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Research

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Kin recognition and kin selection have long been known to occur in animals where they shape altruistic behavior towards relatives. More recently, studies have found that kin recognition and altered behavior towards kin can also occur in plants. However, inferring the underlying mechanism responsible for variation in plant performance in experimental studies is challenging as often, results can be explained by alternative and non-exclusive mechanisms such as niche differences, kin competition avoidance and genetic variation in growth rate and competitive ability. Plant–plant interactions may change with the life stage of plants, and competition is often most intense towards the end of plants growing season. However, changes in plant–plant interaction intensity across plants life cycle are rarely considered in kin interaction studies. Here, we adapt a model of plant growth over time modified to specifically include effects of kin and non-kin competition. The model decompose competitive interactions at different stages during plant growth from initial growth to the end of the growing season. It estimates genotype specific variation in growth rate, and how sensitive individual genotypes are to competition from neighbors. Furthermore, it estimates size asymmetry among plants accounting for both variation in growth rate, neighbor relatedness and resource variation (here water availability). We use this model to analyze the results from a competition experiment where plants grew in mini-populations with neighbor plants that were either kin or non-kin. We find that when applied to our experiments, this approach can disentangle kin effects from other effects caused by genotypic variation in growth rate and competitive response to neighbors, and thus significantly help to detect whether plants exhibit kin-cooperative behavior.

Keywords: competition, kin specific growth response, plant–plant interactions

Introduction

How plants respond to conspecific neighbors based on their degree of relatedness (i.e. kin versus non-kin) is a question that has received growing interest in ecology over the past decade (recently reviewed by Anten and Chen 2021). The findings that some plant species recognize their kin neighbor and modulate their competitive growth to

reduce competition with kin, suggests that kin recognition and kin selection have important consequences for plant fitness (File et al. 2012, Ehlers and Bilde 2019). Kin cooperative behavior may modify competition within a species and facilitate the growth of closely related conspecifics. This may for examples affect crop yield in agroecosystems, and depending on the genetic relatedness of conspecific neighbors, kin cooperative behavior can alter the strength of intraspecific competition relative to interspecific competition that affect species co-existence in natural communities (Ehlers et al. 2016, Murphy et al. 2017, Subrahmaniam et al. 2021). Despite the potential for kin interactions to affect plant interactions across organizational levels, we still know little about this topic, and studies have so far provided conflicting results.

Conflicting results may, in part, be related to the way kin interactions are measured. Experiments that measure plant's root behavior toward their neighbors have been performed and, due to the experimental constraints of determining root behavior for the entire life cycle, have been limited to the early life stages (Dudley and File 2007, Bhatt et al. 2011, Tomiolo et al. 2021). Alternatively, plants are grown with neighbors of varying relatedness (kin versus non-kin) and their final biomass or reproductive output after a growing season are used to test whether kin competition is more or less intense than non-kin competition (Cahill et al. 2005, Masclaux et al. 2010, Biernaskie 2011, Simonsen et al. 2014, Tomiolo et al. 2021). It is known that different mechanisms affect plants during their life cycle, leading to shifts in the outcome of plant–plant interactions across time (Schiffers and Tielbörger 2006, Soliveres et al. 2010, le Roux et al. 2013); yet, temporal variation in the outcome of plant–plant interactions has, to our knowledge, not been considered in the study of kin interactions.

