

Size inequality and the tragedy of the commons phenomenon in plant competition

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Abstract

Game theory predicts that the evolutionarily stable level of root production is greater for plants grown with neighbours compared to plants grown alone, even when the available resources per plant are constant. This follows from the fact that for plants grown alone, new roots compete only with other roots on the same plant, whereas for multiple plants grown in a group, new roots can also compete with the roots of other plants, thereby potentially acquiring otherwise unavailable resources at their neighbours' expense. This phenomenon, which results in plants grown with neighbours over-proliferating roots at the expense of above-ground biomass, has been described as a 'tragedy of the commons', and requires that plants can distinguish self from non-self tissues. While this game theoretical model predicts the evolutionarily stable strategies of individual plants, it has only been tested on average allocation patterns of groups of plants. This is problematic, because average patterns can appear to reflect a tragedy of the commons, even when none has occurred. In particular, assuming (1) a decelerating relationship between individual plant biomass and the amount of resources available, and (2) greater size inequality in plants grown with neighbours compared to plants grown alone (due to asymmetric competition), then plants grown with neighbours should, at least on average, be smaller than plants grown alone. This is a manifestation of 'Jensen's Inequality', which states that for decelerating functions, the average value of the function is less than the function of the average value. We suggest that Jensen's Inequality should serve as an appropriate null hypothesis for examining biologically-based explanations of changes in biomass allocation strategies.

Plants compete in two distinct arenas: above- and below-ground (e.g., Clements et al. 1929; Donald 1958; Wilson 1988b; McPhee and Aarssen 2001). Above-ground, plant leaves and shoots compete primarily for light, while below-ground, roots compete for water and several macro- and micro-nutrients. Plant traits that confer a high competitive ability for acquiring each of these resource

types (i.e., above- vs. below-ground resources) are obviously quite different and trade-offs between the two major components of plant competition are likely to arise (Mooney 1972; Wilson and Tilman 1993). One important example of such a trade-off is the often-observed negative correlation between a plant's shoot to root ratio and the ratio of light to nutrient availability (Chapin

1980; Hunt and Nicholls 1986; Boot and Mensink 1990).

The adjustment of the allocation to shoots and roots in response to competition between plants may depend on more than resource ratios (e.g., Ballaré et al. 1987; Aphalo and Ballaré 1995). Specifically, a plant's strategy may also depend on the strategies of its competitors. To this end, Gersani et al. (2001) conducted a game theoretical analysis to determine the root allocation patterns expected to emerge under different competition scenarios, assuming that plants plastically allocate above- and below-ground biomass in a way that maximizes whole-plant fitness. Our goal here is to explore the assumptions of Gersani et al.'s model, and to examine the possibility that the effects of asymmetric competition and size inequalities (which were not dealt with in Gersani et al. 2001) can lead to similar shoot-root patterns, albeit by a very different process.

According to the game theoretical model, plants growing alone should proliferate their roots until the marginal return (i.e., 'benefit') of new roots equals the marginal cost of new roots, in a classic case of profit maximization. When plants grow with neighbours, however, the *average* return per unit root mass becomes increasingly important in their root proliferation 'decisions', assuming that plants can detect the difference between self and non-self tissues and thus distinguish neighbours (Gersani et al. 2001). For a nutrient uptake vs. total root production curve that passes through the origin and decelerates (i.e., when a group of neighbouring individuals receives, on whole, diminishing returns on its root investment), the average return per unit root exceeds the marginal return for any given level of root production. Hence, as more individuals compete for resources, the evolutionarily stable profit diverges from, and becomes lower than, the maximum profit. If profit is related to above-ground biomass or reproductive yield, then plants grown with neighbours will have a lower above-ground biomass or reproductive yield than plants grown alone – even when the total available resources per individual plant is constant (see Gersani et al. 2001; Maina et al. 2002 for details).

Gersani et al. (2001) identified this phenomenon as an example of a 'tragedy of the commons' (Hardin 1968). It is a tragedy in the sense that the above-ground and reproductive output could be

greater for the population as a whole, and indeed for all the plants involved, if they could somehow cooperate and not over-proliferate their roots in response to competition. (Such a scenario would not be evolutionarily stable, as plants that adopted this benign strategy would likely be out-competed by plants that adopted the overexploitation strategy.)

The game theoretical model makes three primary predictions (Gersani et al. 2001): (1) plants growing with neighbours will produce more root mass and less above-ground mass or reproductive yield compared to plants growing alone, (2) as a result, individuals' shoot to root ratios will be lower when growing with neighbours than when growing alone, and (3) these results should be independent of the cultivation technique used. While Gersani et al. refrained from predicting the relationship between the presence or absence of neighbours and *total* (i.e., above- plus below-ground) biomass, we predict that (4) plants growing with neighbours will have a lower total biomass than plants growing alone. This prediction follows from the possibility that above-ground biomass (especially leaves) can subsidize the cost of its own construction through photosynthesis, while root biomass cannot.

