Commentary

Competitive optimization models, attempting to understand the diversity of life*

The complex interplay between the abiotic and biotic components of plant communities is precisely what makes them so fascinating to study. This complexity, however, is also what makes building predictive models of plant responses to climate change particularly difficult. Prediction into the novel environmental conditions that climate change brings requires mechanistic understanding of the scaling of abiotic and biotic feedbacks from individual plants to the landscape level. In this issue of *New Phytologist*, van Loon *et al.* (pp. 1253–1265) have taken on this challenge for soybean plants in competition for light. They have built a model that includes the physiology needed for quantitative predictions, while also including the influence of competitive plant interactions on determining dominant individual strategies. This model accurately predicts the response of soybean plants to experimental manipulations of atmospheric CO_2 and, through comparison of model scenarios, shows quite clearly the importance of individual-based competitive interactions in predictive models of plant responses to climate change.

The importance of the details in competitive games

Van Loon *et al.* find that soybean plant responses to CO_2 fertilization are consistent with predictions from a model in which selection at the individual-level leads to a community with suboptimal collective and individual resource-use efficiency. This counterproductive dynamic often occurs when individuals of a community share a limiting resource, appropriately called the 'Tragedy of the commons' (Hardin, 1968). Two examples of this phenomenon, meant to illustrate its fundamental components, are illustrated in Fig. 1. Individuals in the community share a limiting resource (light) such that if an individual invests more in resource uptake than its neighbors (here height for ease of illustration), it will get a greater share of the resource. The optimal community for resource-use efficiency is not a stable community, evolutionarily (Maynard Smith & Price, 1973), and is not the one we should expect to see in nature. It can be invaded by individuals with greater investment in resource uptake. In competition with individuals of the optimal resource-use efficiency community, individuals with

greater investment in resource uptake utilize a greater share of the resource, have higher reproductive output, and will take over the community. However, this individual-level benefit vanishes as the community becomes dominated by individuals of the greater uptake strategy. Because total resource availability has not changed, the individuals of the new strategy no longer have higher resource uptake but still carry the costs of their more competitive strategy, lowering community and individual-level resource-use efficiency (see a–c in Fig. 1). In the simplest models, invasions by individuals with greater investment in resource uptake continue until the resource-use efficiency approaches one (Fig. 1e), or the costs of taking up a resource are equal to their gains. This is a 'complete' tragedy of the commons. In this case, individuals in the evolutionarily stable community are just as well off as if they had not taken up any resource at all. For essential resources like light, water, and nutrients, this model is clearly too simple; resource-use efficiency for essential resources must be greater than one in order for individuals to grow and reproduce.

One common reality that keeps plant communities from reaching a complete tragedy of the commons is partial territoriality, or spatial segregation, of resource uptake (depicted in the lower panels (f–j) of Fig. 1). If individuals have ownership over a resource, any investment above the level needed to take up the resource is a waste. Partial territoriality limits the rewards of having greater investment in uptake than neighbors to only the shared portion of the resource (see partial self-shading of individuals in Fig. 1g,i). This restraint on the tragedy of the commons is found to be important in the van Loon *et al.* model where soybean plants are competing for light (as in the example in Fig. 1, but instead of differing in height, individuals differ in investment in leaf area). The authors found model predictions to be particularly sensitive to the parameter defining degree of aboveground overlap, or the degree of resource sharing, among individuals.

'The complex interplay between the abiotic and biotic components of plant communities is precisely what makes them so fascinating to study. This complexity, however, is also what makes building predictive models of plant responses to climate change particularly difficult.'