One main challenge in studying plant kin interactions is associated with the interpretation of experimental results. Theory predicts that plant growth can be affected by niche complementarity and by kin cooperation (Chase and Leibold 2003, File et al. 2012, Ehlers and Bilde 2019). When different processes have opposing effects, one process may mask the presence of the other. For instance, among kin, plants may reduce the competitive effect on a related neighbor plant, while among non-kin, plants may differ more in niche and nutrient requirements, which reduces their competition and increase growth. These two mechanisms could therefore result in comparable plant performance among kin and non-kin even if shaped by different processes (Biernaskie 2011, Ehlers and Bilde 2019, Anten and Chen 2021, Tomiolo et al. 2021). Additionally, interaction outcomes are affected by the degree of difference in competitive ability, growth and resource acquisition rate among the interacting genotypes. In kin interactions, size asymmetry is expected to be small because related plant genotypes are expected to have more similar growth. Conversely, in non-kin interactions, competitively superior genotypes may grow much larger than competitively inferior ones. This size asymmetry can result in a lower mean performance (i.e. lower mean biomass or mean seed set) of plants in non-kin interactions, due to diminishing returns of

investments in resource uptake and growth (Masclaux et al. 2010, Simonsen et al. 2014, Ehlers and Bilde 2019). A higher mean performance of plants growing with kin compared to plant growing with non-kin is therefore not a proof of a kin cooperative growth response as it could simply be explained by higher size symmetry due to similar competitive abilities and growth among kin plants (Simonsen et al. 2014, Ehlers and Bilde 2019).

Another challenge for interpreting competition experiments that rely on plant measures taken at the end of plants' life cycle is that, by the end of the growing season, plants that have grown together with limited space and resources will compete irrespective of whether they are kin or not. The strength of competition may override other mechanisms that operated during prior life stages when plants were smaller and space limitation less strong. This consideration is supported by many studies showing that the intensity of competitive interactions among plants changes as a function of life stage (Goldberg et al. 2001, Schiffers and Tielbörger 2006, Schlau et al. 2021) and resource limitation (Gaucherand et al. 2006, Liancourt et al. 2017, Klanderud et al. 2021). Competition is often strongest among plants towards the end of the growing season, whereas facilitative effects may be more dominant during early life stages (Goldberg et al. 2001, Schiffers and Tielbörger 2006, Liancourt et al. 2017, Schlau et al. 2021). Similarly, competition is stronger in the most productive environments and under higher resource availability (Schiffers and Tielbörger 2006, Klanderud et al. 2021). Thus, comparing differences among plants grown in kin versus non-kin pots at the end of the growing season, where plants often have very limited space and resources left, may not be the most informative time point for detecting if plants modulate competition intensity in response to their neighbor's identity. Competitive response to neighbors and potential kin competition avoidance may vary in importance across life stages, and go undetected if interaction intensity is interpreted from a single time point (Schiffers and Tielbörger 2006).

To disentangle the different processes that may simultaneously affect plant competition among kin and non-kin, we propose here a model of plant growth over time that can be parameterized to measure how kin interactions differ from non-kin during different growth phases. The model estimates individual (genotype) specific variation in growth rate, and parameterizes how sensitive individual plants are to competition from kin versus non-kin neighbors. Furthermore, it estimates size asymmetry among plants in a pot, accounting for both variation in growth rate, neighbor relatedness and resource variation (here water availability).

Our purpose was to ask whether an explicit plant growth model can increase our ability to detect kin specific effects in a competition experiment performed in pots. By dividing the plant growth process into initial growth (plants not likely affected by neighbors), mid growth (plants begin to interact physically with other plants in the pot) and end of growing season (plant growth is mainly determined by limited pot space), we estimate different factors affecting plant growth during the experiment (Fig. 1). We show that when applied to potting

experiments such a modelling approach can disentangle kin effects from other effects caused by genotypic variation in growth rate and competitive response to neighbors, and thus help detect whether plants exhibit kin-cooperative behavior.

Methods

The experimental data used to parameterize the model

We used data from a greenhouse experiment aimed at testing the combined effects of genetic relatedness and abiotic stress on intraspecific interactions. In this experiment, we set up mini-populations of the annual legume *Medicago truncatula*, composed of kin or non-kin plants.