While the game theoretical model makes predictions for the optimal allocation strategies of *individual* plants, logistical considerations – in particular the difficulty of assigning severely entangled roots to individual competitors – make it much easier to examine properties of *groups* of plants, for instance the average below-ground biomass per plant. As a result, the game theoretical model makes the ancillary prediction that the averages of the various biomass components within groups of plants (growing either with neighbour interactions allowed or prevented) will follow the same trends as predicted for individual plants.

The first two primary predictions of the game theoretical model have been tested (using averages of multiple plants, i.e., at the 'group level') in two empirical studies, both of which found that as predicted, plants grown alone out-yielded plants grown with neighbours (with the amount of resources per plant held constant) and had greater above- to below-ground biomass ratios (Gersani et al. 2001; Maina et al. 2002). The results of these studies were therefore taken to be consistent with the game theoretical model of root allocation.

Confidence in these findings, however, relies on the assumption that the average biomass allocation patterns of *groups* of plants accurately reflect the strategies of *individuals*. Indeed, the existence of a single evolutionarily stable level of root production under the game theoretical model implies that all else being equal, the competing plants will all end up with the same biomass as one another, which equates with average biomass.

Yet, all is often *not* equal, and size inequalities among individuals within groups of plants frequently develop. Size inequalities can emerge for a number of reasons (Weiner 1985; Schwinning and Weiner 1998): episodic (e.g., age differences leading to ‘initial advantage’), abiotic (e.g., micro-site differences) and biotic (e.g., genotypic differences among individuals). Although root competition is generally size-symmetric, where competitive effect is proportional to plant size (e.g., Weiner and Thomas 1986; Wilson 1988a; Weiner et al. 1997; Cahill and Casper 2000; Blair 2001), competition for light is generally size-asymmetric (e.g., Weiner and Thomas 1986), with large plants having a disproportionately large effect compared to small plants. Light competition is asymmetric because of its directional nature – generally speaking, a large plant can shade a smaller plant, but not vice versa. Since both modes of competition will frequently be present or absent simultaneously (due to the physical connection of roots and shoots), plant resource competition as a whole should be at least slightly asymmetric (and it is, with some exceptions; Weiner 1990; Schwinning and Weiner 1998).

The relevance of size inequalities to the apparent tragedy of the commons phenomenon is potentially profound, because they can provide a mechanism whereby average biomass allocation patterns of groups of plants appear to follow the predictions of the game theoretical model, even though the allocation strategies of individual plants do not. To see why this is so, consider the relationship between soil volume and individual plant size (Figure 1). Here, soil volume is a proxy for available below-ground resources. As soil volume increases, so should plant size, due to the increase in resources. However, this curve should decelerate since the value of additional soil attenuates with increasing soil volume, as the maximum species-specific plant size is approached. Now consider two plants, each sharing an equal portion of a total soil volume $2v$ (i.e., each plant gets the

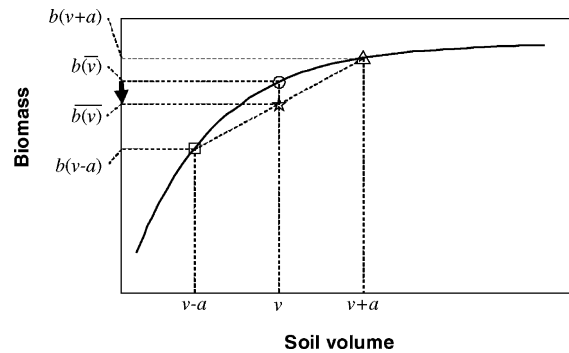


Figure 1. The consequences of size inequality and the relationship between individual plant biomass and soil volume on average plant biomass. The biomass-soil volume curve (for individual plants) decelerates as it approaches the maximum potential species-specific plant size. When two plants each capture the resources in a patch of soil of volume v , they each yield $b(v)$; hence, the average biomass of the two plants is also $b(v) = b(\bar{v})$ (circle). However, when size inequality is present, and one plant manages to capture the resources in a soil patch of volume $v + a$ (and attains a biomass of $b(v + a)$; triangle), the other plant is left with a soil volume of $v - a$ (attaining a biomass of $b(v - a)$; square). The average biomass in this case, $(b(v + a) + b(v - a))/2 = \bar{b}(\bar{v})$ (star), is constructed graphically as the intersection of the line connecting $(v + a, b(v + a))$ and $(v - a, b(v - a))$ with the vertical line where soil volume is v (which remains the average soil volume captured by the two plants). Due to the deceleration of the biomass curve, $\bar{b}(\bar{v}) < b(\bar{v})$ (the ‘aggregation bias’ of Jensen’s Inequality; Ruel and Ayres 1999); the decrease is indicated with an arrow.

