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Kin discrimination causes plastic responses in floral and clonal allocation

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The composition of a plant's neighbourhood shapes its competitive interactions. Neighbours may be related individuals due to limited seed dispersal or clonal growth, so that the ability to recognize and respond to the presence of kin is beneficial. Here, we ask whether plants plastically adjust their floral and clonal allocation in response to their neighbour's identity. In a species that reproduces both sexually and clonally, we test the following predictions in response to neighbouring kin: (i) a reduction in floral display will occur to minimize costly floral structures and pollinator competition, as well as to mitigate inbreeding; and (ii) a decrease in clonality will occur to minimize resource competition and overcrowding among kin. We grew focal individuals of *Mimulus guttatus* (syn. *Erythranthe guttata*) surrounded by neighbours of varying relatedness (non-kin, outcross siblings or self siblings) and measured a suite of vegetative, floral and clonal traits. Consistent with our predictions, focal plants reduced floral and clonal allocation in the presence of kin. Moreover, focal plants increased their floral and clonal allocation when surrounded by non-kin neighbours that were high-performing. Together, we demonstrate a clear and predictable response to kin, which has general implications for the structure and function of plant neighbourhoods.

1. Introduction

Many plants live in spatially structured populations where they interact closely with their neighbours [1]. Because plants are sessile and cannot directly control their dispersal, they have little power over the composition and features of their neighbourhoods. Thus, plasticity in both vegetative [2,3] and reproductive traits [4,5] can allow individuals to increase fitness by adjusting their strategies to their neighbourhoods. A classic and well-studied example of this is individuals growing in dense patches that elongate their stems to access more light [6,7]. Yet, plants within a population frequently grow near relatives due to limited pollen and seed dispersal or clonal expansion [8]. In these cases, the fitness outcomes of neighbour associations depend not only on the direct consequences of plasticity for the focal individual but also on the indirect consequences for relatives through inclusive fitness [9,10].

Altruistic behaviour directed towards relatives can increase an individual's fitness, provided that direct costs incurred by the focal individual are counterbalanced by the benefits conferred to its relatives [10,11]. A costly trait associated with helping can evolve in this context because it increases indirect fitness—a process known as kin selection [11,12]. Kin recognition can promote the evolution of kin selection because individuals are able to discriminate between kin and non-kin and direct help towards relatives [9]. Kin recognition was long thought not to occur in plants, yet research has demonstrated that neighbour phenotypes can affect a focal individual's fitness [13], and plants have the ability to recognize neighbour relatedness through both belowground (e.g. root exudates [14]) and aboveground signals (e.g. red : far red light ratios [15]). Similarly, a growing number of studies have documented plasticity in response to kin in a range of traits from root allocation [16] and branching architecture [17] to floral display size [18,19].

One important interaction among plants within a patch is competition for limited resources [20]. Increased allocation to more competitive traits can compromise investment in reproduction, but individuals cannot decrease competitive measures, lest they cede resources to their neighbours [21]. However, if neighbours are genetically related, then the most favourable strategy may be to reduce competition and share resources with neighbours [9,22,23]. The potential for cooperation between plants should be especially high in species that bear clonal offspring through creeping stems or roots, where competition with related genotypes occurs frequently. Indeed, when clonal plants of *Potentilla anserina* were grown in high density and competed directly with daughter ramets, mother ramets decreased their allocation to clonal structures and instead invested in other aspects of growth or reproduction [24]. However, the degree to which plasticity in clonal allocation in response to competition interacts with neighbour relatedness is unknown.