Medicago truncatula is a widespread annual legume native to the Mediterranean basin. The species reproduces predominantly by selfing (Bataillon and Ronfort 2006, Jullien et al. 2019), and has high levels of homozygosity, where maternal progenies share the same genotype (i.e. kin). Because of a mixed dispersal strategy where pods of the legume either can

fall close to the maternal plant or be passively dispersed over larger distances by attaching to the hair of small mammals, populations of *M. truncatula* are characterized by a strong genetic structure. Individuals of this species can thus occur in dense patches of closely related individuals (kin), or can be surrounded by different genotypes (Bonnin et al. 2001, Siol et al. 2008).

We used nine genotypes originating from natural populations located in the south of France, Algeria, Cyprus and Morocco (Supporting information). These genotypes belong to a core collection (CC16) maintained at INRAE Montpellier (INRAE *M. truncatula* Stock Center: <www1.montpellier.inra.fr/BRC-MTR/>), and were chosen because they capture the range of simple-sequence repeat (SSR) diversity found in a worldwide collection of naturally occurring lines (Ronfort et al. 2006). The seed lots used for this study were obtained after at least three successive generations of self-fertilization, and can thus be considered as homogeneous inbred lines. Although strong patterns of isolation by distance have been observed within populations of *M. truncatula*, the degree of genetic differentiation among neighboring
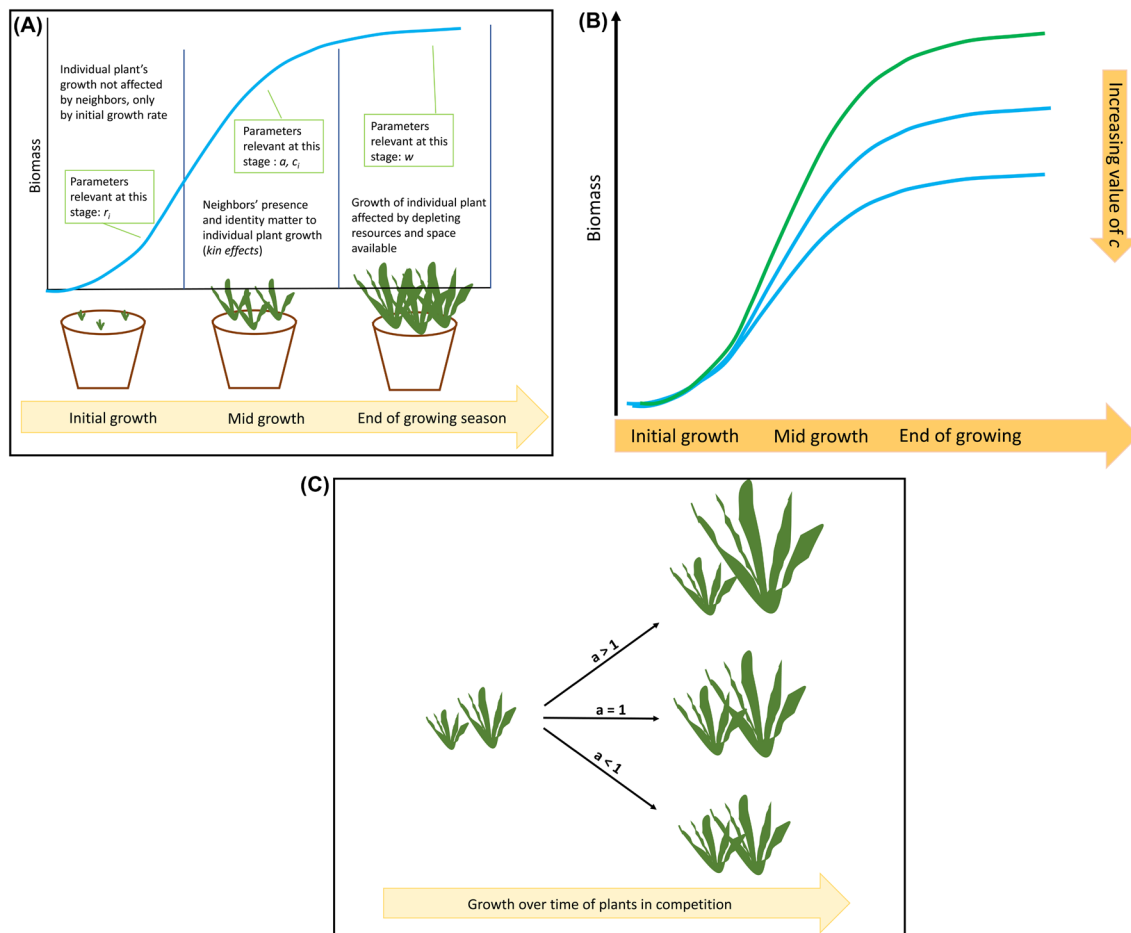
Figure 1. (A) Schematic overview of plant growth indicating the stages where model parameters are most relevant. (B) Conceptual illustration of plant growth. Green line: sigmoidal growth of a plant growing alone (without competition), blue lines: growth of plants in competition. The larger c, the earlier (smaller size) a plant's growth is limited by its neighbors. (C) Conceptual illustration of the degree of asymmetric growth of interacting plants under different values of the size asymmetric growth coefficient a.

