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Modelling the effect of size-asymmetric competition on size inequality: Simple models with two plants

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ABSTRACT

The concept of size asymmetry in resource competition among plants, in which larger individuals obtain a disproportionate share of contested resources, appears to be very straightforward, but the effects of size asymmetry on growth and size variation among individuals have proved to be controversial. It has often been assumed that competition among individual plants in a population has to be size-asymmetric to result in higher size inequality than in the absence of competition, but here we question this inference. Using very simple, individual-based models, we investigate how size symmetry of competition affects the development in size inequality between two competing plants and show that increased size inequality due to competition is not always strong evidence for size-asymmetric competition. Even absolute symmetric competition, in which all plants receive the same amount of resources irrespective of their sizes, can, under some assumptions, result in higher size inequality than when competition is absent. We demonstrate our approach by applying it to data from a greenhouse experiment investigating the size symmetry of belowground competition between pairs of *Triticum aestivum* (wheat) plants. The effects of size symmetry/asymmetry on size inequality are dependent on (1) the individual plant growth model, (2) the parameters of the growth model that are affected by competition and (3) the initial sizes and growth rates. Across a range of reasonable assumptions, very general patterns that have been considered evidence for or against size-asymmetric competition do not always hold. Our results emphasize the need for explicit growth models, even very simple ones, for making inferences about the effects of competition on plant growth and size inequality.

1. Introduction

Competition is a key process in agricultural as well as natural plant populations and communities. Numerous studies have shown that the survival and growth of an individual plant is usually highly influenced by competition from its neighbors (e.g. Connell, 1983; Goldberg, 1987; Schoener, 1983; Wilson and Keddy, 1986). Competition leads not only to an overall decrease in individual plant size, it often increases size inequality (Weiner and Thomas, 1986).

The basic concept that larger plants have a large competitive advantage over smaller plants has been described by the term "asymmetric competition" (Wall and Begon, 1985; Weiner, 1990), but it has also been referred to as "one-sided competition" (Kikuzawa, 1999) or "dominance and suppression" (Schmitt et al., 1986; Turner and Rabinowitz, 1983).

The concept of size asymmetry has been in use for decades, but has not always been defined in the same way. Some have used the term "size-asymmetric competition" to simply mean any competitive advantage for a larger individual or species (e.g. Goldberg, 1990). Others follow the terminology of Begon (1984) to distinguish size-proportional from over-proportional effects and reserve the term asymmetry for the latter case.

The study of size inequality within plant populations started with a focus on the effects of density. Such studies predicted that populations grown at higher densities (without mortality) should show greater size inequality than populations grown at lower densities over the same period if competition is size-asymmetric (Weiner and Thomas, 1986). The idea is that, although size inequality may increase in the absence of competition if plants vary in their growth rates, size-asymmetric competition will act to increase this variation and therefore increase size inequality over what it would be if plants had grown without competition. Similarly, unchanged or decreased size inequality at higher densities has been interpreted as evidence for size-symmetric competition.

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Table 1
Suggested modification of the definition of competitive size symmetry of resource uptake from Schwinning and Weiner (1998) and of competitive size symmetry of growth from Weiner and Damgaard (2006), so they are based on the effects of size on the reduction in resource uptake and reduction in growth respectively, rather than on resource uptake and growth themselves. The terminology of Weiner (1990) is used. The first three cases are generally referred to as size symmetry and the last two cases as size asymmetry.