same level of resources as if it alone controlled a volume of v), and each attaining a size (biomass) $b(v)$. The average biomass of these two plants will also be $b(v) = b(\bar{v})$. If, on the other hand, one of the plants captures more than its share of the soil volume (i.e., $v + a$ in Figure 1), it would be able to attain a larger size of $b(v + a)$. The other plant, left with a soil volume of $v - a$, would only be able to attain the smaller size of $b(v - a)$. The average size of the two plants, $(b(v + a) + b(v - a))/2 = \bar{b}(\bar{v})$, can be determined by the intersection of the line connecting the points $(v + a, b(v + a))$ and $(v - a, b(v - a))$ with the vertical line through soil volume v . Due to the deceleration of the plant size curve, this point of intersection will always have a biomass value less than $b(\bar{v})$. This scenario, whereby $\bar{b}(\bar{v}) < b(\bar{v})$, is a special case of the mathematical principle known as Jensen’s Inequality (Jensen 1906), and the magnitude of the decrease has been referred to as an ‘aggregation bias’ (Ruel and Ayres 1999). Indeed, for *any* function that is decelerating over an interval, the

average value of the function is less than the function of the average value (for other applications to ecology see, for example, Smallwood 1996; Ruel and Ayres 1999). As a increases (or as size inequality increases when there are more than two plants under examination), the point of intersection is driven down further, resulting in an expected negative correlation between average plant biomass and size inequality for populations of plants grown with neighbour interactions permitted. If inequalities are greater in groups of plants growing with neighbours compared to groups of plants with exclusive access to their own soil – as is likely to be the case, given the ‘snowball’ effect of asymmetric competition (Newman 1973) – then the average plant growing with neighbours will have a lower total biomass compared to the average plant growing alone. This holds true even in the absence of differing biomass allocation strategies between plants growing alone vs. those growing with neighbours, such as those predicted by Gersani et al.’s (2001) game theoretical model.

Note that unlike the game theoretical argument, size inequalities are not necessarily detrimental to all the players. Some plants will benefit by capturing a disproportionately large share of the available resources, while other plants will suffer the effects of being left with a disproportionately small share. The ‘tragedy’ – if it can even be called one – only occurs at the level of the group of plants, reflected by a decrease in the average plant biomass. To reiterate, while a decrease in biomass within individual plants implies that the average biomass of groups of plants will follow the same pattern, the logic is not reversible: We cannot assume that patterns relating to group averages necessarily imply the strategies of individual plants. Indeed, in the case of the size inequality model, average plant size decreases when neighbours are present, just as in Prediction 4 of the game theoretical model, yet the decrease is a simple mathematical consequence of a non-linear size-resource curve and increased size inequality, rather than a shift in tissue allocation strategy. Further, because of shoot/root growth allometry, whereby smaller plants tend to have lower shoot to root ratios (e.g., Cahill 2003), a decrease in plant size is likely to produce a reduction in shoot to root ratios (as in Gersani et al.’s (2001) Prediction 2, see above) that is also unrelated to changes in the biomass allocation strategies of individual plants.

We do not present the preceding ideas on how size inequalities can lead to group-level biomass allocation patterns resembling a ‘tragedy of the commons’ as a mutually exclusive alternative to Gersani et al. (2001) and Maina et al.’s (2002) game theoretical model, nor do we seek to refute their findings in general. Indeed the *absolute* increase in root biomass found in plants with neighbours (Prediction 1 of Gersani et al. 2001, also found by Maina et al. (2002)) is consistent with the game theoretical model, and not the size inequality model. However, there is no reason to predict that both processes could not occur simultaneously, and we expect that the realized level of biomass in those two studies, for example, was the net effect of plastic biomass allocation strategies (according to the game theoretical model) and differences in size inequality acting in concert to determine average and individual biomass allocation patterns. Hence, an important task will be to separate the effects, or partition the importance of the two processes. One method would be to look for differences in the assumptions or predictions of the game theoretical and size inequality models. For example, the game theoretical model requires that plants can distinguish physiological self from non-self (Gersani et al. 2001), while the size inequality model does not. Therefore, a possible approach could be to investigate situations where the ability of plants to distinguish self from non-self is manipulated. However, this in itself is problematic, since even physically separated clones can potentially distinguish between themselves (Falik et al. 2003).

Alternatively, the size of the aggregation bias of Jensen’s Inequality could be estimated using (1) a characterization of the response function between plant size (both above- and below-ground) and available resources, paying particular attention to the concavity of the relationship, and (2) estimates of the size inequality (e.g., the coefficient of variation or the Gini coefficient; Weiner 1985; Weiner and Thomas 1986) – or a more detailed characterization of the plant size distributions – for plants grown with or without neighbours, with the same amount of available resources per plant. The predicted changes in biomass allocation could then be compared to the observed changes, to determine if these observed changes had a biological basis, or a strictly mathematical explanation (see Ruel and Ayers 1999 and citations therein for a

number of similar examples). In other words, Jensen's Inequality should serve as an appropriate null hypothesis for examining biologically-based explanations of changes in biomass allocation strategies.

More broadly, we wish to emphasize that in ecological systems where there is individual variability, such as the size inequality that frequently develops in groups of competing plants, great care must be taken when attempting to link average, group-level patterns to individual-level patterns and the processes that produced them. We advocate that researchers explicitly consider the implications of individual variability and size inequality, and incorporate these implications into their experiments and models of allocation and plant competition.

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