

Competition, herbivory and plant size variability: *Hypochaeris radicata* grazed by snails (*Helix aspersa*)

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Summary

1. To investigate the interaction of competition and herbivory in influencing plant size variability, *Hypochaeris radicata* plants were grown in containers in a glasshouse at two densities and with three densities of snails (*Helix aspersa*).
2. There were significant effects of both plant and snail density on total above-ground biomass and mean plant biomass with no evidence of interaction.
3. There was a significant interaction between plant and snail density in influencing variation in plant size. As in most previous studies, variability in plant size was higher at high plant density. At this density, herbivory had very little effect on plant size variability, perhaps because the primary effect of snails was to reduce plant density slightly. At low plant density, a high level of herbivory increased plant size variability by reducing the size of some plants while not affecting the largest individuals.

Key-words: Inequality, plant–animal interactions, variation

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Introduction

While there has been much interest in the factors that determine size variability in plant populations (e.g. Benjamin & Hardwick 1986; Weiner 1988), very little is known about the influence of herbivory on plant size distributions. There is no clear theoretical expectation of how herbivory should influence plant size variability. There are so many forms of herbivory and different types of plant communities with which herbivores interact, that it may not be meaningful to discuss the influence of herbivory on plant size variation as a general phenomenon. Yet since so little is known, we must begin here.

In the few studies to date, herbivory has usually resulted in an increase in plant size variability. When insect herbivory in early successional communities was reduced with insecticide, variability in leaf number decreased in several herbaceous plant species (Gange & Brown 1989). In monocultures and mixtures of aphid-resistant and non-resistant genotypes of barley, plant size variability increased over time in the presence of aphid parasitism, but not in its absence (Windle & Franz 1979). Grazing of winter wheat by rabbits usually increased variability in weight of wheat plants, but a low level of rabbit herbivory decreased variability by removing or reducing the size of the largest individuals (Crawley & Weiner 1991). Slug grazing of mixtures of *Trifolium repens* and *Dactylis glomerata* increased mean plant size of *Dactylis* and decreased mean plant size

of *Trifolium*, but the size variability of both species was increased (Cottam 1986).

Other studies that did not directly address this question suggest effects of herbivory on size variability. In natural populations of *Impatiens pallida*, smaller individuals were more likely to experience extensive herbivore damage than larger individuals (Thomas & Weiner 1989). If herbivore damage is not fatal, this type of size-dependent herbivory would be expected to increase plant size variability. Although size variability was not evaluated, grazing by livestock altered the population structure of the perennial bunchgrass *Schizachyrium scoparium* by fragmenting large genets into smaller ones (Butler & Briske 1988).

In nature, the most important effects of herbivory on plant size may occur through interactions with competition (Weiner 1988). Since the above-mentioned studies either did not vary plant density or did not contain information on plant density, it is unclear if the results were due to the direct effects of the herbivores, or if the effects were mediated by competition. Ecologists must go beyond the study of simple effects to look at the interactions between the major factors which influence organisms and populations. The interaction between competition and herbivory on plant size variability is an example of such an interaction.

Competition is the one factor influencing plant size variability which has been studied extensively (reviewed in Weiner 1988). Plant size variability

generally increases at higher plant densities, although there may be exceptions when competition occurs only below ground (Weiner 1986; Wilson 1988), or when plants grow only taller but not wider when competing (Ellison 1987). The data suggest that asymmetric competition among plants may be primarily due to competition for light (Weiner 1990).

Based on simple principles, Weiner (1988) constructed several scenarios for how competition and herbivory could interact to influence plant size variability:

1. If competition is intense and asymmetric (a) herbivory can reduce competition and thus decrease the size variability which asymmetric competition generates. This could occur if the herbivore randomly reduces biomass without killing plants, or if the herbivore reduces plant density by removing individuals. Alternatively (b) if herbivore attack is size dependent, even limited herbivory could have a major effect on asymmetric competitive interactions. This might occur because such herbivory could increase or decrease size differences among individual plants which could be exaggerated by competitive asymmetry.

2. If plant competition is not intense and/or if herbivory is very intense, the effects of herbivory on plant size distributions are less likely to be mediated by competition. Here consideration should be given to the size dependency of herbivore attack and the compensation responses of individual plants which are not competing to see how herbivory influences plant size distributions.