Term	Resource uptake		Growth	
	Schwinning and Weiner (1998)	New definition	Weiner and Damgaard (2006)	New definition
Absolute symmetry	All plants receive the same amount of resources, irrespective of their size	Competition reduces resource uptake of all plants equally, irrespective of their size	All plants have the same absolute growth rate irrespective of their size	Competition reduces growth of all plants equally, irrespective of their size
Partial size symmetry	Uptake of contested resources increases with size, but less than proportionally	The reduction in uptake of contested resources due to competition decreases with size, but less than proportionally	The growth rate is less than proportional to the size	The reduction in growth due to competition decreases with size, but less than proportionally
Relative size symmetry	Uptake of contested resources is proportional to size (equal uptake per unit size)	The reduction in uptake of contested resources due to competition is proportional to size	The growth rate is proportional to the size	The reduction in growth due to competition is proportional to size
Partial size asymmetry	Uptake of contested resources increase with size, and large plants receive a disproportionate share	The reduction in uptake of contested resources due to competition decreases over-proportionally with size	The growth rate is more than proportional to the size	The reduction in growth due to competition decreases over-proportionally with size
Absolute size asymmetry	The larger plant gets all the contested resources	Resource uptake of the largest plants is not reduced by competition. Only smaller plants are affected	Limiting case where only the very largest plants are growing	Growth of the largest plants is not reduced by competition. Only smaller plants are affected

The inference that increased size inequality at higher density is strong evidence for size-asymmetric competition has since been questioned (Bonan, 1991; Miller and Weiner, 1989; Weiner et al., 2001a).

Using simple models, it has been demonstrated that size-asymmetric competition results in a higher size inequality than when plants are not competing (Aikman and Watkinson, 1980). Furthermore, exponential and sigmoidal models of plant growth under extremely size-symmetric competition, in which competition reduces the growth of all individuals by the same proportion, predict lower or unchanged size inequality after a period of growth (Weiner and Thomas, 1986). This is because this type of competition reduces the variance in growth rate, and this reduces the variation in size after a period of growth. However, the effects of the more realistic "relative size-symmetry", in which plants obtain resources in proportion to their size, have not been well studied with simple models.

Instead of looking at size inequality as a function of density at one point in time, as in most experimental and many modelling studies, it can be more useful to observe how size inequality develops over time. Plants grow in a "sigmoidal" fashion, with a period of exponential-like growth, a period of almost linear growth and a period in which growth is leveling off. The effects of competition on size inequality may be different in these periods. Differences in initial size and growth rate among competing plants due to other factors may not simply reinforce the effects of competition but may completely change the pattern of how size inequality develops, as we show here with theoretical simulations.

More complex models, including spatial patterns or the effect of facilitation, have been developed to describe the effect of competition on growth and size structure (e.g. Chu et al., 2009; Weiner et al., 2001b). However, even in very simple models, the effects the symmetry/asymmetry of competition on the development of size inequality are not always straightforward.

The definitions of the different degrees of size symmetry/asymmetry of competition by Schwinning and Weiner (1998) focus on resource-mediated competitive interactions, but they do not consider differences in resource uptake originating from other factors such as soil heterogeneity or size-dependent growth.

Here we argue for a further clarification of the definition of size asymmetry to improve inferences concerning competition-induced changes in resource uptake and growth, even when there are other causes of differences in resource uptake. We use very simple individual-based models, in which plants grow linearly or exponentially and where growth rate reflects resource uptake, to analyze how the size symmetry of competition relates to size inequality. We show that neither higher size inequality due to competition, nor increasing size inequality over time is always strong evidence that competition is size-asymmetric.

The models are used to explore theoretical cases and the linear model is applied to data from a greenhouse experiment designed to ask if belowground competition between pairs of wheat plants is size-asymmetric. The analysis and interpretation of the results of this experiment provided the initial motivation for the present study.

1.1. *Defining size symmetry/asymmetry*

The size symmetry/asymmetry of competition has been described as a theoretical continuum ranging from absolute symmetry, in which resource uptake among competitors is independent of plant size, to absolute size asymmetry, where the largest plants obtain all of the contested resources (Schwinning and Weiner, 1998; Weiner, 1990). However this way of describing size symmetry/asymmetry of competition does not consider the possibility that resource uptake may differ among competing plants due to factors other than competition, such as variation in individual growth potential or heterogeneity of resource availability.

If a larger and a smaller plant compete and the larger plant has either a higher or lower growth rate due to factors other than competition, then the degree of size asymmetry in competition can be over- or underestimated. Larger millet plants (*Pennisetum americanum*) intercepted a greater fraction of the available light per unit ground area in the field than smaller plants, but they occupied less