and spatially distant populations can be similar (Bonnin et al. 2001, Ronfort et al. 2006). Thus, when comparing individuals from different populations, the correlation between spatial distance and genetic relatedness is expected to be low.

Seeds of *M. truncatula* were germinated in trays, and subsequently even-sized seedlings were transplanted into pots, which were filled with a mixture of greenhouse soil:sand:vermiculite (1:1:1). Within each pot, seedlings were planted equidistant to ensure an equal access to space and resources.

Experimental mini-populations, composed of three individuals, were grown in 5 l pots (diameter = 23 cm, height = 17.9 cm). In each pot, focal individuals were exposed to either two neighbors of the same genotype (kin) or to two neighbors of a different genotype (non-kin). This resulted in 25 different genotype combinations (Table 1). Each of these combinations was exposed to two water treatments, where mini-populations were watered for either eight minutes per day (high water treatment) or two minutes per day (low water treatments). Each genotype combination at both water treatments was replicated three times.

Starting one week after setting up the experiment, we monitored the growth of all plants by measuring their mean diameter and height using a ruler, and counting number of leaves of all plants. These measures were taken for five consecutive weeks. Plant diameter and height was used to estimate plant volume approximating the plant to a cylindrical shape ($\pi \times r^2 \times h$). We then estimated final plant volume in leaves equivalents, based on regressions between leaves number and plant volume (Supporting information).

The model

We adapted the Birch growth model (Birch 1999) proposed by Damgaard and Weiner (2008) to the growth data. This allows modelling the plant growth of individual plants that are affected by the size of the neighboring plants. Such a plant growth model is instrumental in decomposing the competitive interactions at various stages during plant growth (Birch 1999). Furthermore, it accounts for size-asymmetric competition that occur when larger or fast-growing plants preempt resources faster and at the expense of smaller plants (Damgaard and Weiner 2008). We modified the growth model of Damgaard and Weiner (2008) to specifically

Table 1. List of genotypes of *Medicago truncatula* used for this experiment and combinations of genotypes used for kin and non-kin minipopulations. In total, 25 different mini-populations were created.

Provenance	Accession	Combined with
Algeria	A_05	A_05, A_11, A_14
Algeria	A_08	A_08, A_05, A_14
Algeria	A_11	A_11, A_05, A_14
Algeria	A_14	A_14, A_05, A_08
France	F_07	F_07, F_13, F_15
France	F_13	F_13, F_07, F_15
France	F_15	F_15, F_07, F_13
Cyprus	C_02	C_02, M_12
Morocco	M_12	M_12, C_02

