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Asymmetric competition and the evolution of propagule size

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Summary

1 In an asexually reproducing plant (*Potamogeton pectinatus* L.) the competitive advantage of a larger propagule over a smaller one was determined by a single parameter (α, the competitive asymmetry coefficient), independent of sowing density or average propagule size. Competitive advantage was determined by the relative size difference between propagules instead of their absolute difference.

2 Productivity per germination site increased with the number and size of propagules present, even at densities high enough to result in decreased per capita yield due to plant competition.

3 Both the number of propagules produced by a plant and their size increased with increasing per capita resource capture. Therefore, propagule size was neither equal to the size of the propagule from which the plant germinated nor independent of resource status.

4 Our results clarify what assumptions should be made in ecological and evolutionary models dealing with competition for resources between seedlings. In particular, the use of relative size differences instead of absolute ones should lead to the evolution of smaller propagules than those expected if competitive advantage grew with absolute propagule size.

Key-words: Competitive advantage, germination sites, *Potamogeton pectinatus* L., seed size.

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Introduction

Propagules enable many plants to survive adverse periods in addition to their dispersal function. Propagule size is a trait that shows large variability both between and within plant species (Silvertown 1989; Westoby *et al*. 1992), although this variation is limited in comparison with associated variation in propagule number. Fecundity and survival normally increase with propagule size (Westoby *et al*. 1992; Geritz 1995; Westoby *et al*. 1996; Mack 1998; but see Hulme 1998; Yamada & Suzuki 1999), but if a plant only has a limited amount of resources that it can invest in propagules, it can produce either many small propagules or fewer larger ones, i.e. there is a trade-off between propagule size and propagule number.

Many models have studied the ecological and evolutionary implications of this trade-off, postulating a number of different, often incompatible, hypotheses concerning competition for resources between seedlings. Our goal was to use asexual propagules (tubers) of *Potamogeton pectinatus* L. (fennel pondweed) to test the validity of three specific assumptions, made in the model of Geritz *et al*. (1999). We chose this particular model because it makes specific assumptions concerning the competition process between individual seeds and each of these will be compared with alternatives proposed by other authors in different contexts.

GERITZ'S MODEL FOR THE EVOLUTION OF SEED SIZE

The model presented in Geritz *et al*. (1999) is based on discrete 'germination sites', each containing a fixed amount of resources, R, which can be converted into propagules. Each germination site is occupied by a number of propagules of different sizes. In a site with n propagules, of sizes $m_1, \dots m_n$, a plant i grown from a propagule of size m_i obtains an amount of resources equal to

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$$r_i = R \cdot \frac{e^{\alpha \cdot m_i}}{\sum_j e^{\alpha \cdot m_j}}, \quad (j = 1, \ldots n). \qquad \text{eqn 1}$$

If $\alpha = 0$, competition is symmetric and all plants in a germination site obtain the same amount of resources, but if $\alpha = \infty$, competition is extremely asymmetric: the largest propagule monopolizes all the resources, and all other propagules die. We will therefore refer to α as the 'competitive asymmetry coefficient'. The resources obtained by a plant are converted into propagules. At the end of the season, individual propagules are distributed randomly among germination sites and a new cycle starts within each site.

By studying the fate of small mutations, Geritz *et al.* (1999) concluded that, at evolutionary equilibrium, the number of propagule sizes coexisting in a population increases with the competitive asymmetry coefficient. We performed two experiments in order to test three of the model's assumptions:

Assumption 1: (i) A single parameter, α, governs competition for resources at all densities and (ii) the competitive advantage of a given propagule over a smaller one is determined by their absolute size difference.

Both parts of assumption 1 are implicit in equation 1. For a simplified case with only two propagules, of sizes m_1 and m_2, competing for resources at one site, the proportion of resources captured by the first plant will be

$$f_1 = \frac{e^{\alpha \cdot m_1}}{e^{\alpha \cdot m_1} + e^{\alpha \cdot m_2}} = \frac{1}{1 + e^{\alpha \cdot (m_2 - m_1)}}. \qquad \text{eqn 2}$$

According to equation 2, the amount of resources that a plant obtains depends only on the difference $m_1 - m_2$. An alternative is that the competitive advantage of a large individual over a smaller one depends on their relative size difference. We therefore compare the predictions of the original model (the absolute-difference model) with those of a relative-difference model, according to which the proportion of resources at a germination site that a plant obtains is

$$f_i = \frac{e^{\alpha \cdot \log(m_i)}}{\sum_j e^{\alpha \cdot \log(m_j)}}, \qquad \text{eqn 3}$$

which, for the particular case of two propagules, becomes

$$f_1 = \frac{1}{1 + e^{\alpha \cdot \log(m_2/m_1)}} = \frac{1}{1 + (m_2/m_1)^{\alpha}}. \qquad \text{eqn 4}$$

In order to determine the factors affecting the asymmetry of competition, α, and to compare the absolute- and relative-difference models, we measured the strength of competition for different tuber sizes and planting densities.

