**The Tragedy of the Commons in Plant Root Competition**

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1) Motivation As ecologists and economists have recognized since the 1960's, a Tragedy of the Commons (ToC) may arise in a broad array of competitive interactions when gains accrue to individuals but costs are shared with competitors. Existing empirical research demonstrates that, under certain conditions, plants competing for soil resources mediated by root uptake may over-invest in root production at the direct expense of their ability to generate reproductive mass. This can produce a ToC because nutrient uptake benefits individual plants but depletes the shared nutrient pool. But if the plants sharing the nutrient pool behaved cooperatively--in the same way that roots of an individual plant behave toward each other--they could each generate more reproductive mass than under the competitive ToC scenario. This inefficiency offers a means of directly quantifying the scope of the ToC in a given system by finding the ratio of reproductive yield of plants with root systems separated by a barrier to those with directly competing root systems. While existing research confirms that root competition can give rise to a ToC in some systems, others do not appear to exhibit ToC effects. Exactly what conditions and factors give rise to a ToC in plant root competition remains unknown.

2) Research Questions What factors determine whether plants under root competition produce a Tragedy of the Commons? What systems have evolved in nature to help manage these ToC effects? Do these questions have direct agricultural implications? Which empirical studies will most productively address these questions?

3) Methodology Formally, this situation comes under the heading of competitive game theory, or contest games. We use a spatially explicit simulation model to solve the game and generate predictions about the conditions that produce a ToC, and the extent of ToC effects. We assume that a single soil nutrient (typically nitrogen) limits plant growth. The model features a heterogeneous resource landscape, so as the simulated plants draw down nutrient levels, the nutrient diffuses across the landscape down the concentration gradient. Nutrient that remains unallocated to root growth serves as a proxy for reproductive mass.

4) Results Simulated plants in the model produce ToC effects when competing directly. Separating the simulated plants into separate plots eliminates these effects. Separating the plants with a semi-permeable membrane that allows plausible rates of nutrient diffusion across the membrane but prevents roots from directly overlapping makes any ToC effects insignificant. Clonal plants that can pass nutrient between themselves experience no ToC effects, and generate similar root landscapes to those of plants separated by either type of barrier.

5) Discussion A Tragedy of the Commons can emerge in any situation in which the costs and the benefits of a decision get distributed unevenly between decision making agents. In this example, each additional unit of root mass added to the system benefits the plant that produced it, while it reduces the efficiency of the roots of all competing plants. When a plant exploits a nutrient pool in the absence of competition, it balances the costs of roots with the benefits of nutrient uptake, ultimately maximizing its own reproductive capacity. In competitive systems, however, each plant adds root mass past the point of maximum efficiency, because some of the efficiency costs get borne by the other plant. The simulation model presented here suggests numerous potentially productive lines for future empirical research. The lead author's immediate research plans center on testing the model's prediction that plants separated by a semipermeable membrane will behave like plants separated by a completely impermeable barrier. Subsequent research will include studies comparing root behavior of connected ramets to that of separate ramets. Developing a better understanding of the Tragedy of the Commons has value both for biologists addressing natural systems and for social scientists considering interactions between humans and between human institutions.