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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 ground relative to their size (Schwinning, 1996). This is because larger plants suffered more self-shading than smaller plants. Therefore larger plants had no overall competitive advantage over smaller plants, which in some cases resulted in convergence in plant size over time. If a larger plant has a growth disadvantage compared to a smaller plant, the size asymmetry of competition will only be expressed in increased variation if the intensity of competition is large enough to offset and reverse the intrinsic differences in growth rate (Schmitt et al., 1987; Schwinning, 1996).

Therefore we propose a refinement of the definition of size symmetry of competition that differentiates between competition-induced differences in resource division and other potential causes. Competition in general acts to reduce resource uptake by individual plants, because resources must be shared with other individuals. Therefore, our new definition address how competition reduces resource uptake under different degrees of size symmetry/asymmetry (Table 1), which is the assumption made in most models of growth and competition among individual plants.

Different terms have been used for the different degrees of size symmetry/asymmetry. We prefer the complementary terms "absolute" and "relative" used by Weiner (1990) over the less informative "complete" and "perfect" used by Schwinning and Weiner (1998). According to our definition "Absolute symmetry" means that competition reduces resource uptake of all plants equally, irrespective of their sizes. "Absolute size asymmetry" is when resource uptake by the largest plants is not reduced by competition – only smaller plants suffer – and "relative size symmetry" is the case in which the reduction in uptake of contested resources due to competition is proportional to size. In between these specific situations lies partial size symmetry and partial size asymmetry.

It is common in studies of size-asymmetric competition to define size asymmetry in terms of resource pre-emption, but it is usually observed and measured as the disproportionate size advantage in the growth of larger individuals in crowded populations, i.e. size-asymmetric growth (Weiner and Damgaard, 2006). Plant growth does not necessarily reflect resource uptake, however, so the size symmetry of growth does not necessarily reflect directly the size symmetry of competition. The definitions of different degrees of size symmetry of competition by Schwinning and Weiner (1998) have been mapped into definitions of the size symmetry of growth (Weiner and Damgaard, 2006). We propose modifying this definition as well, focusing on how competition reduces the growth rate of competing plants, rather than the growth rate of a plant itself (Table 1).

Emphasizing that our modified definitions focus exclusively on competition-induced changes in resource uptake and growth respectively, we find it descriptive to use the expressions "competitive size symmetry of resource uptake" and "competitive size symmetry of growth" instead of "size symmetry of competition" and "size symmetry of growth".

For young and relatively small plants, the assumption that the growth rate reflects resource uptake may be reasonable, as the plants are not yet burdened by their need for resources to maintenance or other activities (Amthor, 1984; Penning de Vries, 1975). Furthermore it has been argued that there is no single unified concept of size for plants (Weiner and Thomas, 1992) and therefore no measure of size perfectly reflects resource uptake, even for young plants. Dry mass is a widely used measure for many purposes. Plants are primarily composed of carbohydrate, so the dry biomass of most plants is usually proportional to the plant's energy content (Hickman and Pitelka, 1975). Thus, a plant's biomass tells us something about the energy potentially available for reproduction (Reekie and Bazzaz, 1987) and thereby the plant's potential fitness. Biomass is usually measured destructively, so the biomass of a plant can only be accurately measured once. Researchers sometimes rely on non-destructive measures of size, such as height, diameter or leaf/branch length. The advantage of non-destructive measures is that one obtains a direct measure of growth for individual plants, while the disadvantage is that the different measures of size are not always well correlated (Hara, 1988). In addition, plant growth is allometric, i.e. the growth rate changes with size. For example a wheat (*Triticum aestivum*) plant produces leaves and tillers in its first growth stages, which increases plant biomass and total leaf length but not always height proportionally. Only when plants are larger and enter the stem extension stage does height increase. A further complication is that competition often changes the relationships among different aspects of plant size (Weiner and Thomas, 1992). Plants grown at high densities tend to be taller and narrower than solitary plants, reducing the negative effects of competition for light. Such plasticity acts to reduce the degree of size asymmetry in competition (Stoll et al., 2002).