Assumption 2: The productivity per site is independent of (i) the number and (ii) the size of the propagules growing there, where productivity refers to the total amount of resources allocated to propagule production at a given germination site. These two assumptions are a consequence of equation 1, but (i) is unlikely because the total amount of resources used by the plants is often an increasing function of the number of propagules present (see Weiner 1988 for a review) and (ii) is also unlikely to hold if larger propagules make larger plants, which can gain access to more resources.

Assumption 3: The size of the propagules produced by a plant is independent of the plant's productivity. Assumption 3 is not generally true: propagule size has been reported to increase with plant resource status (defined as the total amount of resources converted into propagules; see Venable 1992 for a review). Our aim was therefore to quantify any relationship between available resources and the size of the tubers produced by *P. pectinatus*.

To test assumptions 2 and 3, we planted tubers of a wide range of sizes and at different planting densities, and calculated the effect of tuber size and planting density on tuber production and on the size of newly produced tubers.

An alternative model (Rees & Westoby 1997) assumes, contrary to assumption 1, that competitive asymmetry is governed by relative size differences (as in equations 3 and 4). They use a population-dynamic approach that is not spatially explicit, but assumes that the total amount of resources captured by an individual plant is independent of the propagule from which it originates (i.e. only the second part of assumption 2 is necessary). Other modelling approaches make rather different assumptions. Thus, Venable (1992) shows that under certain conditions the optimal strategy of a plant would be to adjust the size of the propagules it produces to the amount of resources available. This would be predicted by the model of Rees & Westoby (1997), were these authors to relax their implicit assumption that all individuals of a given species obtain exactly the same amount of resources. A growing literature on the dynamics of plant populations uses yet another approach whereby competition kernels predict the growth of individual plants as a function of the degree of competition they face (see Purves & Law 2002 and references therein) instead of assuming that the habitat is divided into a set of germination sites.

Materials and methods

STUDY SPECIES

Potamogeton pectinatus L. (fennel pondweed) is a pseudo-annual submerged angiosperm with a cosmopolitan distribution (Casper & Krausch 1980; Wiegleb & Kaplan 1998). In temperate areas it grows from late spring to early autumn, overwintering by means of underground asexual propagules (tubers) formed at the end of the growing season (Van Wijk 1988). Yearly recruitment depends almost exclusively on these tubers (Van Wijk 1988, 1989) and their production is therefore a good correlate of fitness.

GENERAL METHODS

Tubers originated from a clonal line developed from a single tuber collected at the Babbelaar (Lake Lauwersmeer, the Netherlands; 53°20′ N, 6°13′ E) and maintained since 1995 under standardized growth conditions. We divided tubers into five size classes, such that there was the same number of tubers in each class. Limits (average fresh weight, fresh wt. ± SD) were: ≤ 20 mg (class 1: 14.50 ± 2.91 mg), 21–35 mg (class 2: 27.32 ± 3.17 mg), 36–50 mg (class 3: 42.58 ± 3.76 mg), 51–80 mg (class 4: 65.11 ± 6.54 mg) and > 80 mg (class 5: 124.36 ± 42.23 mg). Tubers were weighed individually (accuracy ± 1 mg) and pre-sprouted in microtiter trays filled with sand and placed in a container of water (as below) for 6 days. We planted sprouted tubers in pots (10.2 cm high, 10.9 cm upper diameter, 8.9 cm base diameter) filled with 0.67 L of a mixture of sand and potting clay (3 : 1 by dry weight) on 15–16 June 2000. Pots were placed in five containers (surface dimensions 0.9×1.1 m^2, water depth 0.55 m) inside a greenhouse. The pots of the two experiments were randomly interspersed, subject to the conditions that: (i) each container had the same number of pots from each experiment, and (ii) the pots of each planting density (see below for details) were evenly distributed among the containers. A few *Daphnia magna* individuals (from a commercial source for aquarium fish) effectively controlled phytoplankton growth. We covered the containers with neutral-density shading nets (25% PAR reduction) supported slightly above the water surface, in order to reduce light levels to these typical of the shallow eutrophic lakes inhabited by *P. pectinatus* and to prevent insects and debris particles from falling into the water.