To study the interaction of competition and herbivory and test the above predictions, an experiment was performed in which both plant and herbivore density were independent variables.

Materials and methods

Hypochoeris radicata L. (Asteraceae) seeds, purchased from John Chambers Wildflower Seeds (Kettering, UK), were planted in 20.5 cm high, 45.7 cm² containers (Stewarts 18 inch plastic tubs) in a mix of two-thirds peat moss and one-third coarse sand with slow release N-P-K fertilizer (J. Arthur Bowers Growmore Granules 7-7-7) added at the rate of 1 kg m⁻³. Containers were filled to 10 cm from the top of the containers, giving a soil volume of approximately 21 000 cm³ per container. The containers were placed on benches in a heated glasshouse without supplemental lighting at the Department of Biology, Imperial College at Silwood Park, UK. Seeds were sown in a hexagonal pattern through masonite templates at a density of 56 per container (282 m⁻²) for the low density or 480 per container (2370 m⁻²) for the high density. There were 12 containers for each density. Seeds were then covered to a depth of 0.5 cm. Seeds were sown on the dry soil on 15–17 December 1989, and all the containers were first

watered on 17 December. Germination was approximately 70% within 2 weeks after sowing. On 31 December, seedlings that had been planted at the same time were transplanted into missing locations in the low density units and, to the degree possible, in the high density units. On 3 March 1990, 0, 2 or 10 snails (*Helix aspersa* Müller) of uniform size (approximately 3 cm diameter), which had been collected locally from Silwood Park, were added to the containers, which had been placed on wooden blocks in 5 cm high plastic trays which were filled with water. These water-filled trays served as moats which kept the snails from travelling. Every morning for the duration of the experiment, snails found on the outside of the containers were put back into the containers. Snails found in the water were replaced. The temperature in the glasshouse was kept above 10°C, and it reached as high as 25°C on sunny days. The experimental design was factorial, with:

two plant sowing densities (282 and 2370 seeds m⁻²)
three snail densities (0, 2, 10 snails per container)
four replicates

In addition, six plants were grown individually in the same containers to obtain an estimate of the size that the plants would achieve in the same environment in the absence of competition. On 24–27 March 1990, the plants were harvested. Each individual plant was cut at ground level, placed in a paper bag, dried in a drying oven, and weighed. Whether a plant was within 4 cm of the edge of the container was recorded. Coefficient of variation was used as a measure of inequality; data were analysed using analysis of variance.

Results

Both plant and snail density had a significant effect on total above-ground biomass, but there was no significant interaction (Table 1). Total biomass increased with increasing plant density and decreased with increasing snail density (Fig. 1). Herbivory by two snails reduced total above-ground biomass by 5.74 g (13%) and 10 snails reduced biomass by 12.07 g (27%) on average compared to populations without herbivory. On average, total above-ground biomass was 7.53 g (22%) higher at high density than at low density. Similarly, the main effects of plant and snail density were highly significant, but their interaction was not, when mean weight, log mean weight, or log plant weight ($n = 3813$) was the dependent variable. The results were similar for analyses of variance with log weight of each plant as the dependent variable. The mean weight of the six individually grown plants was 6.567 g (SD = 2.394). This compares with mean weights per plant of 0.743 g and 0.173 g at low and high plant density respectively in the absence of snails.

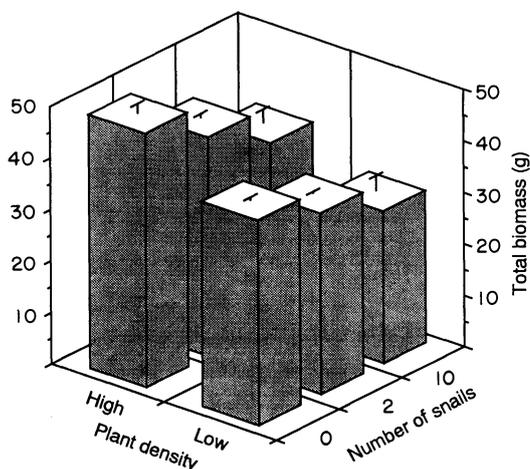


Fig. 1. Total above-ground plant biomass per container as a function of plant density and number of snails. Error bars represent + 1 SD ($n = 4$).