Table 2
Definition of the constant, C for larger and smaller plants depending on the size symmetry/asymmetry of competition in the models. r is the average reduction competition causes on the growth rates, i is the initial size and $\bar{y}$ is the mean plant size.

	C_{larger}	$C_{smaller}$
No competition	1	1
Absolute symmetry	r	r
Relative size symmetry	$r * i_{larger}/\bar{y}$	$r * i_{smaller}/\bar{y}$
Absolute size asymmetry	1	0

2. Methods

To examine how competition reduces plant growth under different degrees of size symmetry/asymmetry, and thereby affects the development of size inequality, we use simple individual-based models of two competing plants. The plants are defined by their initial size and growth rate, and we assumed that growth is proportional to resource uptake.

Simple assumptions about plant growth are the necessary starting point for such models, which can be extended with more complex growth models (e.g. Damgaard and Weiner, 2008) in the future. Therefore we use the simplest models of growth: linear (Eq. (1)) and exponential (Eq. (2)). Even though plants grow in a "sigmoidal" fashion, growing exponential-like before entering a period of linear-like growth, we here present the linear model first, because it is the simplest.

$$y_k = i_k + AGR_k * C_k(y_{larger}, y_{smaller}) * t \quad (1)$$

$$y_k = i_k * (1 + RGR_k * C_k(y_{larger}, y_{smaller})^t) \quad (2)$$

where y is the size of plant k at time unit t, i is the initial size, and C is a constant defining the reduction in growth rate depending on the size symmetry/asymmetry of competition (Table 2). For linearly-growing plants, growth is described by the absolute growth rate (AGR), and the reduction in growth due to competition is modeled as a reduction in the AGR. For exponentially-growing plants, the growth is described by the relative growth rate (RGR), and the reduction in growth due to competition is modeled as a reduction in the RGR. In both cases competition sets in at a certain point in time and acts with a constant strength thereafter.

The reduction is calculated in relative terms, meaning that the growth is reduced by a certain fraction. Absolute symmetric competition is modeled as an equal reduction in growth rate of both plants. For relative size-symmetric competition, the reduction in growth rate is proportional to relative initial plant size. Apart from the case in which two linearly-growing plants with equal absolute growth rate compete relative size symmetrically, the size difference between the two plants changes with time. This calls for a recalculation of C for every time unit as C depends on the relative sizes of

Table 3
Growth rate for larger and smaller plants when not exposed to competition and size of initial larger plants.

Growth model	Case 1	Case 2	Case 3	Case 4
Linear growth				
Absolute growth rate of larger	0.2	0.5	0.5	0.2
Absolute growth rate of smaller	0.2	0.2	0.2	0.4
Size of initial larger plant	1.5	1.5	3.0	1.5
Exponential growth				
Relative growth rate of larger	0.10	0.15	0.15	0.10
Relative growth rate of smaller	0.10	0.10	0.10	0.25
Size of initial larger plant	1.5	1.5	3.0	1.5

the two plants, meaning that the growth curves are no longer linear or exponential respectively. We present only the simplest version here, where the proportion in initial plants' sizes is used.

In case of absolute size-asymmetric competition, the larger plant gets all the contested resources and continues to grow as if there is no competition, whereas the small plant does not grow at all, but maintains the size it achieved before competition began, although in reality the plant would eventually die (Table 2). Partial size-symmetrically competing plants show growth rates in between absolute symmetric and relative size-symmetrically competing plants, and partial size-asymmetrically competing plants show growth rates in between relative size-symmetrically and absolute size-asymmetrically competing plants.