EXPERIMENT 1: EFFECT OF SIZE DIFFERENCE ON ASYMMETRIC COMPETITION

To test whether the competitive asymmetry coefficient, α, is a constant or depends on factors such as planting density and mother-tuber size, we planted tubers of various sizes at different densities. The unit of analysis (replicate) is a set of four plants, grown from two small and two large tubers. There were two levels of planting density, four tubers per pot, in which the four plants of a replicate were grown in the same pot, and two tubers per pot, where two pots each contained one large and one small tuber.

Tuber sizes were chosen at random, subject to the following conditions: (i) the small and large tubers were in different size classes, (ii) the two small (and the two large) tubers of a replicate had the same fresh wt. (± 5%), (iii) for each replicate, there was a replicate in the other density treatment that had the same tuber sizes (± 5% fresh wt.). There were 40 replicates for each planting density. Within each pot, we chose at random whether to mark the small or the large tuber(s) by wrapping a piece of plastic straw around the sprout and placing a small stick at the closest point on the rim of the pot.

When tuber production is completed, the plants are fully senescent and it is impossible to determine which individual plant has produced each tuber. However, because plant biomass in mid-season is a good correlate of tuber production at the end of the season (L. Santamaría, unpublished data), we carefully washed plants free of sediment, separated individual plants and measured above-ground, below-ground, mother-tuber, newly formed tuber and seed biomass (dry wt., after 48 h at 70 °C) after 40 days (mid-July).

EXPERIMENT 2: EFFECT OF TUBER SIZE AND PLANTING DENSITY ON YIELD

Our aim was to estimate per capita yield at different planting densities and for different tuber sizes. We used densities of 0.5, 1, 2, 4, 6 and 8 tubers per pot (equivalent to 0.7, 1.5, 3, 6, 9 and 12 tubers per L of sediment). To achieve 0.5 tubers per pot while keeping a comparable surface : volume ratio in the pots, we created 'double pots' by removing *c.* 30 cm^2 of the pot's side and joining two pots together. In order to estimate the yield from approximately the same number of plants at all planting densities, we planted more pots with the lower densities (40, 40, 20, 10, 10 and 10, respectively, for the five densities). Within each pot, all the tubers were of the same size (± 1 mg fresh wt.). For each density, there were equal numbers of pots with tubers of each size class thus, for example, there were eight double pots with tubers from each size class. We harvested half of the pots in July, when the plants were green and healthy and took the same measurements as in Experiment 1. The remaining pots were randomly placed in two of the previously used containers in order to maintain a comparable above-ground density. We harvested these pots 119 days after planting (October, when tuber production had ceased) and collected tubers from all the pots. We weighed these tubers individually (fresh wt.) and calculated their dry weight (dry wt.) from a regression based on a randomly chosen subsample of these tubers (dry wt. = $0.3959 \times$ fresh wt.; $r^2 = 0.97$, $n = 55$). We calculated, for each pot, the average tuber productivity per plant. Pots were randomly assigned to the two harvests, with the condition that half of the pots of each size–density combination were collected at each harvest.

To check whether per capita productivity increased at densities below 0.5 tubers per pot, we also planted tubers of six different sizes in six large square pots (one tuber per pot, pot volume 5.9 L, depth 10 cm, filled with 5.7 L sediment) and placed them in a separate container. These larger pots were harvested in October.