The mating environment has a critical role in shaping opportunities and constraints for kin selection. Plants invest in showy floral displays to encourage pollinator visitation [25], although large displays can reduce the resources available for seed set [26]. Individuals in densely flowering patches can gain pollinator visits through facilitative effects [27], setting the stage for dynamics at the patch level [28]. On the one hand, if plants gain indirect fitness from greater pollinator visitation to kin neighbours, kin selection may lead to increased floral displays [29]. Indeed, previous research has found that plants growing with kin increased floral display effort relative to individuals in non-kin groups [18]. However, increasing floral display may intensify the occurrence of geitonogamy (inter-floral selfing mediated by pollinators visiting flowers on the same genetic individual [30]); and pollen and ovule discounting (where low-fitness self-fertilization reduces the number of gametes available for outcrossing [31]). Thus, when inbreeding reduces fitness, increasing floral display when surrounded by kin neighbours may not be beneficial as pollinators may transfer pollen between genetically related flowers. Consequently, the direction of response to kin could depend on the degree of inbreeding depression, with selection for increased floral display among kin when selfing is absent or inbreeding depression is low and selection for reduced floral display when inbreeding depression is high. Furthermore, competition for pollinator attraction could also influence the direction of floral responses to kin. Greater competition to attract pollinators among non-kin could select for increased floral display to increase a plant's share of visitation. Thus, it remains an open question how competition, cooperation and mating influence flowering responses in the presence of kin.

Here, we determine whether kin recognition can cause plasticity in floral and clonal allocation in a herbaceous plant. In particular, we used plants of perennial *M. guttatus* (syn: *E. guttata*, Phrymaceae) surrounded by neighbours of three types of relatives (self siblings, outcross siblings or non-kin). In its perennial form, *M. guttatus* reproduces sexually with hermaphroditic flowers and clonally with aboveground stolons. Mixed mating, limited seed dispersal and clonal reproduction mean that plants interact closely with relatives in some populations [32,33]. To test the prediction that social interactions differ depending on the relatedness of neighbours, we measured allocation to floral display and clonal stolons in experimental pots with neighbours that differed in relatedness. In particular, we set out to establish (i) whether plants experience competition when grown with neighbours and (ii) whether there is plasticity in allocation to floral display or clonal stolons when neighboured by kin versus non-kin. Given our findings that plants reduce floral and clonal allocation in the presence of kin, we then test (iii) whether ecological niche partitioning and/or inbreeding depression may explain our findings. Together, our results provide evidence of kin recognition in *M. guttatus* by demonstrating that plants reduce their allocation to floral display and clonal stolons in the presence of kin and support the roles of competition and inbreeding avoidance in shaping responses.

2. Methods

(a) Study species

Mimulus guttatus (syn: *E. guttata*, Phrymaceae), the common yellow monkeyflower, is a herbaceous angiosperm native to western North America. It has self-compatible hermaphroditic flowers that are pollinated mostly by bumblebees (*Bombus* spp.), producing up to hundreds of small seeds with no specialized dispersal mechanisms [34]. The species comprises populations that are either annual plants that reproduce exclusively through seeds or perennial plants capable of both sexual and clonal reproduction. Perennials produce aboveground clonal runners (stolons) from the base of the primary shoot so that patch relatedness is higher in perennial populations as neighbours can be ramets from the same clonal plant [33]. In addition, extensive literature has documented inbreeding depression in almost every fitness-related trait (e.g. [35–38]), as well as geitonogamous and biparental inbreeding in natural populations [32,39,40].

(b) Experimental design

To test the prediction that kin recognition leads to plasticity in floral and clonal allocation, we experimentally manipulated patch relatedness for perennial *M. guttatus* plants in greenhouse conditions. The seed originated from 36 open-pollinated seed families from a perennial population near Sequoia National Forest, California (N35°57'30.06", W118°36'47.46"), from which approximately 500 plants were randomly outcrossed for three generations in the greenhouse. Thus, we are confident that there are no lingering maternal effects. Moreover, research using the same seed families demonstrated no difference in a suite of phenotypic traits after three generations in the greenhouse compared to ancestral plants [41].