The size inequality is measured as the coefficient of variation:

$$CV = s/\bar{y} \tag{3}$$

Where s is the standard deviation of the two plants' sizes and $\bar{y}$ is the mean plant size. Other measures of inequality, such as the Gini coefficient, originally developed to measure economic inequality (Sen, 1973) have been used (Weiner and Solbrig, 1984), but the measures are very highly correlated in this context (Bendel et al., 1989).

2.1. Theoretical simulations

To demonstrate how differences in growth rate due to factors other than competition influence the development in size inequality among competing plants, we run the model using different combinations of growth rates and initial sizes. The specific values are arbitrarily chosen to produce illustrative results, since we are interested in general trends, not specific values. Competing and non-competing pairs of plants are modeled for 16 time units, starting at time 0 where it is also assumed that competition sets in. The initial smaller plant is size 1 at time 0, and we used two initial sizes for the larger plant (Table 3). The initial size differences may be interpreted as a result of earlier sowing of the larger plant. The average reduction competition r causes on the growth rates is 50% in all cases, representing very strong competition. Four cases are modeled for both linear and exponential growth (Table 3). In Case 1 growth rate is equal for both the larger and the smaller plant, when exposed to competition. In Case 2 and 3 the initially larger plant has higher growth rate, whereas in Case 4 the initially smaller plant has higher growth rate. Case 2 and 3 differ in the initial size of the larger plant. As the two plants could be any plants competing, meaning conspecific plants as well as plants of different species with very different growth strategies, we consider all four cases reasonable.

2.2. Experimental data

We applied the model to a subset of the data from a large greenhouse experiment. The experiment is described elsewhere (C.R. Rasmussen, A.N. Weisbach, K. Thorup-Kristensen, J. Weiner, unpublished; Weisbach, 2011), but we describe those aspects relevant to our analysis here. It was conducted in the greenhouses of the University of Copenhagen, Frederiksberg, Denmark. Pairs and individuals of larger and smaller winter wheat (*Triticum aestivum* L. var. Audi) plants were grown in 100 cm tall, 7.5 cm diameter containers. There were four replicates. Plants grown in pairs were able to compete below- but not aboveground. The results analyzed here ask if low nutrient levels and high competition intensity could make belowground competition size-asymmetric.

The growth media consisted of a low nutrient clay soil mixed with one third of sand. The same volume of soil was added to each container and 1.98 g of ground fertilizer/container (4% P, 20.8% K, 7.4% S, 1.2% Mg, and 0.1% Cu; PK Gødning, Kolding Omegns Foderstof, Kolding, Denmark) was mixed into the soil before adding it to all containers and compacting the soil. This left N as the primary limiting soil resource. The soil contained 3.7 mg N/kg, which corresponds to 26.9 mg N/container. Aboveground competition was prevented by white plastic dividers, 42 cm wide and 30 cm tall, which divided the space above the soil in two equal halves and extending beyond the edges of the containers. Plants grown alone had dividers mounted as well. Larger plants were sown one week ahead of smaller plants, and the plants were grown for 62 days after sowing the smaller individuals. Three seeds were sown near the edge of the container in each location and thinned to one seedling one week after germination. A week after sowing the first germination was observed. The plants did not grow long enough to produce tillers or begin flowering. Shoot growth, measured as total leaf length, that is the sum of the length of all leaves was measured 14, 21, 28, 35, 42, 49, 56 and 62 days after sowing smaller plants. To measure the strength of competition, we calculated the competitive intensity (Miller, 1996):

$$CI = (P_{alone} - P_{comp})/P_{alone} \tag{4}$$

where P_{alone} is the mean performance of plants grown alone, and P_{comp} is the mean individual performance of plants grown with competition, i.e. performance is averaged between the two plants in each container. Performance is measured as total leaf length. CI measures the accumulated competitive effect from onset of competition to the day CI is measured. The period with the steepest increase in CI shows the strongest competition.