Both plant and snail density had significant effects on the variability in plant size (Table 2), but in this case the interaction was significant ($P < 0.01$). Coefficient of variation of plant dry mass was always higher at high plant density (Fig. 2). At high density, the presence of snails had very little effect on inequality in plant mass. At low plant density, the presence of two snails decreased variability slightly, but herbivory by 10 snails increased variability greatly (Fig. 2). Only at low plant density and high snail density did herbivory have a major effect on plant size variation.

Snails reduced plant biomass per container by reducing plant density as well as mean plant weight. Snail density as well as initial plant density had a highly significant effect on final plant density in a two-way ANOVA, demonstrating there was significant mortality due to snails. At high plant density, the mean number of surviving plants per container was 285, 270 and 244 in the presence of zero, two and 10 snails, respectively. This represents a 5.26% reduction in density from two snails and a 14.4% reduction by 10 snails. At low plant density the mean number of surviving plants per container was 53.5, 47.25 and 48.25 in the presence of zero, two and 10 snails, respectively, a reduction by approximately 10% by two or 10 snails. Because seedlings of the same age were transplanted to replace seeds which did not germinate in the low density containers (this could not be done to the same extent in the high density units), it was not possible to perform an analysis of the proportion of seeds sown which survived until the end of the experiment.

Plants within 4cm of the edge of the containers were smaller than those towards the centre in the presence and in the absence of snails. When position (centre vs edge) was added to snail and plant density as a factor in an ANOVA of coefficient of variation (CV), it was significant ($P = 0.01$); edge plants were

Table 1. Analysis of variance of total above-ground plant biomass per container

Factor	df	Sum of squares	<i>P</i>
Plant density	1	530.8	0.0001
Snail density	2	584.1	0.0001
Interaction	2	13.7	NS
Residual	18	249.3	

Table 2. Analysis of variance of the coefficient of variation of individual plant mass

Factor	df	Sum of squares	<i>P</i>
Plant density	1	2347.6	0.0001
Snail density	2	387.0	0.0136
Interaction	2	437.7	0.0074
Residual	18	603.1	

Table 3. Three-way ANOVA of coefficient of variation of individual plant mass on plant density, snail density and plant position in container (edge vs centre)

Factor	df	Sum of squares	<i>P</i>
Plant density	1	4590.5	0.0001
Snail density	2	1129.6	0.01
Plant position	2	728.8	0.0135
Plant density × snail density	2	1502.6	0.0027
Residual	18	4481.0	

significantly more variable in size than centre plants (Table 3). Of the four interaction terms in this three-way ANOVA, only the plant density × snail density interaction was significant. Although the CV cannot be decomposed into between- and within-subpopulation components, this result suggests that the effects of herbivory on plant size variation, as well as its effects on plant density and mean plant size, were concentrated on the edge plants.

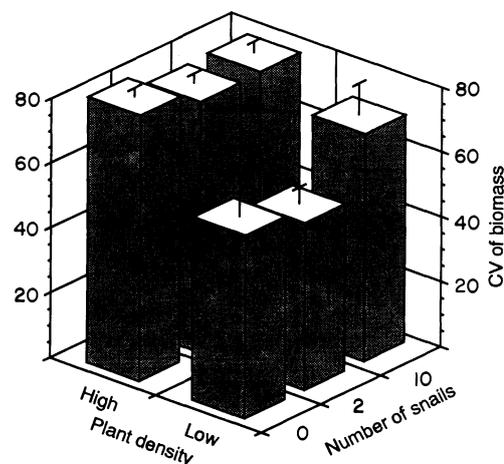


Fig. 2. Coefficient of variation of individual above-ground plant biomass as a function of plant density and number of snails. Error bars represent + 1 SD ($n = 4$).

Competition changed the growth form of *Hypochaeris radicata*. Plants grown in isolation had large flat rosettes, with their leaves appressed to the soil surface. At low density, the rosettes were less flattened, and at high density the leaves were much more upright. Plant competition also affected snail foraging behaviour. Single snails were added to three of the six containers with single plants, but there was no snail herbivory on these large plants. Snails appeared to have an aversion to feeding in this low-cover environment, and were often found on the outside of the containers.