STATISTICAL ANALYSIS

Experiment 1

To analyse the relationship between α, tuber size and planting density, we calculated the proportion of biomass, $f_{ij,obs}$, corresponding to each plant j within the i-th replicate (i.e. for $j = 1, \ldots 4$):

$$f_{ij,obs} = \frac{s_{ij}}{\sum_{k=1}^{4} s_{ik}}, \qquad \text{eqn 5}$$

where s_{ik} is the dry weight of the k-th plant in the i-th replicate and thus the denominator represents the total biomass produced by the four plants in the i-th replicate. According to the absolute-difference model (equation 1), the predicted proportion of biomass corresponding to plant j would be:

$$f_{ij,pred}(\alpha) = \frac{e^{\alpha \cdot m_{ij}}}{\sum_{k=1}^{4} e^{\alpha \cdot m_{ik}}}, \qquad \text{eqn 6}$$

where m_{ik} is the size of the tuber from which the k-th plant in the i-th replicate grew. For each replicate we used a single measure of the discrepancy between predictions and observations, namely the function $\delta_i(\alpha)$:

$$\delta_i(\alpha) = \sum_{j=1}^{4} (f_{ij,pred}(\alpha) - f_{ij,obs})^2 \qquad \text{eqn 7}$$

The function $\delta_i(\alpha)$ is equal to zero if the four plants in the i-th replicate have the sizes that the model predicts, and becomes increasingly larger as the observations depart from the model predictions.

We fitted the model to the data by finding the values of α that minimize $\delta_i(\alpha)$, such that the data from the four plants in a replicate are summarized in this single parameter, α_i^*. We then used an ANCOVA to test whether planting density (two or four tubers per pot), average mother-tuber size (per replicate) and size asymmetry (the absolute size difference between the large and small mother-tubers in the replicate) had an effect on the value of α_i^*. The null hypothesis was that a single α properly describes the complete data set (assumption 1). The same analysis was repeated using the relative-difference model (equation 3) instead of the absolute-difference model (equation 1) to calculate $f_{ij,pred}$.

ANCOVAS on competitive asymmetry coefficients, α_i^*, were performed using the General Linear Models module of Statistica (StatSoft 1995). We used a full factorial design with a categorical variable (planting density) and two continuous variables (average mother-tuber size and size asymmetry). Because the interaction terms were not significant, we performed a second set of ANCOVAS without them. This resulted in increased model r^2 and model significance and only the results of the simplified analyses are reported.

To compare the absolute-difference and relative-difference models, we first defined the quantities

$$\Delta_X(\alpha) = \sum_i \delta_{i,X}(\alpha) \qquad \text{eqn 8}$$

where the sum is done over all the replicates and the subscript X refers to whether $f_{ij,pred}$ in equation 7 were calculated with the absolute-difference (*abs*) or relative-difference (*rel*) models. For each model, we calculate the value of α, α_X^*, that minimizes the total sum of squares in equation 8. If the relative-difference model provides a better description of the data than the absolute-difference model, $\delta_{i,rel}(\alpha_{rel}^*)$ will be significantly smaller than $\delta_{i,abs}(\alpha_{abs}^*)$ when we compare them in a paired t-test. Notice that although the i-th replicate (a set of four plants) provides two data points (one for each model), the paired t-test examines whether the mean of the *differences* between these two values is different from zero. It therefore uses a single value per replicate so that no pseudoreplication is involved.

Experiment 2

Statistical analyses consisted of stepwise backward multiple regressions and ANCOVAS (StatSoft 1995). In the backward regressions, we removed factors with $P > 0.10$ starting with the (non-significant) interaction terms and continuing with the (non-significant) main factor effects. Variables were $\log_{10}$ or square root transformed if they were not homoscedastic (ANCOVA) or the residuals not normally distributed. For the analyses of tuber size, data from individual tubers were $\log_{10}$ transformed before taking the average for each pot. In the multiple regressions, the independent variable 'planting density' (x) had to be transformed to match the type of non-linearity observed in the data (of the family $y = x^{-c}$). For this purpose we obtained the parameter c^* that minimized the sum of squares of the fit $y = x^{-c}$, entered x^{-c^*} as an independent variable in the multiple regression analysis and subtracted one degree of freedom from the error's d.f. We chose to use this approach instead of an inverse transformation of the dependent variable, because it resulted in a clearer interpretation of the fitted model effects.

ANCOVAS on tuber size and number were performed using the General Linear Models module of Statistica (StatSoft 1995), using a full factorial design with a categorical variable (planting density) and two continuous variables (tuber production and mother-tuber size). Because mother-tuber size and its interactions were never significant, we report only on a second set of ANCOVAS without this factor (i.e. only planting density and tuber production included), which resulted in increased model r^2 and model significance.

Results

EXPERIMENT 1

The values of the competitive asymmetry coefficient (α^*) according to the absolute- and relative-difference models were 9.81 and 0.70, respectively, whereas the average (± SD) values of the within-replicate discrepancy, $\delta(\alpha)$, were 0.037 (± 0.002) and 0.024 (± 0.001). Goodness of fit was significantly better for the relative-difference model ($t = 3.28$, $n = 80$, $P = 0.002$, paired t-test; Fig. 1).