3. Results

3.1. Theoretical cases

In Case 1, the two non-competing plants have equal growth rates. In the linear growth Case 1, they continue to have the same absolute difference in size, resulting in a decreasing CV. This also applies to absolute symmetrically competing plants. The CV for two non-competing plants decreases faster than CV for two plants competing absolute symmetrically, as the non-competing plants are larger at any point in time. In reality the non-competing plants would at some point in time reach the leveling off phase and stop growing, and if the absolute symmetrically competing plants continue growing beyond this point in time, they would, at some point, reach the same low CV. If the competing plants are not able to keep up before they reach the leveling off phase, however, absolute symmetric competition will be a relative advantage for the larger plant compared to no competition. Relative size-symmetric competition results in unchanging size inequality. Absolute size-asymmetric competition results in increasing size inequality because only one of the plants grows (Fig. 1).

In the exponential Case 1, the two non-competing plants with equal absolute growth rates continue to have the same relative

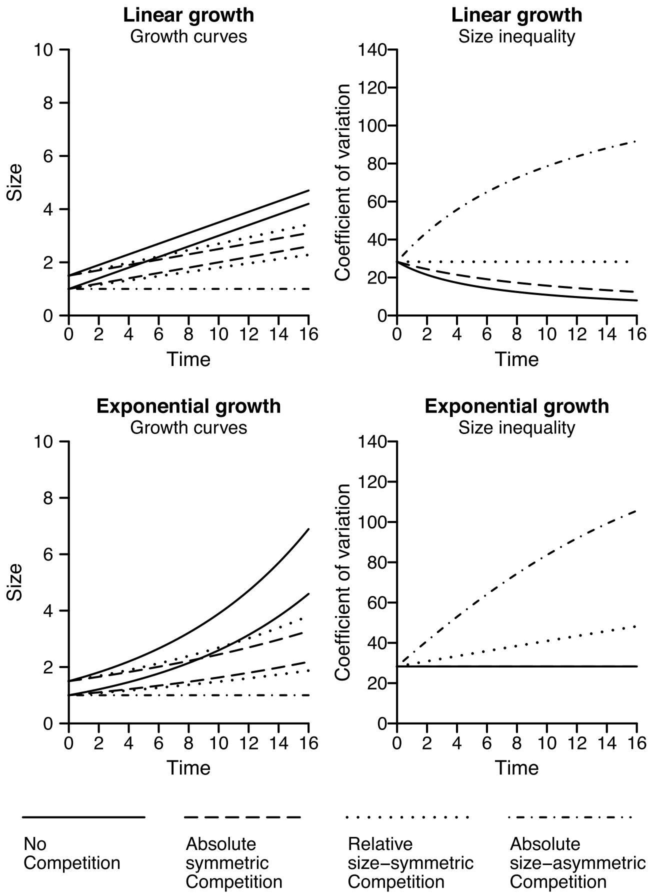

Fig. 1. Growth curves and development in size inequality (coefficient of variation) for competing and non-competing plants with linear and exponential growth for Case 1, in which pairs of non-competing plants have equal growth rates. Growth curves for non-competing and absolute symmetrically competing plants that are larger than their competitor are identical. The CV for non-competing and absolute symmetrically competing plants is identical when plants grow exponentially.