Discussion

The effects of plant and herbivore density on total above-ground biomass (or mean plant mass) were straightforward and additive. Total biomass was 22% higher at high plant density than at low plant density. Thus, the lower (and perhaps the higher) plant density was below that which would result in maximum yield under these growing conditions. However, competition was important even at the lower density: mean plant mass at low plant density (without snails) was one-tenth that of the six individually grown plants.

Total biomass decreased with increasing herbivore density in all cases. The effect of 10 snails on total biomass was only twice that of two snails, suggesting either a density-dependent response of the snails, or increased compensation by plants at the higher level of herbivory.

Although there was no interaction between plant and herbivore density with respect to total biomass per container or mean plant biomass, there was a significant interaction in their influence on plant size variability. As in previous studies (see Weiner & Thomas 1986), plant size variability was higher at higher plant density. Further evidence of the effect of plant density on size variability is that the CV of plant weight for the six individually grown plants was only 36.5%, which is much lower than the CV for any of the experimental treatments. The effect of density on plant size inequality was much smaller at high herbivore density than at low or zero herbivore density. The highly skewed, unequal weight distributions in the high density treatments (Fig. 3) are typical of plant populations growing in crowded conditions (Harper 1977).

There was very little effect of herbivory on plant size variability at high plant density. At low plant density, however, two snails decreased the CV by 4%, but 10 snails increased it by 14%. It seems likely that the effect of high levels of herbivory on plant size distributions at low plant density occurs through the size dependency of herbivore attack. High herbivore abundance seems to reduce the number of large individuals and increase the number of small plants (Fig. 3). Unlike rabbits (Crawley & Weiner 1991),

snails did not usually reduce the size of the largest individuals. This is because snail herbivory does not affect all individuals. Plants not attacked will be as large or larger (because of reduced competition) than they would be if no herbivores were present.

Herbivory had a major effect on plant size variation only when density was low and herbivory was high. This is the situation in which the effect of herbivory on mean plant mass (although not total biomass) was greatest and competition least important. Contrary to scenario 1b, increased competition seems to reduce the effects of herbivory on plant size variation. This would occur if the primary effect of snail herbivory at high density is to kill plants, rather than make some of them smaller. A small reduction in density (5.3%, on average, with two snails and 14.4% with 10 snails) would have relatively little effect on plant size variability, possibly reducing it slightly by reducing asymmetric competition. This is consistent with what was observed. On the other hand, at low density, plants are larger and less likely to suffer mortality if attacked. In this case, the effects of herbivory on plant size distributions occur through the size dependency of herbivore attack, as suggested in scenario 2. The data on plant density provide some support for the following interpretation: while snails reduced final plant density at both low and high initial plant density, the effect was greater at high initial density.

How did herbivory increase the size variability of plants at low plant density? Since herbivory was concentrated near the edge of the containers, many plants in the centre of the area will have suffered no herbivory. Indeed, the size of the largest plants was not affected by herbivory (Fig. 3). The reduction in size of some of the plants at the edge will result in an increase in size variation by reducing the modal and median sizes.

In summary, at low plant density snails reduced the size of many plants without affecting the largest plants. This resulted in an increase in plant size inequality. At high plant density, the primary effect of snails was to reduce plant density. This had little effect on plant size variation, although it may have decreased it slightly by reducing competition.

The effects of snail herbivory were concentrated near the edge of the container. This is a reflection of snail foraging behaviour; snails prefer to forage near relatively large objects, in this case the edge of the container. Snails do not forage randomly or uniformly, even if the vegetation is random or uniform, so the effect of snails on a plant size distribution has a spatial component.

The analysis of size variability in plant populations is hampered by the confounding effects of mortality. Since only variability among survivors is considered, variation present is conditional upon survival. A plant which has died does not contribute to this variability whereas a very small plant, just before its