include the effect of kin and non kin competition, by adding a kin-term to the parameters accounting for population level asymmetric growth, and the competitive response of individual plants (see further below). In short, assuming n competitively interacting plants, the Birch model predicts the size of plant i at time t ($v_i(t)$) as a function of the plant's initial relative growth rate (r_i), the plant's size when growth stops (w), the inflection point of the growth curve (c_i) and the size-asymmetric growth coefficient in plants of the same population (a), as follows:

$$\frac{dv_i(t)}{dt} = \frac{r_i(v_i(t)+1)^a - 1}{a} \frac{nw - \sum_{k=1}^{n} v_k(t)}{nw - \left(1 - c_i \sum_{k=1}^{n} v_k(t)\right)} \quad (1)$$

where $v_i \geq 0$, $a \neq 0$, $r_i > 0$, $w > 0$, $c_i \geq 0$.

In Eq. 1, the size of plant i at time t ($v_i(t)$) is modeled by taking into account both individual (genotype)-specific growth properties of the plant (r_i and c_i) and growth properties at the population level (a and w).

The parameter r_i (Eq. 2) describes the initial growth rate of a plant before experiencing competition (i.e. the initial slope of the growth curve). The value of r_i depends on genotype identity, and variation within genotypes (Eq. 2).

The parameter c_i (Eq. 3) describes the inflection point of the curve, a positive parameter describing the size of a plant where the absolute growth rate is at its maximum and starts to decrease. For plants growing in competition, c_i describes the size of a plant when competition from neighbors becomes important and the plant starts reducing its growth (Fig. 1A). The parameter c_i depends on the identity of the individual plant (i.e. genotype), and describe how sensitive a given genotype is to competition from neighbors. Increasing values of c indicate that competition from neighbors is important early on in life, when the plant is still small (Fig. 1B). In addition to c_i, we included a population level term c_k that allow a plants sensitivity to competition from neighbors to also be modified by the identity of its neighbor (here either kin or non-kin). Thus, for a given plant, the effect of competition from neighbors depends on the plants genotype-specific c_i, and on the population-level neighbor identity effect; c_k (kin or non-kin).

The size-asymmetric growth coefficient a (Eq. 4) describes the variation in growth among plants within a population. Differences in plant size translates into differences in growth rate, where the relationship between growth and size is assumed to follow a power law characterized by the parameter a (Fig. 1C). If $a = 1$, then the difference in growth rate between plants will be directly proportional to their difference in size. If $a < 1$, then differences in growth rates will be less than proportional to the differences in size. The smaller a, the more growth rates become similar between competing plants, irrespective of their size. If $a > 1$, larger plants will gain a more than proportional advantage in growth rate

compared to smaller plants and this will exacerbate differences in growth rates. In the extreme case, this may allow large plants to potentially deplete a resource making it unavailable to smaller plants (Fig. 1C, Schwinning and Fox 1995, Schwinning and Weiner 1998). In our model, the size asymmetric growth is broken down into three components: the population mean size-asymmetric growth (a_0) caused by variation in growth rates, the size-asymmetric growth caused by micro-environmental properties, such as resource availability (a_w) (here as the variation in water availability), and the size-asymmetric growth due to neighbor relatedness, i.e. kin or non-kin (a_k).

Finally, the parameter w (Eq. 5) describes the average plant size when growth has stopped (i.e. when plant growth has reached the asymptotic part of the growth curve at the end of the growing period, Fig. 1A). This parameter varies as a function of resource availability (here water availability).

The four parameters described above are therefore modeled as follows:

$$r_i = \mu_r + \sigma_r \varepsilon_{r,i} \tag{2}$$

$$c_i = \mu_c + c_k I_k + \sigma_c \varepsilon_{c,i} \tag{3}$$

$$a = a_0 + a_w I_w + a_k I_k \tag{4}$$

$$w = w_0 + w_w I_w \tag{5}$$

where I is an indicator variable for the amount of water available to a population (I_w) or for whether the neighbours in a population are kin or non kin (I_k). I_w equals 1 in high water availability and 0 in low water availability. I_k equals 1 in populations of kin and 0 in populations of non-kin. The parameter μ_r represents the mean growth rate of genotypes within a population, and μ_c the mean effect of neighbors on the inflection point. c_k is the effect of neighbor type (i.e. kin or non-kin) on c. The parameters $\sigma_r \varepsilon_{r,i}$ and $\sigma_c \varepsilon_{c,i}$ represent the genotypic variance of r_i and c_i respectively.