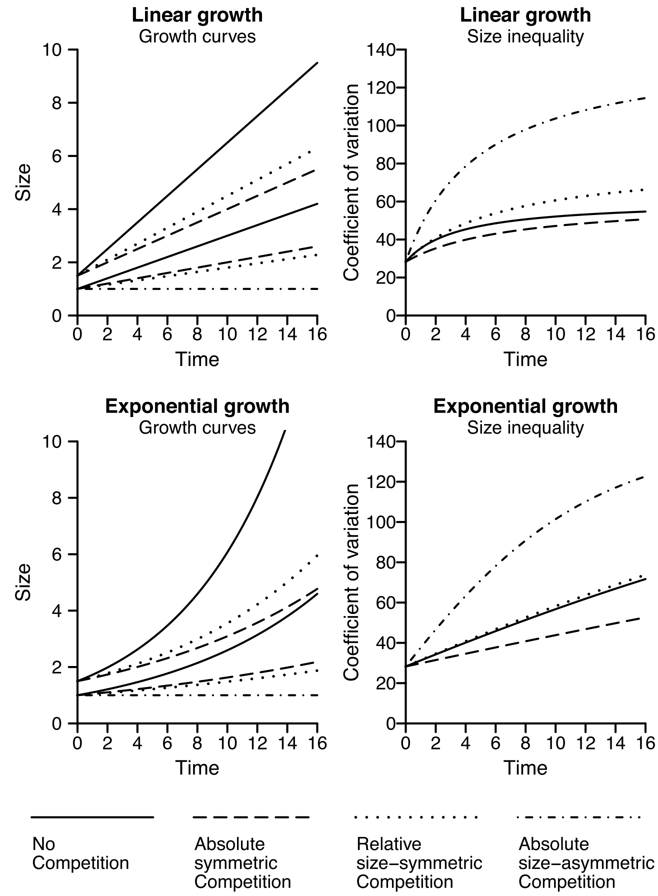

Fig. 2. Growth curves and development in size inequality (coefficient of variation) for competing and non-competing plants with linear and exponential growth for Case 2, in which the two non-competing plants differ in relative growth rate, and the initially larger plant has the higher growth rate. The growth curves for non-competing and absolute symmetrically competing plants are identical for the larger plants.

difference in size, resulting in constant CV over time. The same applies to absolute symmetrically competing plants. Both relative size-symmetric competition and absolute size-asymmetric competition result in increasing size inequality, where the latter increases faster than the former (Fig. 1).

In Case 2 the two non-competing plants differ in growth rate, and the initially larger plant has the highest growth rate. In both the linear and the exponential growth model, CV increases over time in all situations, as the absolute difference in size increases more than mean plant size. The increase in CV is faster for absolute size-asymmetrically competing plants and relative size-symmetrically competing plants than for non-competing plants, whereas CV for absolute symmetrically competing plants is increasing more slowly (Fig. 2).

In Case 3, as in Case 2, the two non-competing plants differ in growth rate, and the initially larger plant has the higher growth rate, but in Case 3 the initial size differences are larger than in Case 2. The increase in initial size difference does not change the pattern of development in CVs in the exponential case, but in the linear case the CV for non-competing and for absolute symmetrically competing plants decreases over time, whereas they increase in Case 2. The CVś for non-competing and absolute symmetrically competing converge on the same asymptote, even though they have different starting points (Figs. 2 and 3).

In Case 4 the initially smaller plant has the higher growth rate, so at some point in time it becomes larger than the initially larger plant. The shift in relative size causes a shift in CV in both the linear and the exponential model, making the degree of asymmetry resulting in the highest CV time dependent (Fig. 4).

3.2. Experimental data

Belowground competition was very intense, and the competitive intensity (CI) was significant from day 28, when it reached 20.7% (Confidence interval: 14.5–27.0 %). By the end of the experiment the CI had reached 41.7% (confidence interval: 33.4–50.0%). The development in CI was approximately linear from day 28 ($r^2 = 0.734$; Fig. 5), so we modelled the data from day 28 onward. During this period, growth was linear ($r^2 = 0.991$), so we use a linear model to fit the data (Fig. 6). The average reduction in AGR due to competition was 54%.

CV of non-competing pairs decreased over time but increased for competing pairs.

Applying the linear model to the data shows that the modelled growth rate of the competing plants lies in between that of theoretical absolute size-asymmetry and relative size-symmetry. This is reflected in the CV for the competing plants, which also lies between absolute size-asymmetric and relative size-symmetric competition, indicating that competition was size-asymmetric (Fig. 6).