We conducted controlled crosses to establish 25 focal families containing sets of outcrossed and selfed seeds. For each cross, we removed the anthers from a fresh flower on the pollen donor (paternal plant) and tapped the pollen onto a glass slide before hand-brushing it onto the stigma of its assigned ovule recipient (maternal plant). To create each outcrossed family, we paired one pollen donor with one unrelated ovule recipient, for a total of 50 parents and 25 unique families. The pairing of paternal and maternal plants was random, and each pollen-donor father was used for a single family. We pollinated an additional flower on the 25 maternal plants with self-pollen, for a total of 25 selfed-sibling families. Thus, the 25 selfed-sibling families share the same maternal genotype as the 25 outcrossed-sibling families. From a separate set of eight plants in the same population, we randomly paired four pollen-donor plants with four ovule-recipient plants to create four outcrossed 'non-kin' families. These four non-kin families were unrelated to each other and to all 25 sibling families and were used as neighbours in the non-kin treatment.

We sowed seed from each of the 25 outcrossed and 25 selfed families and from the four extra families in individual wells of trays filled with Sunshine Mix no. 1 (Sun Gro Horticulture). Germination in this species is very high (>95%) and highly synchronous (within 1–2 days). As soon as seedlings had open cotyledons, we transplanted them over a two-day period into three experimental neighbour treatments that manipulated patch relatedness. Seedlings were randomly selected for transplant and showed little variation in size within or between families. In the first treatment ('self sibs'), we surrounded a selfed focal plant from each of the 25 selfed-sibling families with four neighbours from the same selfed-sibling set. In the second treatment ('outcross sibs'), we surrounded an outcrossed focal plant from each of the 25 outcrossed families with 4 neighbours from the same full-sibling outcrossed set. In the third treatment ('non-kin'), we surrounded an outcrossed focal plant from each of the 25 outcrossed families with 4 non-kin neighbours, 1 from each of the 4 unrelated families. Focal plants and their neighbours were grown in 6" (1.6 l) round pots. All neighbour plants were placed in a square formation around the focal plant, approximately 3.7 cm from the focal plant and 5 cm from the nearest neighbour. We replicated each treatment three times for each of the 25 families. In total, we had $n = 225$ focal plants (25 families × 3 neighbour treatments × 3 replicates) and 900 neighbours.

To test for the effects of competition and inbreeding depression, we simultaneoulsy grew additional plants in solitary treatments (i.e. without neighbours) in a 6" (1.6 l) round pot, replicated twice for outcrossed and selfed plants from each family ($n = 50$; 25 families × 2 mating systems).

We randomly distributed pots into five blocks, with each family represented at least twice per block. Following standard conditions for growing *M. guttatus* in the greenhouse, we bottom-watered pots to saturation by flooding with RO water for 1 hour daily. We fertilized pots using water-soluble 20-20-20 fertilizer (Master Plant-Prod). The greenhouse was held on a 16 : 8 light cycle and at 21°C day/18°C night for the duration of the experiment. To account for minor greenhouse environmental differences, we rotated blocks three times weekly, haphazardly redistributing the pots within each block during rotation.

(c) Phenotypic measures

We measured a suite of vegetative and floral traits in focal plants at early (4 weeks post-germination), reproductive (6 weeks post-germination) and post-reproductive (9 weeks post-germination) stages. We quantified clonality by recording the number of stolons and the length and thickness of the longest stolon. To quantify vegetative traits, we recorded the number of nodes and branches, stem thickness (at the midpoint between the first and second nodes) and the length of the first true leaf. For reproductive traits, we recorded the date and node of first flowering, measured the corolla length and width of the flower from the third flowering node, and counted the cumulative number of open and spent flowers at week 6 and week 9. In addition, we recorded the number of flowers on the four neighbours in each pot (week 6). This species sets very little autonomous seed in greenhouse conditions, so we do not measure fruiting or seed set. Of the 225 focal plants, 22 plants never flowered and were excluded from analyses of flowering (self-kin treatment: 8 plants; outcross-kin treatment: 5 plants; non-kin treatment: 9 plants). These were excluded because we expect that failing to transition to flower is a different process to low flower investment. Although plants are perennial, their growth slows, their leaves senesce and they stop producing new flowers after about 9 weeks in the greenhouse (in nature, their above-ground material senesces at the end of summer). Thus, after week 9, we separated each focal plant into clonal stolons and rosette (all other vegetative and floral material) and placed them in paper bags. We harvested the four neighbours from each pot in a single paper bag. Plants were dried at 65°C for 4 days. We weighed all samples on an analytical balance (Mettler-Toledo).