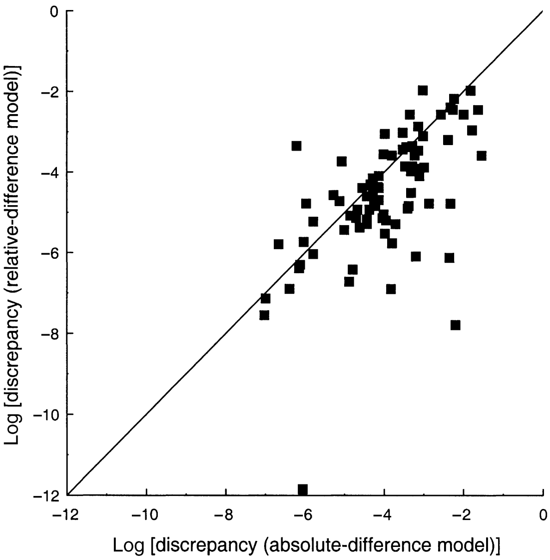
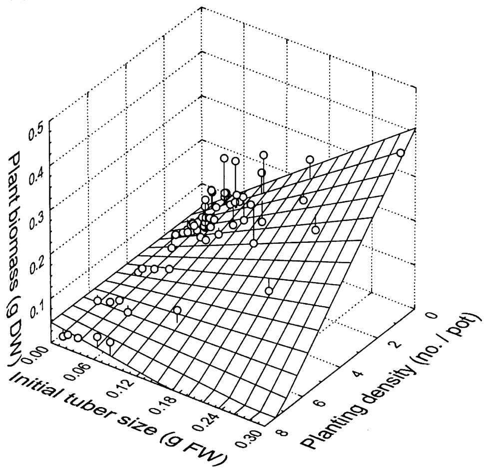


Fig. 1 Goodness-of-fit of the absolute- and relative-difference models. For each replicate, the natural logarithm of the discrepancy between predictions and observations, equation 7, according to the relative-difference model, $\log[\delta_{i,rel}(\alpha^*_{rel})]$, is plotted against the logarithm of the discrepancy according to the absolute-difference model, $\log[\delta_{i,abs}(\alpha^*_{abs})]$. The diagonal represents the line of equality.

(a) $z = 0.047 + 1.21 \times y - 0.187 \times x \times y$



(b) $z = 10\text{\^{}}(0.7 - 0.25 \times \log10(x + 1) - 0.78 \times y) - 1$

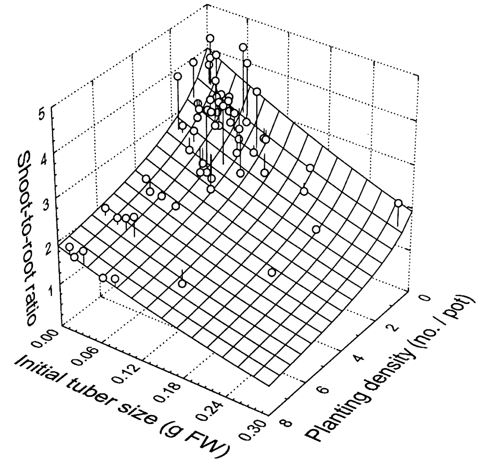


Fig. 2 Effect of planting density (number of tubers planted per pot) and mother-tuber size (FW = fresh weight) on (a) the biomass yield per individual plant (DW = dry weight) and (b) plant shoot-to-root ratio (mother-tuber's biomass excluded). The surface displayed was fitted using backward stepwise multiple regression (see Table 2 for statistical details of the fits).

Competitive asymmetry coefficients of individual replicates were affected by average mother-tuber size and absolute tuber size difference in the absolute-difference model ($P = 0.00003$ and $P = 0.018$, respectively; Table 1), but not according to the relative-difference model ($P > 0.8$, Table 1). Planting density had no effect on the competitive asymmetry coefficient, regardless of the model used for the calculations ($P > 0.15$, Table 1).