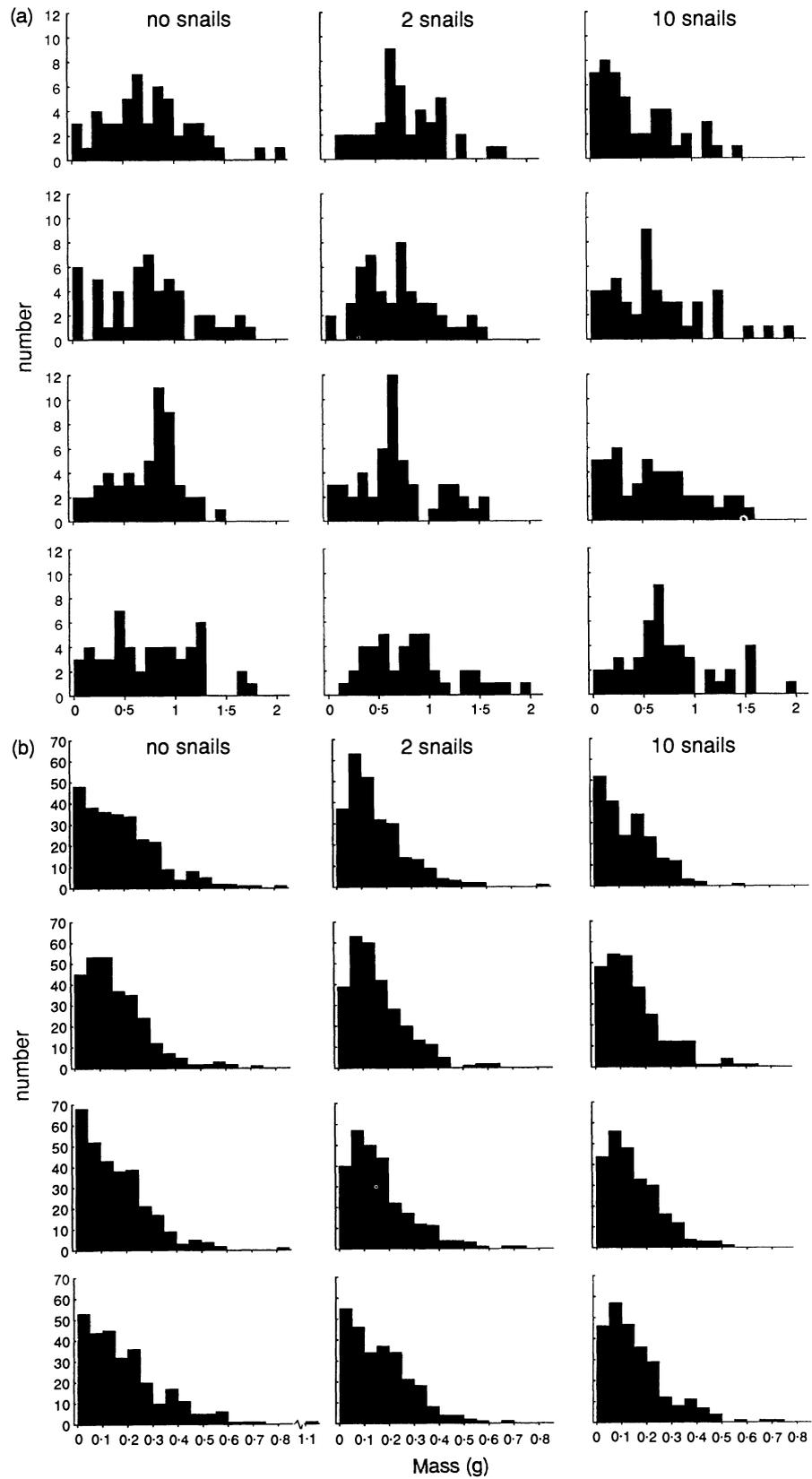


Fig. 3. Distributions of above-ground dry mass of *Hypochaeris radicata* plants grown at (a) low plant density and (b) high plant density with three densities of snails (*Helix aspersa*).

death, will contribute to variability. Statistical methods are needed that can consider size and mortality together (Weiner 1988). One way to do this is to consider those plants which die to have a size equal to zero. When the analysis of the CV as a function of snail and plant density was performed this way by assuming that no mortality occurred in the absence of snails and assigning a biomass of zero to the 'missing' plants, the results (not shown) were slightly different. Plant size variability always increased with increasing snail and plant density and there was no significant interaction between the two. This view of variation and its causes are very different, depending upon whether or not the difference between the living and dead is considered to be a form of variation. The observed interaction between plant and herbivore density in determining plant size variability is mediated by herbivore-induced mortality.

