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A holistic tree seedling model for the investigation of functional trait diversity

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Abstract

Improved insights into the basis for the large variation in plant traits observed in nature are expected from the development of more holistic optimization models. Holistic approaches emphasize the effects of interactions and tradeoffs among multiple traits on whole plant fitness rather than studying individual traits in isolation. Using this holistic approach, we developed a general model of tree seedling form and function. Here we present this new model and examine its realism and utility. The modeled growth of tree seedlings reproduced natural patterns accurately, including subtle ontogenetic shifts and environmental responses. The underlying processes of resource acquisition also behaved realistically, including the key process of stomatal control. Due to its holistic approach and the generality of the tradeoffs on which it is based, the model is well suited to investigating both general laws governing alternative designs for tree seedlings and the nature of trait adaptation in response to competition and environmental differences.

Keywords: Plant functional traits; Growth analysis; Optimal stomatal control; Optimization model; Trait evolution; Tree mechanics; Tree seedlings

1. Introduction

One of the most striking observations about plant communities everywhere is the high level of quantitative variation in functional traits among plant species both within sites (Westoby et al., 2002) and among sites (Niinemets, 2001; Wright et al., 2004; Maherali et al., 2004). This trait diversity is not only fascinating to naturalists, but also of ecological importance since it affects species distributions (Guthrie, 1989; Roderick et al., 2000; Prior et al., 2003) as well as ecosystem processes (Shugart, 1997; Díaz et al., 2004; Suding et al., 2005). Although progress has been made in understanding some dimensions of plant trait variation (Westoby et al., 2002; Reich et al., 2003), much still remains to be elucidated. Through an original application of an optimization modeling approach our study aims to improve this understanding.

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We chose an approach based on optimization since optimization models have important advantages over more empirical and statistical models in investigating patterns of trait variation (Maynard Smith, 1982; Mooney and Chiariello, 1984; Givnish, 1986a; Parker and Maynard Smith, 1990; Farnsworth and Niklas, 1995; Mäkelä et al., 2002; Sutherland, 2005). Most significantly, optimization models are derived from first principles (Parker and Maynard Smith, 1990; Sutherland, 2005), which allows the mechanisms underlying plant function to be investigated directly. Furthermore, since first principles apply generally, optimization models can be used to make predictions about responses under new conditions (Sutherland, 2005).

These advantages have allowed optimization models for particular elements of plant function to provide insights into diverse aspects of plant function: nitrogen allocation (Hilbert et al., 1991; Van der Werf et al., 1993; Hikosaka and Hirose, 1998; Buckley et al., 2002), root-to-shoot ratio (Orians and Solbrig, 1977; Schulze et al., 1983; Hilbert, 1990; Chen and Reynolds, 1997; Stuefer et al., 1998; Magnani et al., 2002), shoot architecture (King, 1981, 1990; Niklas, 1994c), specific and canopy leaf area (Schieving and Poorter, 1999; Farquhar et al., 2002), stomatal control (Cowan and Farquhar, 1977; Hari et al., 1986; Givnish, 1986b; Mäkelä et al., 1996), and water-use (Schwinning and Ehleringer, 2001; Zavala, 2004). To advance this line of inquiry, we have developed a more holistic optimization model, the Tree seedling Adaptive Designs (TAD) model that considers a broad array of elements in plant function influencing tree seedling growth and survival. Here we present the TAD model as well as demonstrating its realism with a particular focus on seedling growth analysis.

TAD advances plant optimization models in four important ways. First, while fitness is known to be affected by multiple traits and may be limited by multiple resources (Mooney and Chiariello, 1984; Körner, 1991; Gutschick, 1999), TAD is to our knowledge the first optimization model to incorporate key traits associated with the economy of all four primary resources for plant growth: water, nitrogen, light and carbon.

Second, many plant organs perform multiple tasks and consequently their traits must reflect a compromise optimizing performance across a set of individual tasks (Mooney and Chiariello, 1984; Körner, 1991; Farnsworth and Niklas, 1995; Gutschick, 1999). Few optimization models have addressed the challenge of multiple plant functions, and those that have typically used a multi-objective optimization approach which is difficult to justify biologically (Niklas, 1994c). A more elegant solution is to integrate multiple functions into a single fitness measure as in TAD where growth rate is maximized, but with prevention of carbon starvation, dehydration, and mechanical failure acting as constraints. The combination of survival and maximization of growth is a well accepted fitness measure for tree seedlings, since maximal seedling growth increases the chance to survive into adulthood and increases lifetime reproductive potential (Van Valen, 1975; Harcombe, 1987; Oliver and Larson, 1996; Landis and Peart, 2005). Thus the fitness measure in TAD is biologically realistic and can be easily interpreted.

Third, the variation in individual traits cannot be fully understood without taking into account the direct and indirect effects of other traits (Mooney and Chiariello, 1984; Körner, 1991; Gutschick, 1999). In other words, the conclusions from studying traits at the organ level in isolation do not necessarily scale up to the whole plant. For example, the values for leaf traits that maximize nitrogen-use-efficiency at the leaf level are not the same as the values for leaf traits that maximize nitrogen-use-efficiency at the whole plant level (Aerts and Chapin, 2000). This interdependence requires taking a whole plant approach. Furthermore, ecophysiology can be directly linked to population and community ecology only at the whole-plant level of trait organization (Mooney and Chiariello, 1984). Some other optimization models recently have moved toward this holistic approach (Schwinning and Ehleringer, 2001; Zavala, 2004), but not as comprehensively as TAD.

Fourth, plant traits modify the environment and thereby also the selection on traits (Van Valen, 1977; Laland et al., 2004). In TAD these feedbacks on the environment are modeled in a spatially explicit manner. Consequently TAD is capable of accounting for the effects of neighbor–neighbor competition. Some previous optimization models (Cohen, 1970; Iwasa et al., 1984; King, 1990, 1993; Schieving and Poorter, 1999; Schwinning and Ehleringer, 2001) have also included these feedback effects, but none has considered competition for light, nitrogen, and water all at the same time. Because of this and also the preceding points, TAD represents a significant advance in optimization modeling