(d) Data analysis

(i) Competitive tolerance and genetic variation

To determine whether plants experienced competition, we used a test of tolerance. Tolerance of competition is defined as the ability to preserve fitness from non-competitive settings in competitive ones and is conventionally quantified as the fitness of plants grown in competition relative to the fitness of the same genotype when grown alone [42]. To this end, we compared the values of fitness components [43] for focal plants growing with non-kin neighbours to focal plants from the same family growing alone. We evaluated the effects of competition on flower number and clonal biomass using a general linear mixed model in the *lme4* package [44] in R [45] with neighbour presence/absence as a fixed effect and random slopes and intercepts for the family to account for genetic variation in tolerance. To test the significance of random effects, we used log-likelihood ratio tests between full models and reduced models [46].

(ii) Allocation responses to kin versus non-kin neighbours

To determine whether focal plants adjusted their allocation in response to their neighbours, we tested whether flower number and stolon biomass depended on neighbour identity, accounting for plant size in the model. We constructed linear mixed models with either flower number or clonal biomass (both log-transformed) as the response variable, and neighbour type (self-kin, outcross-kin or non-kin) as a fixed effect. We included the number of nodes of the focal plant (week 6) as a covariate for plant size because we were interested in relative allocation to sexual and clonal reproduction. Node number was highly associated with other measures of plant size (e.g. biomass; $F_{1,\,219.06} = 424.65$; $p < 0.001$). We included family as a random effect. We used linear mixed-effect models (*lme4*) and the *emmeans* package [47] to compare among fixed effects and log-likelihood ratio tests between full models and reduced models to test for significance.

We next tested whether the productivity of the neighbourhood affected focal plant responses differently depending on the relatedness of their neighbour competitors. We tested for an interaction between the fixed effects of treatment (self sibs, outcrossed sibs or non-kin neighbours) and either total neighbour flowering or total neighbour biomass. The models were fit with a response variable of either the number of flowers or the biomass of stolons produced by the focal plant (both log-transformed). We included focal plant size as a covariate and family as a random effect. We used log-likelihood ratio tests between full models and reduced models to test for significance.

(iii) Potential contributors to allocation differences

We evaluated potential factors influencing the plasticity in allocation across treatments. We first tested whether the results could be due to more efficient niche partitioning of soil resources between plants in the non-kin treatments compared with plants growing with relatives. Under niche partitioning theory, unrelated plants share a lower overlap in resource needs, which could effectively give the focal plant in non-kin treatments access to more resources and account for differences in allocation between kin and non-kin groups. To test this, we compared the total above-ground biomass of non-kin pots to kin pots. We used a linear mixed model with family as a random effect and treatment as a fixed effect. Additionally, we tested whether the productivity of the neighbours differed between treatments (i.e. excluding focal plants) for both the number of flowers and total above-ground biomass, using a linear model with treatment as a main effect. Second, we tested whether inbreeding depression negatively affected the performance of selfed plants compared with outcrossed plants. To do this, we used the solitary plants and compared the trait values between selfed and outcrossed individuals (fixed effect of the mating system) with a random effect of family. Note that we could not do this analysis using the plants in the neighbour treatments, as we did not have a treatment that varied the mating system of the focal plant independent of the mating system of its neighbours.

3. Results

(a) Competitive tolerance and genetic variation

We compared the fitness components (flower number and stolon biomass) of a focal plant growing alone with those of a focal plant surrounded by non-kin neighbours. Plants grown alone produced significantly more flowers and more stolons than those in the non-kin competition treatment (flowers: $F_{1,67.05} = 52.13$, $p < 0.001$; stolons: $F_{1,74.40} = 93.36$, $p < 0.001$). All families had lower trait values when grown in competition than when grown alone, and there was no significant interaction between treatment and family (flowers: $X^2 = 23.18$, $p = 0.20$; stolons: $X^2 = 21.21$, $p = 0.55$). There was significant genetic variation in fitness-related traits (main effect of family, flowers: $X^2 = 211.12$, $p < 0.001$; stolons: $X^2 = 215.73$, $p < 0.001$).