EXPERIMENT 2

Plant size in July ranged from 24 mg to 365 mg dry weight. Backward multiple regression of plant size on mother-tuber size and planting density showed highly significant effects of mother-tuber size and its interaction with planting density ($P < 0.001$, Table 2). Plant size was an increasing function of mother-tuber size. The interaction between tuber size and planting density was negative: plants growing from large tubers were bigger than plants growing from small tubers, but the difference was greater at low than at high planting densities (Fig. 2a).

Table 1 Results of ANCOVAS on competitive asymmetry coefficients. Planting density was entered as a categorical variable, average mother-tuber size and tuber-size difference as continuous variables. Significant factor effects are printed in bold

	Model statistics			Factor effects (F, d.f., P)			
	F (d.f.$_N$, d.f.$_D$)	P	Adjusted r^2	Intercept	Planting density	Average mother tuber size	Mother-tuber size difference
Absolute-difference model	12.2 (3, 76)	10^{-6}	0.30	120.1 (1, 76) 2×10^{-17}	1.98 (1, 76) 0.16	19.9 (1, 76) **0.00003**	5.80 (1, 76) **0.018**
Relative-difference model	0.35 (3, 76)	0.79	< 0.01	34.1 (1, 76) 1×10^{-7}	0.89 (1, 76) 0.35	0.06 (1, 76) 0.81	0.008 (1, 76) 0.93

Table 2 Results of backward stepwise multiple regressions for the effect of planting density, mother-tuber size and their interaction on different plant traits (biomass yield and allocation, morphology, mother-tuber depletion and tuber production). $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

	Model statistics			Parameter estimates (B, significance level, (SE))			
	F (d.f.$_N$, d.f.$_D$)	P	Adjusted r^2	Intercept	Planting density	Mother-tuber size	Density × mother-tuber size
July							
Plant biomass	84.8 (2, 61)	< 0.00001	0.73	0.047	–	1.21*** (0.09)	−0.187*** (0.029)
Shoot-to-root ratio*	39.1 (2, 61)	< 0.00001	0.55	0.70	−0.25*** (0.03)	−0.78*** (0.15)	–
Shoot internode length†	7.10 (1, 63)	0.01	0.09	23.83	–	5.90** (2.21)	–
Mother-tuber biomass utilized (%)†‡	7.52 (1, 63)	0.008	0.09	0.90	–	0.16** (0.06)	–
October							
Tuber biomass per pot§	58 (2, 62)	< 0.00001	0.64	0.18	0.23*** (0.02)	0.73*** (0.16)	–
Tuber biomass per plant§	308 (2, 62)	< 0.00001	0.91	−0.23	0.282*** (0.015)	–	0.67*** (0.15)
Number of tubers per plant§	229 (2, 62)	< 0.00001	0.88	1.98	15.30*** (0.91)	–	18.81* (8.61)
Tuber size¶	49.1 (2, 62)	< 0.00001		0.0076	−0.0040*** (0.0004)	0.0097** (0.0029)	–

*Shoot-to-root ratio and planting density were $\log_{10}$ transformed.

†Mother tuber size was $\log_{10}$ transformed.

‡Percentage of mother-tuber biomass utilized was arcsin (square root) transformed.

§Planting density was x-power transformed ($x^{-0.7}$).

¶Average of all individual tuber sizes from a given plant, $\log_{10}$ transformed before averaging (data strongly right-skewed). Planting density was $\log_{10}$ transformed.

Both tuber size and planting density had significant effects on the shoot : root ratio (Table 2; stepwise backward regression: main effects were highly significant, $P < 0.00001$, interaction term was removed). The proportion of biomass allocated to shoots was smaller for higher planting densities and for larger tubers (Fig. 2b). In other words, when competition for resources was more intense the plants reacted by allocating more resources into roots. At the same time, shoot internode length did not change significantly with planting density (Table 2). This indicates that soil nutrients, and not light, were the limiting factor in our experiment. Plants grown from large tubers used a larger proportion of tuber resources (measured as relative tuber weight loss) than plants grown from small tubers (Table 2).

For the pots harvested in October, the total amount of resources converted into tubers (i.e. tuber production per pot) was significantly affected by the number of competitors present in a pot and by mother-tuber size (i.e. we reject both parts of assumption 2; significant main effects, $P < 0.00001$, and $P < 0.00002$, Table 2). At low planting densities, tuber production per pot was an increasing function of planting density, and it is only at relatively high densities that productivity approaches a plateau (Fig. 3).

