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Plant diversity and drought

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Highlights: We find a phase transition from no species to a highly diverse community, as the drought mortality and water table sharpness increases, but this is not true for water table depth. The species richness is decreasing with drought mortality and water table depth, but not with water table sharpness. Thin crown and intermediate values of photosyntetic efficiency (i. e. productivity) has the highest diversity.

Keywords: root, shoot, evolution, adaptive dynamics, drought

INTRODUCTION

Extreme temperatures and droughts will cause a loss of plant species according to recent studies (Thuiller et al. 2005). Water limitation is a severe obstacle for plant growth and survival. Droughts can cause irreparable damages as air enters the water transportation system, in a process known as cavitation. One way to avoid such damages is that the plant invests in a deep root, a so called taproot.

The conditions for coexistence for plants in a dry environment has not received much attention. Here we extend a static shoot model by Iwasa et al. (1984) with a taproot, able to reach for deep water, and we investigate the model with the techniques of adaptive dynamics. The deep soil water abundance, or potential, is increasing with depth corresponding to a situation often encountered in regions with drought. A taproot reduces mortality, but it is also costly, so investing in a taproot is a strategy with a trade-off.

We find that the shoot and root can coevolve to a common evolutionarily stable strategy (ESS). For the shoot, evolutionary divergence is possible only for large mutational steps. For the root we find one stable strategy, one unstable strategy, and one stable strategy with no root. Surprisingly the stable strategy with a root can result in a larger shoot than the strategy without a root. Deeper soil water levels tend to decrease diversity but more unexpectedly we find a phase transition from zero diversity to high diversity as the drought mortality increases.

SIMULATIONS

We extend the Iwasa el al. (1985) model with a root, which has a quadratic cost like in the original model. There is no competition (or in other words density dependence) for the root. The depth of the root is reducing the non-density dependent mortality from droughts. The reduction is modelled with a logistic function, with initially very low reduction in mortality, an intermediate reduction in mortality when the roots reach the ground water table, and a high reduction at greater depths. Our model has two traits: height of the shoot and depth of the roots. We are interested in the conditions for coexistence and evolutionary divergence.

RESULTS AND DISCUSSION

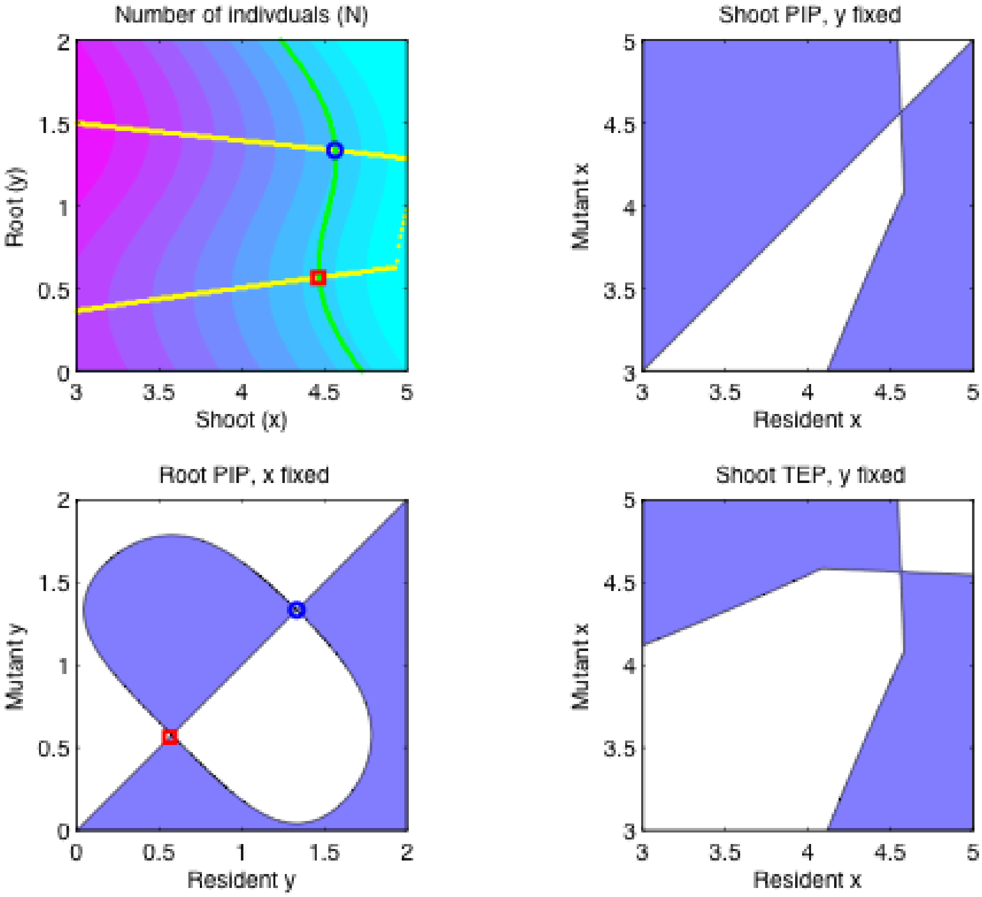

Fig. 1. Isoclines of shoot (green) and root (yellow) plotted on top of the number of individuals (top left). The stable (blue circle) and unstable (red square) intersection of the isoclines is marked in the root PIP (bottom left). The shoot PIP (top right) is always convergence stable, but not evolutionarily stable for large steps. The coexistence area is marked blue in the shoot TEP (bottom right).