(b) Response to non-kin versus kin neighbours

Plants that were surrounded by non-kin neighbours allocated more to flowering than plants that were surrounded by either selfed-sibling or outcrossed-sibling neighbours (figure 1A; table 1A). On average, the flowering allocation for plants in non-kin treatments was 20.1 (95% CI = 19.0–21.3), compared to 18.3 (95% CI = 17.3–19.4) for outcross or 17.6 (95% CI = 16.6–18.7) for self-treatment. The onset of flowering did not differ significantly between treatments (table 2; $F_{2,198} = 2.75$, $p = 0.06$), although selfed plants flowered slightly later than outcrossed ones (table 2). Across all recorded floral traits—corolla length, corolla width, the number of flowers on the focal plant at peak flowering (week 6) and the number of flowers at end of life (week 9)—individuals surrounded by non-kin neighbours had the highest mean trait values (table 2).

We expected that focal plants would increase allocation to clonality in the presence of non-kin neighbours compared with either selfed-sibling or outcrossed-sibling kin. As predicted, we found a significant effect of neighbour treatment (table 1B; figure 1B) on stolon biomass, accounting for plant size in the model. Focal plants with non-kin neighbours allocated the most to stolon biomass (mean = 3.44; 95% CI = 2.89–4.06), compared with focal plants surrounded by outcross-sibs (mean = 2.65; 95% CI = 2.19–3.16) or those neighboured by self-sibs (mean = 2.52; 95% CI = 2.09–3.01). Focal plants with non-kin neighbours had the greatest trait values across all measures of stolon traits (table 2).

We next tested whether the competitive environment, measured as the size of neighbours, affected the allocation of the focal plants. The number of flowers produced by the focal plant was significantly affected by the interaction between treatment

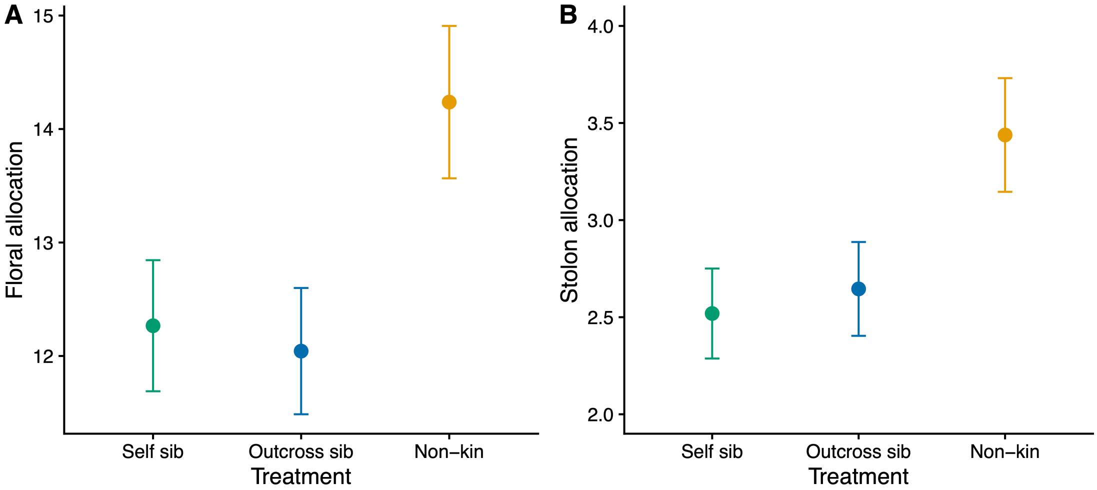

Figure 1. Response of *M. guttatus* plants to kin versus non-kin neighbours for (A) floral allocation (number of open and spent flowers on focal plants after nine weeks, adjusted for plant size) and (B) stolon allocation (stolon biomass of the focal plant after nine weeks, adjusted for plant size). Panels show model-adjusted means and standard errors; see table 1 for statistical details.