Tuber biomass production per plant was a decreasing function of planting density (significant main effect, $P < 0.00001$, Table 2), resulting in a 10-fold decrease in tuber production per plant from the lowest to the highest density (Fig. 3). This effect was more pronounced for large than for small mother-tubers (significant interaction term, $P < 0.0001$, Table 2), although the main effect of mother-tuber size was not significant. While the number of tubers per plant varied likewise (significant effects of planting density and its interaction with mother-tuber size, $P < 0.05$, Table 2),

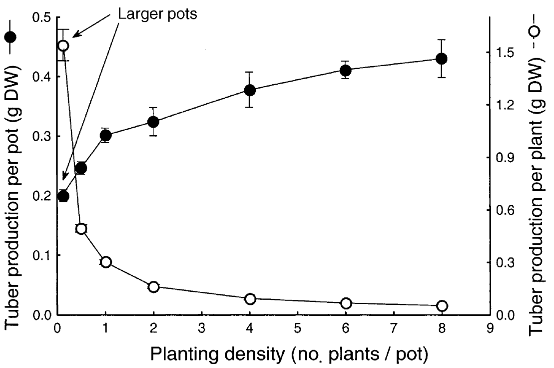


Fig. 3 Effect of planting density (number of tubers planted per pot) on germination site productivity (estimated as tuber biomass production per pot; ●) and per capita tuber production (tuber biomass production per individual plant; ○). DW = dry weight. Planting densities lower than one refer to plants grown in non-standard pots ('double pots' and 'larger pots', see Material and methods); their production is expressed here using 0.67 L as unit of sediment volume. 'Larger pots' refer to the tuber production of plants planted in 5.9 L pots filled with 5.7 L sediment, which were not included in the statistical analysis.

Table 3 Results of ANCOVAs on tuber size and tuber number. Planting density was entered as a categorical variable, tuber production as a continuous one. The three highest planting densities (4, 6 and 8 plants per pot) were pooled in one category. Significant factor effects are printed in bold

	Model statistics			Factor effects (F, (d.f.), P)			
	F (d.f.$_N$, d.f.$_D$)	P	Adjusted r^2	Intercept	Planting density	Tuber production	Density × tuber production
Tuber size†	20.2 (7, 57)	2×10^{-13}	0.68	30.3 (1, 57) 9×10^{-7}	1.29 (3, 57) 0.29	29.6 (1, 57) **0.000001**	3.62 (3, 57) **0.018**
Number of tubers per plant	136 (7, 57)	3×10^{-33}	0.94	24.4 (1, 57) 0.000007	1.14 (3, 57) 0.34	14.86 (1, 57) **0.0003**	0.35 (3, 57) 0.79

†Average of all individual tuber sizes from a given plant, $\log_{10}$ transformed before averaging (data strongly right-skewed). Tuber production $\log_{10}$ transformed.

the size of the newly produced tubers was affected by planting density and mother-tuber size ($P < 0.00001$ and $P < 0.01$, Table 2). This trend was still maintained at very low densities: in the additional low-density pots, tuber production per unit sediment volume decreased even more and tuber production per plant increased further (Fig. 3).

Both the number of tubers per plant and tuber size increased with increasing per capita resource availability (i.e. with the total amount of resources converted into tubers by a plant; $P < 0.001$ and $P < 0.00001$, Table 3). The effect of resource capture on tuber size varied, however, with planting density (significant interaction term, $P < 0.05$, Table 3): the slope of the relationship between propagule size and resource availability was higher at high planting densities (Fig. 4). This effect can be explained in at least two ways: (i) the relationship between resource capture and tuber size varies among planting densities, or (ii) there is a general, non-linear relationship between resource capture and tuber size. Distinguishing between these two hypotheses is difficult because there is little overlap between the amounts of resources captured by the plants at different planting densities (Fig. 4).

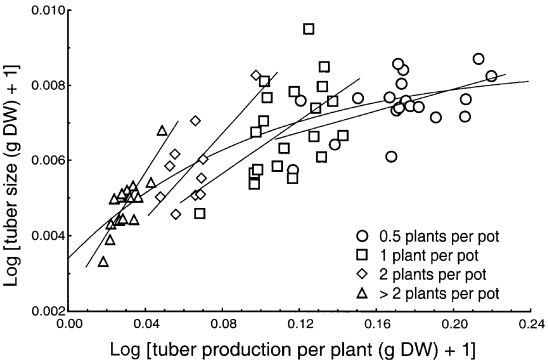


Fig. 4 Effect of per capita resource availability (estimated as the total amount of resources converted into tuber biomass per plant) on the size of newly produced tubers (averaged per pot after $\log_{10}$ transformation, because the distribution of individual tuber weights was strongly right-skewed). DW = dry weight. Continuous line: non-linear fit for the complete data set. Broken lines: separated linear fits for the different planting densities (the three highest densities 4, 6 and 8 plants per pot were pooled in one category: ‘ > 2 plants per pot’).