However, spatial segregation likely plays a small role in limiting tragedies of the commons in belowground competition where individuals' roots often overlap significantly with several other
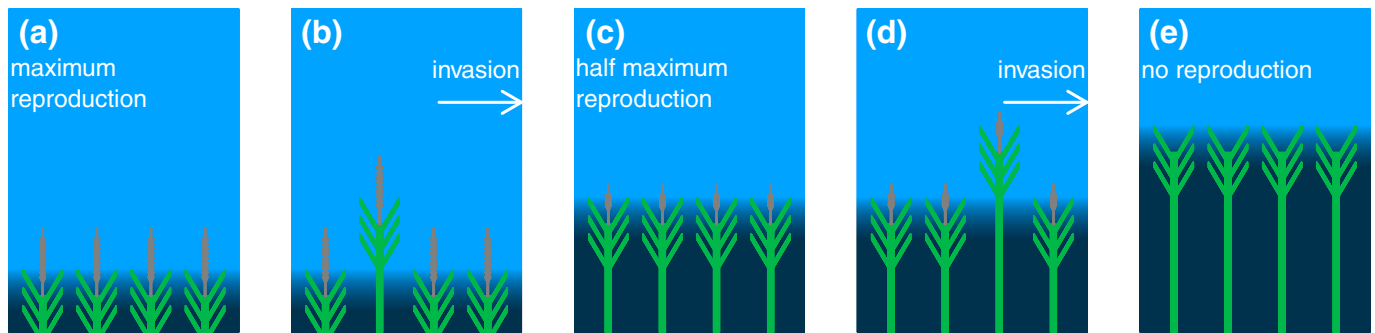
*In reference to Maynard Smith's (1978) paper on optimization models where in conclusion he writes, 'The role of optimization theories in biology is not to demonstrate that organisms optimize. Rather, they are an attempt to understand the diversity of life.'
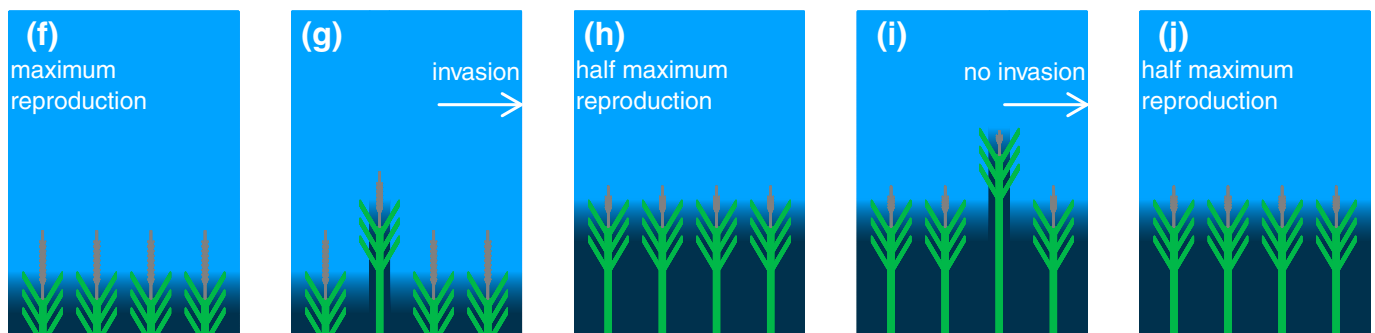
(a–e) Complete sharing of light in the horizontal plane

(f–j) Partial territoriality of light

Fig. 1 If resources are shared, optimization of individual-level fitness often leads to suboptimal community resource-use efficiency, a tragedy of the commons (Hardin, 1968). Here are two examples of hypothetical processes of evolution (or community assembly) for plants that share light completely (a–e) and for plants that only share half of their light (f–j) in the horizontal plane. Individual plants are depicted as a green stem and leaves. Light level is indicated by the brightness of the blue background. Individuals differ in investment in height. To indicate fitness, reproductive output is depicted as seed head length and is proportional to light uptake minus height. Note these examples assume that each community (panel) is large enough that any one individual does not have a measurable effect on the resource level of other individuals. The end point of evolution (or community assembly) for each scenario is pictured in (e) and (j). For the complete-sharing individuals, a dead-end community with no reproduction (e) is arrived at via successive invasions of individuals with greater investment in height (b and d). Increases in height pay off to individuals in competition with shorter individuals, but lead to diminished fitness as the taller individuals come to dominate the community. In competition with one another, these individuals take up the same amount of light as their shorter counterparts, but have greater height costs (compare a, c, and e). If resource uptake is partially territorial however, the end point of evolution is a viable community (j). Here, individuals that are taller than their neighbors (in g and i) receive only half the benefits as they had when resources are shared completely (in b and d) because of the presence of their own self shading. This leads to a community in (h) that cannot be invaded by individuals of greater height (j = h; the taller invader in (i) is unsuccessful). Here self-shading caused by partial territoriality restrains the community from the dead-end scenario in the upper panels. Yet, because resource sharing is still present, the stable community still only has a fraction of the maximum community level resource-use efficiency and reproduction (a and f).