The effect of plants relatedness (kin versus non-kin neighbors) is in our model captured in the parameters c_k and a_k. If c_k is negative, competition from kin neighbors begins to reduce growth of a plant when the plant has attained a larger size (i.e. later in the growing season) relative to competition from non-kin neighbors, and vice versa if c_k is positive. Likewise, if a_k is negative, the population level size asymmetry coefficient is reduced in kin populations. When a is < 1, plants are growing less than proportional to their size, a reduction of a due to a negative a_k is therefore consistent with plants restraining their growth towards neighbor plants when these are kin.

Parameter estimation

We parameterized the model using data from the greenhouse experiment described above. To minimize auto-correlation among the residual variation, we fitted the growth model to the observed growth increments in plant size (Seber and Wild 1989), using an estimate of plant volume in leaves equivalent (Supporting information). The residual error was assumed to increase proportionally with expected plant size and the time-period of growth, and was modeled by a Student's t distribution. The joint Bayesian posterior distributions of the parameters were obtained by a Monte Carlo Markov Chain (MCMC) approach using the Metropolis Hastings algorithm, assuming uniform improper prior distributions in the domains of the parameters. The MCMC iterations converged relatively fast after a burn-in period of 10 000 iterations, and the next 40 000 iterations were used to estimate the marginal posterior distribution and the corresponding 95% credibility interval of each parameter (Damgaard and Weiner 2008). All calculations were performed using the software Mathematica (Wolfram 2003).

Lastly, we performed an analysis of variance (ANOVA) using a single point variable measured at the end of our experiments as response variable. We used our measures of plant volume from our last date of measurement and analyzed plant volume as a function of relatedness (kin versus non-kin), water availability (high/low) and the interaction between these. Estimates of plant volume was square root transformed prior to analysis to fulfill model assumption. We performed this analysis to relate our growth model to a situation where only single point end measures are used.

Results

The model parameters of our growth model, described by the median of the posterior distributions and credibility intervals (2.5 and 97.5 percentiles) are summarized in Table 2 and 3.

The population level size-asymmetric growth coefficient $a = a_0 + a_w I_w + a_k I_k$ was highest in non-kin-populations exposed to low water treatment (0.642) and lowest in kin populations exposed to high water (0.566). The degree of size-asymmetric growth was significantly reduced when plants grew in kin pots ($a_k < 0$, Table 2), indicating reduced competitive effect from neighboring kin plants.

The effect of neighbors on individual plant growth (c_i) varied among genotypes (Table 3), and the negative effect of neighbors on plant growth tended to be reduced when these were kin (median value for $c_k = -0.06$, credibility interval: −0.56; 0.22, Table 2) although this pattern was not statistically significant. As larger values of c indicates that competition from neighbors occur early on in life (Fig. 1A, B), a negative estimate of c_k indicates that the negative effect of neighbor plants on individual plant growth is generally reduced when the neighbor is kin.

The initial growth rates (r_i) also varied among genotypes. Generally, the provenances from Algeria had the highest,

Table 2. Marginal posterior probability distribution of model parameters, median values and the credibility interval (2.5–97.5%). p is the probability that the parameter is larger from zero.