The direct effect of herbivory on a plant size distribution is a function of the size dependency of herbivore attack, and the original distribution. If herbivory is size dependent, this size dependency could be described as a quantitative relationship between the amount of loss to herbivores and the size of the plant (Weiner 1988; Gange & Brown 1989). Such a 'loss-size relationship' would be similar to the 'growth-size relationships' (Weiner 1990), which have been used to describe and characterize the ways in which plant size distributions change during stand development. [Growth-size relationships have also been called 'distribution-modifying functions' (Westoby 1982) and 'G[t,x] functions' (Hara 1984).] Loss-size relationships due to herbivory will be difficult to study except in cases where herbivore attack is relatively brief, because over longer periods the direct effects of herbivory on the size distribution will be confounded by ongoing processes of growth and competition. This confounding may be worsened if there is compensation in the growth of attacked plants. Also, the loss-size relationship will be influenced by the size distributions of the plants, i.e. herbivore behaviour will be influenced by the size distribution of plants presented to the animal. Study of the foraging behaviour of specific guilds of herbivores may provide the basis for testable predictions of loss-size relationships. For example, the effects of plant density on the foraging behaviour of snails might be predictable from models of snail foraging behaviour. This study demonstrates the need for detailed data at the level of the individual plant if models are to be developed which can predict the outcome of snail herbivory on plant size distributions.

Not only would it not be possible to predict the nature of an interaction at a lower level of analysis from information at a higher level, but even the existence of an interaction at a lower level may not be suggested from behaviour at a higher level (Brown &

Allen 1989). In this study, total biomass or mean plant biomass gives no hint of the interactions which influence plant size variability. Studies at all hierarchical levels (plant parts, plant, population and community) are needed if a real understanding of plants' responses to herbivory is to be achieved (Butler & Briske 1988).

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References

- Benjamin, C.R. & Hardwick, R.C. (1986) Sources of variation and measures of variability in even-aged stands of plants. *Annals of Botany* **58**, 757-778.
- Brown, B.J. & Allen, T.F.H. (1989) The importance of scale in evaluating herbivory impacts. *Oikos* **54**, 189-194.
- Butler, J.L. & Briske, D.D. (1988) Population structure and tiller demography of the bunchgrass *Schizachyrium scoparium* in response to herbivory. *Oikos* **51**, 306-312.
- Cottam, D.A. (1986) The effects of slug-grazing on *Trifolium repens* and *Dactylis glomerata* in monoculture and mixed sward. *Oikos* **47**, 275-279.
- Crawley, M.J. & Weiner, J. (1991) Plant size variation and vertebrate herbivory: winter wheat grazed by rabbits. *Journal of Applied Ecology* **28**, 154-172.
- Ellison, A.M. (1987) Density-dependent dynamics of *Salicornia europa* monocultures. *Ecology* **68**, 737-741.
- Gange, A.C. & Brown, V.K. (1989) Insect herbivory affects size variation in plant populations. *Oikos* **56**, 351-356.
- Hara, T. (1984) A stochastic model and the moment of dynamics of the growth and size distribution in plant populations. *Journal of Theoretical Biology* **109**, 173-190.
- Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.
- Thomas, S.C. & Weiner, J. (1989) Growth, death and size distribution change in an *Impatiens pallida* population. *Journal of Ecology* **77**, 524-536.
- Weiner, J. (1986) How competition for light and nutrients affects size variability in *Ipomoea tricolor* population. *Ecology* **67**, 1425-1427.
- Weiner, J. (1988) Variation in the performance of individuals in plant populations. *Plant Population Ecology* (eds. A.J. Davy, M.J. Hutchings & A.R. Watkinson), pp. 59-81. Blackwell Scientific Publications, Oxford.
- Weiner, J. (1990) Asymmetric competition in plants. *Trends in Ecology and Evolution* **5**, 360-364.
- Weiner, J. & Thomas, S.C. (1986) Size variability and competition in plant monocultures. *Oikos* **47**, 211-222.

Westoby, M. (1982) Frequency distributions of plant size during competitive growth of stands: the operation of distribution-modifying functions. *Annals of Botany* **50**, 733–735.

Wilson, J.B. (1988) The effect of initial advantage on the course of plant competition. *Oikos* **51**, 19–24.

Windle, P.N. & Franz, E.H. (1979) Plant population structure and aphid parasitism in barley monocultures and mixtures. *Journal of Ecology* **16**, 259–268.

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