



## Plant diversity and drought: The role of deep roots



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### ABSTRACT

Extreme temperatures and droughts in the wake of climate change potentially threaten plant diversity. A strategy that plants use to improve survival during seasonal drought is to establish deep roots, aptly named tap roots for their ability to tap into groundwater. Little is known, however, about the role of deep roots in maintaining plant diversity. Here, we extend an established model of plants canopies by Iwasa et al. (1985), in which plants of different heights compete for light, to allow strategic investments in an optional tap root. We investigate how emerging diversity varies with water table depth, soil water gradient and drought-induced mortality rate. Having a tap root enables plants to reach deep water, thus reducing mortality, but also carries a construction cost, thus inducing a tradeoff. We find (1) that tap roots maintain plant diversity under increasing drought mortality, (2) that tap roots evolve when ground water is accessible at low to intermediate depths, (3) no viable strategies at high drought mortality and deep water table, and (4) Red Queen evolutionary dynamics in mixed communities with and without tap root.

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### 1. Introduction

As a consequence of global climate change, we may experience decreasing precipitation and increasing evaporation, causing severe and widespread droughts in some regions over the next 30–90 years (Dai, 2013). Due to the fundamental importance of water availability for plants, plant diversity may be at risk in drought-affected areas. Even in the moderate climate-change scenarios, many plant species might be lost. In Europe, the risks are highest in the transition areas, for example between the Mediterranean and Euro-Siberian regions, due to an increase of severe droughts and evaporation (Thuiller et al., 2005). The drought-induced shifts are expected to be largest in ecotones (transition areas between two biomes), and very fast transitions have been reported from for example New Mexico in the 1950s where the ecotone between semiarid ponderosa pine forest and piñon juniper woodland shifted 2 km or more in less than 5 years (Allen and Breshears, 1998). Alarmingly, the drought and climate related mortality of trees has already increased according to a meta-analysis by Allen et al. (2010). To predict and be able to respond to climate

change impacts on plants it is essential to understand the effects of water availability on plant productivity and diversity.

There are a multitude of plant responses to water stress. Fast responses (acclimation) are quite well understood, e.g., closing of stomata, rolling the leaf, and increasing leaf angles (Lambers et al., 1998; McDowell et al., 2008). Slow responses are less well studied. These might include: earlier reproduction (before drought), rigid cell walls or smaller cells to tolerate low water potential (Chaves et al., 2003), and differences in rooting depth (Jackson et al., 1996).

Desert plants exhibit a range of rooting strategies, including shallow-rooted ephemerals, shallow-rooted perennials, and deep-rooted perennials. Such morphological differences suggest alternative strategies for survival under dry conditions (Rundel and Nobel, 1991). However, the mechanistic link between root growth and survival under drought remains unclear. Padilla and Pugnaire (2007) found a negative relationship between root to shoot biomass ratio and survival under drought, while at the same time observing a strong positive relationship between rooting depth and survival in line with other studies (e.g., Fensham and Fairfax, 2007). Thus, it appears that rooting depth, e.g., presence of tap roots, is important for survival under drought whereas the total effect of root growth may be influenced by other factors. More generally it is becoming clear that plant allocation responses to different interacting environmental factors only can be understood from a whole

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plant perspective (Franklin et al., 2012). One must therefore consider the effect of competition for light alongside rooting strategy and how these interact. Furthermore, to model the effect of drought on diversity it is necessary to evaluate not only one plant's drought strategy, but also the potential for coexistence among different drought strategies.

Contrary to common beliefs, deep roots are not only found in arid climate, but also in tropical forests with a dry season. The presence of deep roots can explain why Amazonian evergreen forests extend far into regions with a long dry period. Nepstad et al. (1994) estimate that around half of the closed forests in Brazilian Amazonia rely on deep roots to maintain evergreen canopies throughout the dry season. Roots may be found as deep as 18 m below ground, making it difficult to obtain good data on deep roots.

Recently the importance of drought has been acknowledged in a variety of novel approaches to root modeling, including a stochastic rainfall model by Zavala and Bravo de la Parra (2005) and a model of carbon allocation of trees in competition for water and light by Farrior et al. (2013). However no study has yet investigated the importance of deep roots for upholding diversity in forests where droughts are important. This might include a wide variety of forests, as most forests are likely to operate close to the limits of hydraulic failure (Choat et al., 2012).

To better understand the relationship between plant diversity and drought, we introduce a new eco-evolutionary model of plant root and shoot strategy under different degrees of water limitation. The model is based on an established plant canopy model, which outlines how plants of different height may coexist when competing for light (Iwasa et al., 1985). This model is the only existing evolutionary plant model having a polymorphic equilibrium, i.e., more than one coexisting species, according to a review by Falster and Westoby (2003). We extend the Iwasa model by adding a tap root, defined by its depth, and model the evolution of plant shoot height and tap root depth under different water table depth conditions. The results illustrate how above- and below-ground factors interact to regulate diversity.