Parameter	2.5%	50%	97.5%	P(X>0)
a_0	0.568	0.642	0.716	1
a_w	−0.071	−0.026	0.016	0.13
a_k	−0.089	−0.051	−0.015	0.0035
w_0	60.999	82.537	131.980	1
w_w	73.722	151.709	216.559	1
μ_r	2.031	2.288	2.512	1
σ_r	0.161	0.290	0.490	–
μ_c	0.493	1.063	1.914	1
c_k	−0.559	−0.061	0.223	0.301
σ_c	0.241	0.535	1.033	–
σ	0.244	0.260	0.276	–
V	3.988	5.080	6.542	–

while those from France exhibited the lowest growth rates (Table 3).

The estimated average final plant size (w) was much larger in the high water treatment (234.246 cm³) compared to the low water treatment (82.537 cm³). In accordance with this result, the ANOVA performed on the end point estimates of plants volume (Table 4), showed a strong effect of water treatment. This analysis however did not detect any significant effect of relatedness.

Discussion

We adapted the Birch plant growth model (Birch 1999) to estimate possible kin specific effects in a plant competition experiment consisting of mini-populations of the annual legume *M. truncatula* grown with kin or non-kin neighbors in two different water treatments. We decomposed the plant growth dynamics into initial growth (where plants are unlikely to be affected by neighbors), mid growth (where plants begin to interact physically with other plants in the pot) and end of growth (where plant growth is mainly determined by limited pot space). Our model simultaneously estimates initial growth rates of individual genotypes, competitive responses at the time of plants growth where neighbors interactions are expected to have an effect, and size-asymmetric growth, that can be affected by variations in initial growth rate, neighbor

Table 3. Genotype specific values of r (initial growth rate) and c (effect of growth from neighboring plants) where r_i was calculated as $r_i = \mu_r + \sigma_r \varepsilon_{r,i}$ and c_i was calculated as $c_i = \mu_c + c_k I_k + \sigma_c \varepsilon_{c,i}$, for the situation where genotypes are grown with a non-kin, i.e. $I_k = 0$.

Genotype	r_i	$\varepsilon_{r,i}$	c_i	$\varepsilon_{c,i}$
A_05	2.134	−0.531	1.216	0.285
A_08	2.393	0.361	1.011	−0.098
A_11	2.391	0.356	1.594	0.994
A_14	2.522	0.806	0.812	−0.471
F_07	1.833	−1.567	1.151	0.165
F_13	2.013	−0.948	0.291	−1.445
F_15	1.902	−1.329	1.431	0.688
C_02	2.329	0.141	1.290	0.424
M_12	2.524	0.812	1.679	1.152

Table 4. Results of ANOVA on focal plants volume (n=150) at the end of the experiment as a function of community type (kin/non-kin) and water treatment (high/low). Plant volume was square root transformed prior to analysis.

Term	df	F	p value
Community type (kin versus non-kin)	1	2.057	0.153
Water treatment	1	11.468	< 0.001
Community × water	1	0.811	0.369

relatedness and resources (here water treatment). The purpose of applying this model was to examine whether modelling the growth dynamics of focal plants could increase the ability to detect kin specific effects in competition experiments.

We find a significant negative estimate of the size-asymmetric growth coefficient ascribed to plants relatedness (a_k). This means that when plant neighbors are kins, the size-asymmetric growth coefficient a is reduced and individual plants reduce their growth more than expected given their size, thereby reducing their competitive effect on neighboring plants. The size-asymmetric growth coefficient ascribed to plants relatedness (a_k) is estimated simultaneously with a_0 (population mean size-asymmetric growth) and individual (genotype specific) growth rates (r_i, Table 2), thus taking into account variation in growth rate among plants of different genotypes. Our model provides an efficient way to disentangle the effects of the mean–variance relationship associated with asymmetric competition from the kin specific competitive growth responses.