We use graphical methods to investigate the evolutionary dynamics of our model. A standard tool used in adaptive dynamics is the pairwise invisibility plot (PIP). In this plot the invasion fitness F of a mutant strategy in the presence of a resident strategy is marked either as positive or negative. In the PIP's in Fig. 1 we have marked the positive invasion fitness as blue, and the negative invasion fitness as white. Along the diagonal, when the resident strategy is equal to the mutant strategy we have a zero invasion fitness. A singular evolutionary strategy is easily found in the PIP (Geritz 1998). The singular strategy could be either convergence stable or unstable. If we have a convergence stable strategy (CSS), evolution will move towards this strategy, and if it is convergence unstable evolution will be repelled by this strategy. Once evolution reaches the CSS it can stop there, in this case we have an evolutionarily stable strategy (ESS), or diverge into two new stable strategies. In the root PIP in Fig. 1 the stable point (ESS+CSS) is marked with a green circle and the unstable point with a red square. There is also a stable strategy with no root but this is not marked in the figure, since it is just the point at origo. For the shoot we only find one convergence stable strategy (CSS). This strategy is an ESS for small mutational steps but not for large mutational steps, as can be seen in the blue coexistence area in the shoot trait evolutionary plot (TEP) in Fig. 1 (bottom right). In the TEP the PIP is flipped along the main diagonal and superimposed on the original PIP and the points where both the original and the flipped PIP's are positive are marked as positive (blue) or negative (white). By tracing the singular strategies of one trait as the other trait is varied we can draw isoclines for the traits. When the isoclines cross we have a common singular point for both traits that can be stable or unstable. In Fig. 1 there are two common singular points at the crossing of the shoot isocline (green) and the root isocline (yellow).

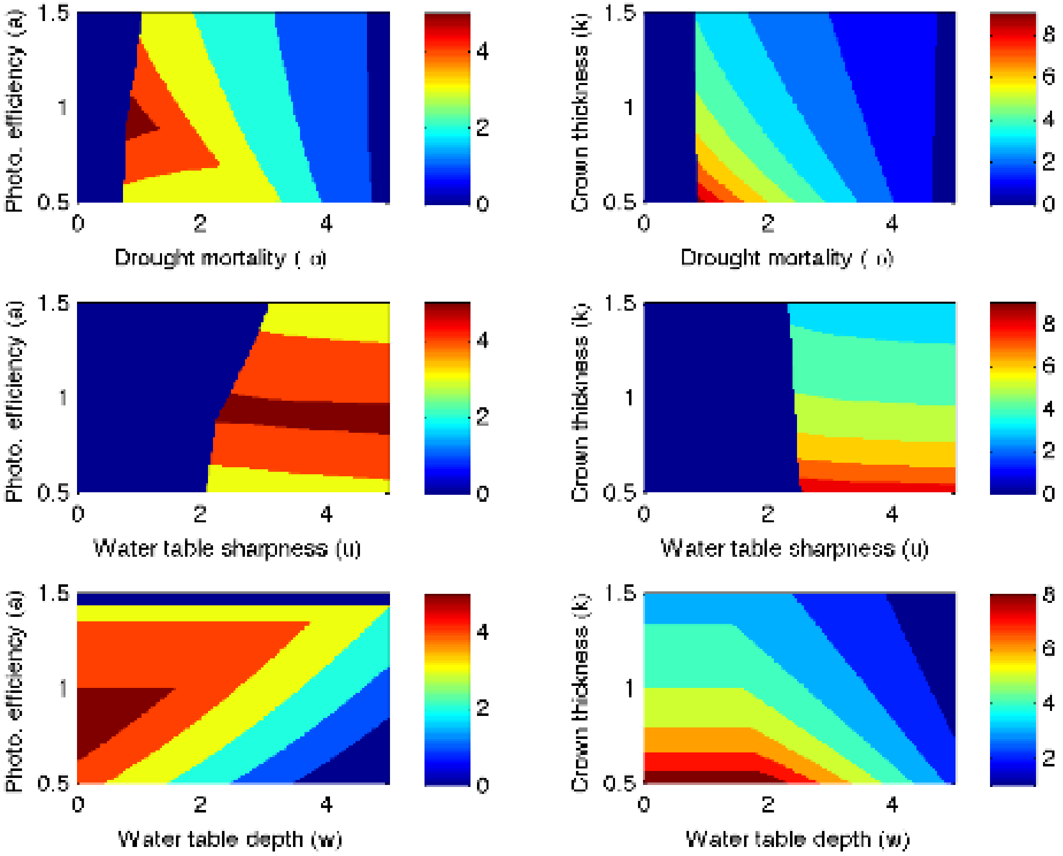

Fig. 2. Number of coexisting species with a taproot, depending on root and shoot parameters.

We investigate the number of coexisting plants dependence on the shoot and root parameters. We find the highest diversity for intermediate levels of photosynthetic efficiency, and low thin crowns (Fig. 2). The diversity is zero for low values of the drought mortality. In this case there is no point in investing in a root, the root and shoot isoclines never cross (Fig. 1), so there is no common singular point. For increasing drought mortality the there is a fast transition to high diversity, and then it decreases slowly. The ground water sharpness has a similar behaviour as the drought mortality but here the high diversity for intermediate values is not disappearing at higher values, and diversity is only affected slightly as drought mortality is increasing. The ground water table depth is lowering the diversity linearly with increasing depth. There is no phase transition as in the case for drought mortality and water table sharpness. For the shoot traits we find the highest diversity for intermediate photosynthetic efficiency, and thin crowns. This pattern disappears for large drought mortality, but not for large water table sharpness.

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