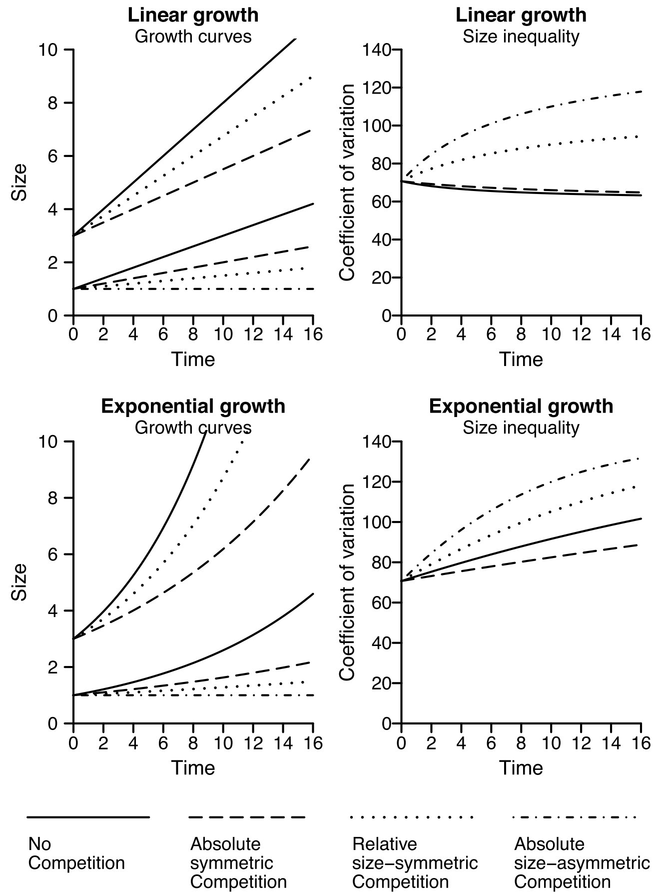

Fig. 3. Growth curves and development in size inequality (coefficient of variation) for competing and non-competing plants with linear and exponential growth for Case 3, in which the two non-competing plants differ in relative growth rate, and (as in Case 2) the initial larger plant has the higher growth rate. The initial size difference is larger in Case 3 than in Case 2. The growth curves for non-competing and absolute symmetrically competing plants are identical for the larger plants.