## 2. Model

A schematic overview of the model is given in Fig. 1. Our treatment of above-ground processes is identical to Iwasa et al. (1985). We extend the study by Iwasa et al. (1985) by incorporating the possibility for plants to grow a tap root (a deep root). Thus, each plant strategy is characterized by two trait values, the height of the shoot,  $x$ , and the depth of the tap root,  $y$ . Since there is no ontogenetic growth of the plants in the model we implicitly assume that only the final height and root depth at maturation are important for calculating the invasion fitness, which we use to find evolutionary outcomes. A tall shoot confers a better ability to compete for available light, while a deep tap root reduces drought-induced mortality. There is a construction cost to having a long shoot or tap root, thus inducing two life-history trade-offs, the total size and the relative size between shoot and root. Such a model is applicable whenever (1) light competition is important and (2) there are occasional periods of drought whose detrimental effects can be mitigated by the presence of a tap root.

The demographic dynamics of a plant strategy with shoot height  $x$  and tap root depth  $y$  are described by the following equations,

$$\frac{dN(x, y)}{dt} = N(x, y)F(x, y, N_C), \quad (1)$$

$$F(x, y, N_C) = f(L(x, N_C)) - c(x, y) - m(y), \quad (2)$$

where  $N(x, y)$  is the density of plants with trait value  $x$  and  $y$  (i.e., the number of plants per area unit) and  $F(x, y, N_C)$  is a function giving the per-capita growth rate of that strategy in its current environment.

The latter term is determined by the photosynthetic assimilation rate  $f(L(x, N_C))$ , the construction cost of supporting tissue like stem root and branches reducing the growth rate  $c(x, y)$ , and a drought-induced mortality rate  $m(y)$ . The term  $N_C$  represents the entire community of strategies that coexist with the focal plant strategy, i.e., the function  $N(x, y)$ . We use the demographic equilibrium condition  $dN/dt = 0$  to find  $N_C$  (see Appendix B).

The photosynthetic assimilation rate

$$f(L(x, N_C)) = a \log(L(x, N_C)) + b \quad (3)$$

is determined by the light intensity  $L(x, N_C)$  at height  $x$ , which is calculated by integrating the shading effects of all coexisting plants with density  $N_C$  and cumulative leaf area  $\rho(z, x)$

$$L(x, N) = L_0 \exp \left( - \int_0^\infty \int_0^\infty N_C(z, y) \rho(z, x) dz dy \right). \quad (4)$$

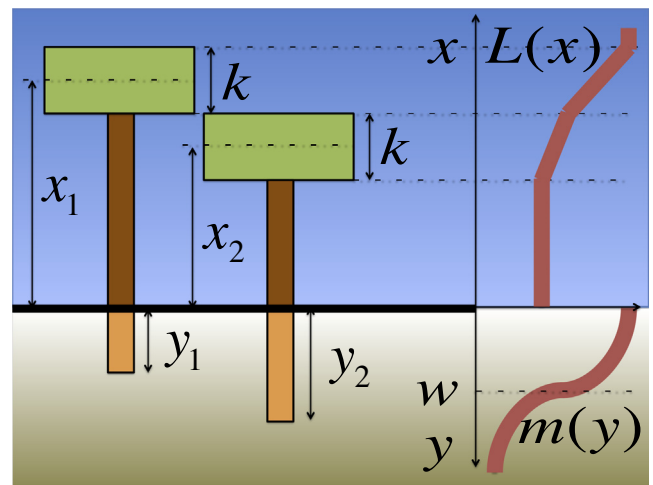
The light intensity is reduced from a maximum of  $L_0$  by shading from other plants coexisting in the community. The cumulative leaf area  $\rho(z, x)$  above height  $x$  on a tree of height  $z$  is defined as

$$\rho(z, x) = \begin{cases} 0 & x \geq z + \frac{k}{2}, \\ \rho_w \left( z - x + \frac{k}{2} \right) / k & z - \frac{k}{2} < x < z + k/2, \\ \rho_w & x \leq z + \frac{k}{2}, \end{cases} \quad (5)$$

based on an assumption of uniformly distributed foliage from height  $z - k/2$  to height  $z + k/2$  for a crown thickness of  $k$ .

The metabolic cost of constructing and maintaining a shoot of height  $x$  and a tap root of depth  $y$  is assumed to increase non-linearly with both shoot and root length:

$$c(x, y) = c_0 + c_2(c_1 x + y)^q. \quad (6)$$



**Fig. 1.** Schematic overview of the model. Plant strategies are characterized by two evolving trait values, the height of the shoot,  $x$ , and the depth of the tap root,  $y$ . Taller plants shade shorter plants, but not vice versa. The light assimilation  $L(x)$  depends on the shoot heights, the crown thickness, and the population equilibrium densities  $N_C$  (this dependence is suppressed in the figure). A tap root reduces the mortality risk of a plant to an extent that depends on the tap root's length and the soil water's vertical distribution. The drought-induced mortality  $m(y)$  is a function of depth reached by the tap root. This function is shown as a solid red line in the lower right. We consider the water table to be located at the depth  $w$  at which this function reaches half of its maximum value, as illustrated by the dotted horizontal line. The crown thickness,  $k$ , influences competition between trees and is assumed to be constant. Subscripts denote different strategies.

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