Discussion

The results of experiment 1 (testing the effect of size difference on asymmetric competition) confirm the validity of a major assumption of the model: namely, that competitive asymmetry can be described with a single parameter, which is independent of planting density and propagule size, at least within the range that we have explored. This is an important result because, to a large extent, it justifies the modelling approach used by Geritz (1995, 1998; Geritz *et al.* 1999), Rees & Westoby (1997) and others.

The results of experiment 1, however, also question the validity of using the absolute size differences between propagules to describe the competitive advantage of larger propagules (assumption 1 (ii)). A better description of the data is that competitive advantage increases with the relative size difference between propagules, as assumed by Rees & Westoby (1997). Indeed, a single competitive asymmetry coefficient, independent of the size of competing tubers, was a good predictor of plant size (assumption 1 (i)) only when it was based on the relative-difference model. It is clear that using relative rather than absolute size differences to model the competition process will affect the quantitative predictions of the model. More important, it might affect the qualitative nature of the predictions (see Rees & Westoby 1997 for an example and discussion). A definite answer to this question, however, requires further analysis.

According to assumption 2, the total amount of resources converted into propagules at a germination site should be independent of the number of competitors present at the site. In experiment 2 (which tested the effect of tuber size and planting density on yield), the tuber biomass produced per pot was an increasing function of planting density (similar results have been reported for a number of seed crops; see Weiner 1988 for a review). It could be argued that, for sufficiently small pots, tuber productivity will be independent of planting density. Nevertheless, we believe that discrete germination sites do not provide a good model of plant competition, because (i) in our experiment, we find that total yield increases with planting density even when individual productivity is resource limited, and (ii) if the germination site is sufficiently small, total yield may well *decrease* as planting density increases (Weiner 1988).

Experiment 2 also shows that, at low planting densities, the tuber biomass produced per pot is not independent of mother-tuber size. A consequence of this result is that plant-competition models that assume that the amount of resources per site is fixed (Venable 1992; Geritz 1995; Geritz *et al.* 1999) underestimate the fitness of plants originating from large propagules. These plant-competition models assume that the advantage of large propagule size is greatest at high densities, when competition for resources is strong. In view of our results, however, it is clear that large propagules have an additional advantage at low densities, where they can produce larger plants that have higher propagule production. It should be added, however, that our results differ from those obtained with seed-producing plants, where seed size had little impact on seed fitness at low sowing density (Gross 1984; Stanton 1984). The relationship between propagule size and plant growth may differ between plants growing from seeds and tubers. For example, Kidson & Westoby (2000) found that species with larger seeds use up proportionally fewer resources than those with smaller seeds ('larger-seed-later-commitment' hypothesis). In our case, plants growing from large tubers used a slightly higher proportion of resources than those growing from small tubers. Although this difference could be caused by the different types of propagules analysed (tubers or seeds), it might also be due to the different type of comparison (within or between species). It would certainly be of interest to find out whether the 'larger-seed-later-commitment' hypothesis applies to within-species variation and what the consequences of proportional seed resource utilization are on plant productivity and size-asymmetric competition.

The results of experiment 2 confirmed that plants produced larger tubers when they had more resources. This agrees with what has been observed in seed-producing species (see Venable 1992 for a review). Hence, the phenotypic expression of seed size varies with the maternal environment, a process ignored by most models.

When modelling processes involving competition between neighbouring plants, our experiments suggest that the strength of the competitive asymmetry should be a function of relative, rather than absolute, size differences and that an approach like the competition kernels used by Purves & Law (2002) is preferable to the use of discrete germination sites. Although assuming that the strength of competitive asymmetries is related to relative, rather than absolute, size differences does not increase the complexity of the model, the use of a competition kernel certainly does. Therefore, under some circumstances it may be justified to use a germination-site approach in order to study a particular problem. Modellers, however, should be aware of the simplification they are making, and they should judge whether it is justified in each particular case.

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