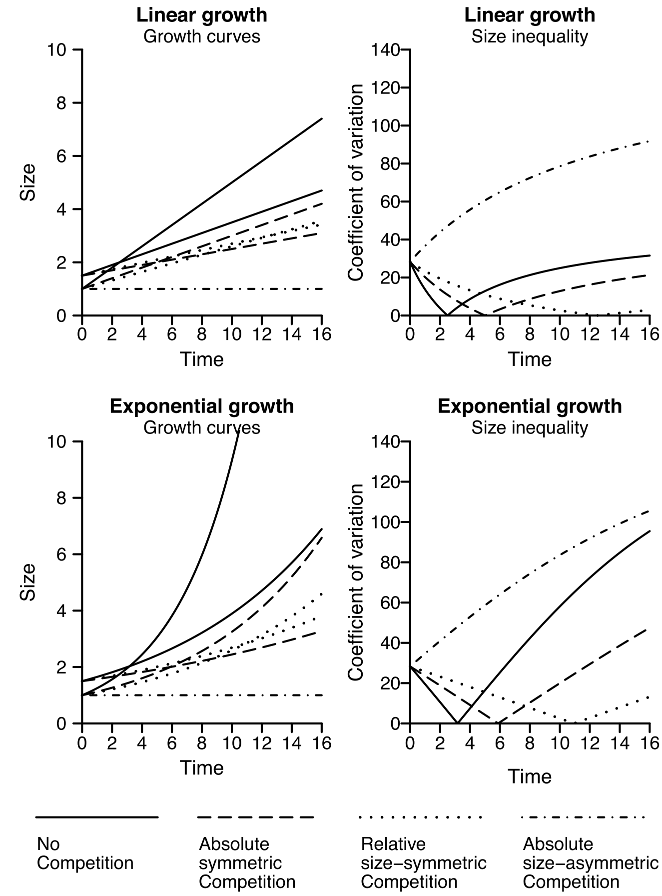

Fig. 4. Growth curves and development in size inequality (coefficient of variation) for competing and non-competing plants with linear and exponential growth for Case 4, in which the two non-competing plants differ in relative growth rate, and the initial smaller plant has the higher growth rate. The growth curves for the non-competing and absolute symmetrically competing plants are identical for the initially larger plants.

4. Discussion

The theoretical cases clearly demonstrate that higher size inequality due to competition is not always strong evidence that competition has been size-asymmetric. In several of the cases, relative size-symmetric competition, which is often the null hypothesis for studies on the size symmetry of competition, results in a higher size inequality than no competition.

The modelled cases confirm earlier findings (Weiner and Thomas, 1986) that size-asymmetric competition results in a higher size inequality than does size-symmetric competition, and that maximum size inequality in most cases occurs under absolute size-asymmetric competition. Our point here is that a certain degree of size inequality observed in an experiment cannot be interpreted as a result of either size-symmetric or size-asymmetric competition if growth is not modelled.

Looking at the development of size inequality over time, we obtain a more detailed picture of how different degrees of size asymmetry influence size inequality. Increasing size inequality over time is not strong evidence for size-asymmetric competition. Size-asymmetric competition will almost always make size inequality increase over time, but relative size-symmetric competition and even absolute symmetric competition can also result in increasing size inequality in some cases.

In the experimental study, growth over the period investigated could be described as linear, and the growth curves for non-competing plants are close to equal, meaning that the experimental

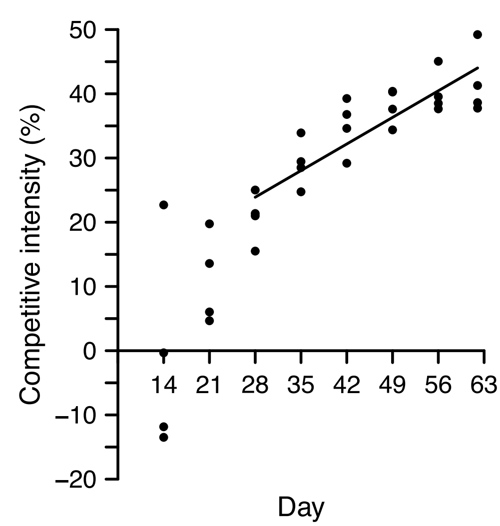

Fig. 5. The development in competitive intensity (CI) during the experiment. The CI was significant and approximately linear ($r^2 = 0.734$) from day 28.

data are an example of the theoretical linear growth Case 1, where only size-asymmetric competition can result in an increase in CV over time. As such, the data presented here do not demonstrate the need for growth modelling to make strong inferences. They do, however, emphasize the need for modelling to provide support