individuals (Casper & Jackson, 1997). Belowground, and in general, there are several other important mechanisms by which plants avoid complete tragedies of the commons like that in Fig. 1(a–e). Here I mention a few I have found to be important in plant communities.

First, the costs or benefits of investment in resource uptake may change with the amount of resource uptake: diminishing returns, increasing costs, or a combination of the two. Diminishing returns in particular are a common feature in biological systems (Foster, 2004). In this case, the additional resource that an individual takes up (by having higher investment in resource uptake than its neighbors) has lower resource-use efficiency than any unit of resource taken up by the neighbors. This limits the tragedy of the commons to that additional or marginal unit of resource. That is, the competitive dominant strategy is one that, when dominant makes the resource-use efficiency of the marginal unit of resource equal to one (e.g. nitrogen in Dybzinski *et al.*, 2011).

A second reality that can limit the tragedy of the commons is fluctuation in resource availability. Plants can only gain an advantage over neighbors through greater resource uptake if that resource is limiting. If fluctuations in resource availability include periods of resource saturation, plant investment in uptake will be restrained from a complete tragedy of the commons by the period of time in resource saturation. In this case, the tragedy is simply limited to the periods of resource limitation. That is, the evolutionarily stable community is composed of individuals whose cost of investment in resource uptake matches the benefits of taking up that resource while it is limiting (e.g. water in Farrior *et al.*, 2013a).

Finally, there may be other, more complex realities that alter competitive games among plants including tradeoffs of uptake with other resources, individual life history, population dynamics, and disturbance regimes that may change the nature of resource limitation and competition. In cases where these components are

important, more extensive individual plant and population dynamics models are necessary to understand the evolutionarily stable strategy.

It is clear that including individual-level optimization within a competitive context is critical to predictive models of plant communities. But, just as critical is sorting out the nature of competition for specific resources by specific vegetation forms. Seemingly small details of competitive games, like those already mentioned, can yield vastly different landscape-level effects and responses to resource additions.

For example, in the van Loon *et al.* model and experiments, soybeans increase leaf area when given additional CO_2. In this model territoriality is the dominant mechanism restraining the tragedy of the commons. Additional resources increase the benefits to an individual for employing more leaf area than its neighbors (imagine greater light levels in Fig. 1). Following the resource addition, invasions will proceed toward higher individual investment in resource uptake until the benefits of the shared portion of the additional resource is again cancelled by the cost of the plant uptake strategy. However, if instead, diminishing returns were the dominant mechanism restraining the tragedy of the commons, resource addition would decrease the rewards to employing more leaf area than neighbors and invasions would proceed in reverse toward a community of individuals with lower investment in resource uptake. The predictive power of these details in plant community responses to simple resource additions has been demonstrated with a grassland model/experiment comparison (Farrior *et al.*, 2013b).

A pathway to including competitive optimization in global carbon cycle models

Plants are currently estimated to take up *c.* 27% of the carbon we are emitting into the atmosphere through fossil fuel burning and land-use change (Le Quere *et al.*, 2014). But our estimates of this percentage in the future still comprise the largest source of uncertainty in the global predictive climate models used to inform policy-makers (Friedlingstein *et al.*, 2014).