Kin cooperative behavior is also supported by the negative (albeit not significant) estimates of c_k, which indicates that competition from neighbors on individual plant growth begins later in the growing period when neighbors are kin. The numbers of replicates per genotype and treatment combination was limited in our experiment (n=3), and this may have resulted in high sampling variances in the estimates of genotype specific parameters. Nevertheless, taken together, these two parameter values (a_k and c_k) support the presence of a kin cooperative behavior occurring during the middle period of plant growth (Fig. 1). It is important to note that restricting the analysis to the final end-point measures of plant volume would likely have led to a different conclusion (no effect of relatedness in the ANOVA analysis). This could be because kin cooperation we detect in our experiments is not strong, and secondly because it would not be possible from the endpoint measure to disentangle effects of possible kin cooperation from other effects such as genetic variation in growth rate and variation in competitive response. Variation in plants volume at the end of the experiment was mainly explained by variation in the environment, here the water treatment.

Our model also estimates the genotype specific inflection point of the growth curves (c_i), which describes the time point in a plant's development when growth becomes negatively affected by presence of neighbors (c_i, Table 2). Larger values indicate that the plant is adversely affected by neighbor presence at an earlier time in its growth relative to smaller values. This parameter is therefore conceptually similar to a

competitive response (Goldberg and Landa 1991, Keddy et al. 1994), in describing how a focal plant's growth is affected by competition from neighboring plants. It can be used to compare plant genotypes, and to obtain a ranking of genotypes in their ability to withstand competition from neighbors. Often, competitive responses are estimated by measuring the reduction in growth due to the presence of neighbors, relative to the situation with no competitors, using a single time point variable (Goldberg and Landa 1991, Armas et al. 2004, Dudley et al. 2013). This is different from c_i in our growth model, which is estimated from temporal data on growth dynamics of a focal plant, and is not closely related to c_i for a plant growing alone. IStudies using the 'traditional' competitive response measure found that the competitive response typically varies with both biotic and abiotic environments (Keddy et al. 1994, Pennings et al. 2005, Wang et al. 2010), and may therefore not necessarily be viewed as a consistent trait for a given genotype. We do not know if this is also the case for c_i. We did not allow c_i to vary with the environment (low versus high water) due to possible over-parameterization of the growth model, and since our main focus was on modelling the kin-specific effects. However, the Birch model approach we present here can easily be further generalized to model such effects.

Where competitive response is used to describe how growth of a plant is affected by competition from its neighbors, the competitive effect, in turn, describes how a plant affects (reduces) the growth of its neighbors (Goldberg and Fleetwood 1987, Goldberg and Landa 1991). Our model parameters c_k and a_k can be understood as population level competitive effect parameters describing the effect plants have on the growth of neighbor plants depending on their relatedness (kin versus non-kin).

In conclusion, our results confirm previous studies (Goldberg et al 2001, Schiffers and Tielbörger 2006, Liancourt et al 2017, Schlau et al 2021, Klanderud et al 2021) emphasizing that plant–plant interactions can change with life stage and with environmental severity. Understanding how plant–plant interactions are shaped by different mechanisms that can vary in importance during the growing season is challenging. We tested the usefulness of plant growth models to separate different mechanisms that can affect plant growth in competition experiments. We show that using an expansion of the Birch growth model adapted to estimate plant growth response to kin and non-kin neighbors allows to estimate kin specific growth responses, which may have gone undetected if only end point measures of plant performance were used. Importantly, this approach can be used more generally to analyse plant–plant interactions over the course of plant growth to disentangle different mechanisms operating over time.

Author contributions

Sara Tomiolo: Conceptualization (equal); Formal analysis (equal); Writing – original draft (equal). **Christian F. Damgaard**: Conceptualization (equal); Formal analysis (equal); Supervision (supporting). **Laurène Gay**: Resources (equal); Supervision (equal); Writing – review and editing (equal). **Joelle Ronfort**: Resources (equal); Writing – original draft (supporting). **Bodil K. Ehlers**: Conceptualization (equal); Formal analysis (lead); Funding acquisition (equal); Project administration (lead); Supervision (lead); Writing – original draft (lead).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sqv9s4n6q> (Tomiolo et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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