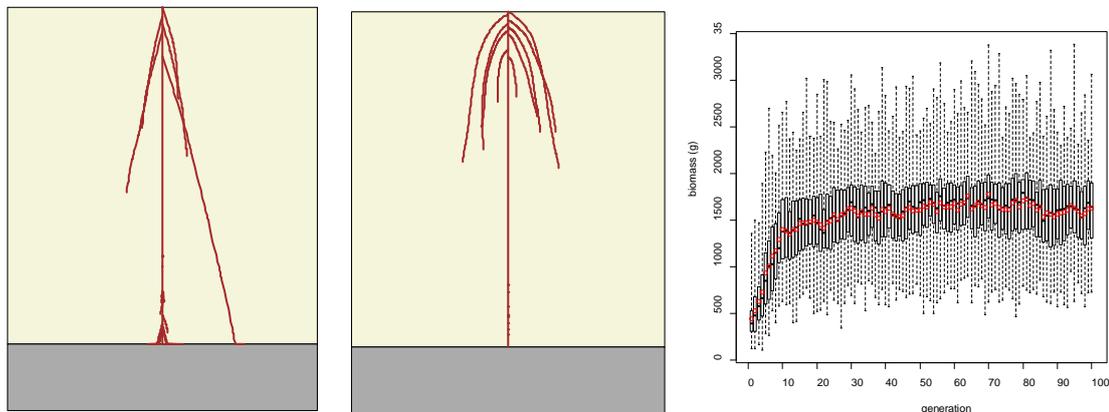


Fig. 2. Example outputs from using TARSIER to simulate the evolution of a plant species that initially has some adaptations to find fissures in underlying rock when ‘fitness’ is defined simply as biomass achieved at the start of the drought season (ie there is no advantage to finding fissures, only in making maximum use of water available over the wet period). Outputs include a typical example phenotype from an initial population (left), a typical example phenotype from the final population (centre) and boxplot showing values of the biomass achieved by individuals within the population changing over generations as evolution occurs (box: interquartile range, whiskers: range, red circle: mean). Note that the species has evolved to have a more superficial root system which leads to it achieving a higher biomass.

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