Certainly including a mechanistic treatment of plant strategies, including those determined by competitive optimization, is an important step. It is clear theoretically (Givnish, 1982; Falster & Westoby, 2003; Franklin *et al.*, 2012), and from simple experiments (Gersani *et al.*, 2001; O'Brien & Brown, 2008), that competitive interactions are drivers of important plant traits, including woody biomass the largest store of carbon in the living biomass. But as explained already, including these mechanisms with the wrong details can lead to wildly inaccurate predictions.

The importance of the details of competitive optimization is what makes models of intermediate complexity, such as the van Loon *et al.* model that succeeds in quantitative comparisons to experimental data, so important. The work clearly demonstrates that mechanistic and quantitative predictions of plant responses to climate change are possible. The work puts forth specific hypotheses of the important details of the competitive games driving soybean investment in leaf area. This is a critical step in calling for the addition of competitive mechanisms in global models.

Caroline E. Farrior

Princeton Environmental Institute, Princeton University,
106 Guyot Hall, Princeton, NJ 08544, USA
(Author for correspondence: tel +1 918 853 1401;
email cfarrior@princeton.edu)

References

Casper B, Jackson R. 1997. Plant competition underground. *Annual Review of Ecology and Systematics* **28**: 545–570.

Dybzinski R, Farrior C, Wolf A, Reich PB, Pacala SW. 2011. Evolutionarily stable strategy carbon allocation to foliage, wood, and fine roots in trees competing for light and nitrogen: an analytically tractable, individual-based model and quantitative comparisons to data. *The American Naturalist* **177**: 153–166.

Falster DS, Westoby M. 2003. Plant height and evolutionary games. *Trends in Ecology and Evolution* **18**: 337–343.

Farrior CE, Dybzinski R, Levin SA, Pacala SW. 2013a. Competition for water and light in closed-canopy forests: a tractable model of carbon allocation with implications for carbon sinks. *The American Naturalist* **181**: 314–330.

Farrior CE, Tilman D, Dybzinski R, Reich PB, Levin SA, Pacala SW. 2013b. Resource limitation in a competitive context determines complex plant responses to experimental resource additions. *Ecology* **94**: 2505–2517.

Foster KR. 2004. Diminishing returns in social evolution: the not-so-tragic commons. *Journal of Evolutionary Biology* **17**: 1058–1072.

Franklin O, Johansson J, Dewar RC, Dieckmann U, McMurtire RE, Brannstrom A, Dybzinski R. 2012. Modeling carbon allocation in trees: a search for principles. *Tree Physiology* **32**: 648–666.

Friedlingstein P, Meinshausen M, Arora VK, Jones CD, Anav A, Liddicoat SK, Knutti R. 2014. Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. *Journal of Climate* **27**: 511–525.

Gersani M, Brown JS, O'Brien EO, Maina GM, Abramsky Z. 2001. Tragedy of the commons as a result of root competition. *Journal of Ecology* **89**: 660–669.

Givnish TJ. 1982. On the adaptive significance of leaf height in forest herbs. *The American Naturalist* **120**: 353–381.

Hardin G. 1968. The tragedy of the commons. *Science* **163**: 1243–1248.

Le Quere C, Peters GP, Anders RJ, Andrew RM, Boden T, Ciais P, Friedlingstein P, Houghton RA, Marland G, Moriarty R et al. 2014. Global carbon budget 2013. *Earth System Science Data* **6**: 235–263.

van Loon MP, Schieving F, Rietkerk M, Dekker SC, Sterck F, Anten NPR. 2014. How light competition between plants affects their response to climate change. *New Phytologist* **203**: 1253–1265.

Maynard Smith J. 1978. Optimization theory in evolution. *Annual Review of Ecology and Systematics* **9**: 31–56.

Maynard Smith J, Price GR. 1973. The logic of animal conflict. *Nature* **246**: 15–18.

O'Brien EE, Brown JS. 2008. Games roots play: effects of soil volume and nutrients. *Journal of Ecology* **96**: 438–446.

Key words: adaptive dynamics, plant competition, resource limitation, responses to climate change, tragedy of the commons.