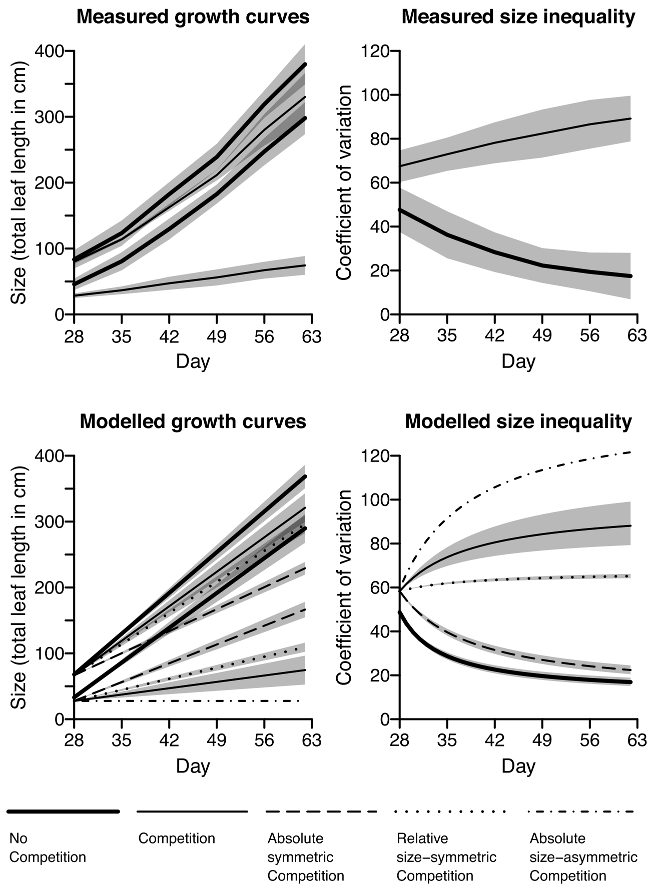

Fig. 6. Growth curves and development in size inequality (coefficient of variation) for larger and smaller competing and non-competing plants from day 28–65 in a root competition experiment, and modelled growth curves and development in size inequality for the same plants. The modelled growth curves for the non-competing and absolute symmetrically competing plants are identical for the initially larger individuals. Bands around the lines represent standard deviation of the slopes.

for conclusions that would be made without modelling, i.e. that competition was asymmetric since the CV was increasing during the experiment. Our message will be more important for experiments with aboveground competition, or between plant species with different growth strategies, or plants established at different times.

In our suggested new definitions of competitive size symmetry of resource uptake and competitive size symmetry of growth, we did not specifically address whether the actual reduction in growth rate should be calculated as an absolute or a relative reduction. In our model we calculated the reductions in AGR and RGR in relative terms, meaning that competition is reducing the growth rate by a certain percent. Another possibility would be to calculate the reduction in absolute terms. Our choice follows from our understanding of the size symmetry of competition. We define relative size symmetry as a size-proportional reduction in uptake of contested resources due to competition. Consequently, when non-competing plants have equal growth rates, relative size-symmetrically competing plants continue to have the same proportions, maintaining a constant CV over time. This would not be the case if the reduction is calculated in absolute terms.

One cannot make strong conclusions about the effects of competition on size inequality without specifying an individual growth model. We can then ask about the effects of different growth models, as well as different treatments. Although we model here only the simplest case: competition between two plants vs. no competition, for simple exponential and linear growth models, the approach we are proposing can be applied to any study in which we have data on the growth of individual plants over time under different competitive regimes/treatments.

Our new definitions of "competitive size symmetry of resource uptake" and "competitive size symmetry of growth" emphasize that the primary effect of competition is a reduction in resource uptake and thereby a reduction in the growth of competing plants compared to no competition. Furthermore, we argue that it is important to use definitions that separate the effect of competition from other effects that can cause differences in growth rate. This allows us to study the effect of competition among plants with different growth rates.

In the models used in this study, we see the sigmoidal growth curve of plants in terms of different phases, and analyze exponential and linear growth separately. The simplification is useful when illustrating how the different growth phases affect the outcome of competition, which is our goal here. Analyzing the impact of competition among plants in different growth phases is not ideal. Further research should focus on developing models for sigmoidal growth curves and clarifying how the parameters of sigmoidal growth models influence the relationship between the symmetry of competition and size inequality (Damgaard and Weiner, 2008).

In conclusion, the effects of size symmetry/asymmetry on size inequality cannot be described independently of an individual plant growth model and specifying the parameters of the growth model that are affected by competition, as well as the initial size and growth rate. By focusing on competition as a dynamic process that alters the growth of individual plants we can advance our understanding of its mechanisms and its effects on plant populations and communities.

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