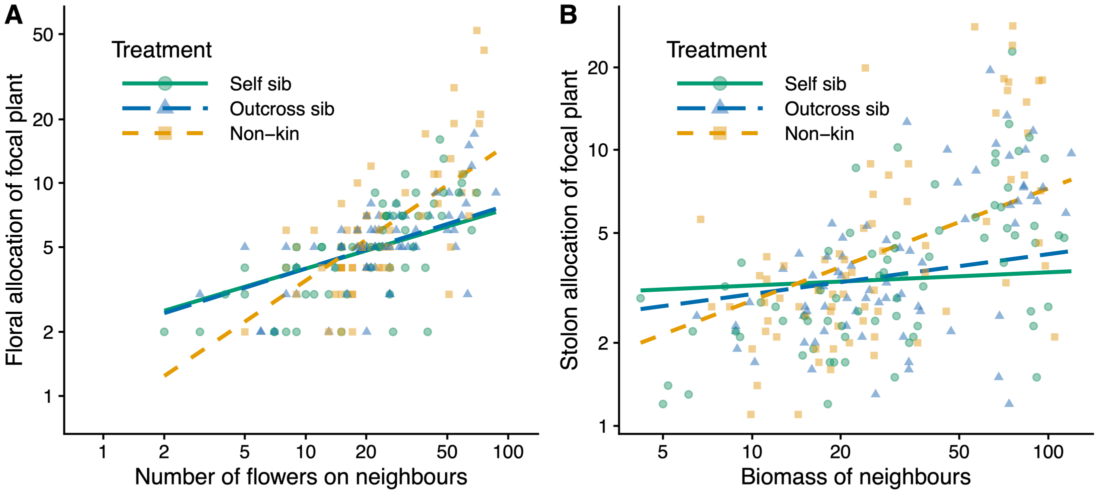

Figure 2. Degree of increase in response to kin versus non-kin neighbours in *M. guttatus* for (A) focal plant floral allocation (number of open flowers on the focal plant after six weeks, adjusted for plant size) in response to the number of flowers produced by plants in its pot, and (B) focal plant stolon allocation (stolon biomass of the focal plant after nine weeks, adjusted for plant size) in response to the total biomass of its neighbours. Panels show raw datapoints with model-adjusted slopes; see table 1 for statistical details. Self siblings in green (solid line, circles); outcross siblings in blue (dotted line, triangles) and non-kin in orange (dashed line, squares).

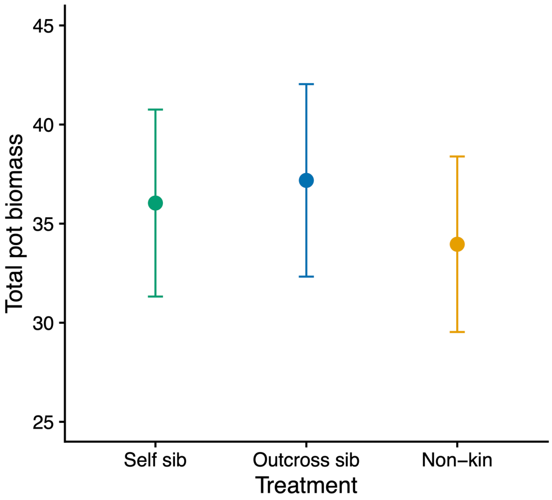

Figure 3. Total biomass of all the plants in a pot for the three treatments of *M. guttatus* to test for ecological niche partitioning. No differences were found between the kin groups: $F_{2,189.3} = 0.57, p = 0.56$.

and the number of flowers produced by neighbours (figure 2A; table 1C). As the number of flowers in the neighbourhood increased, focal plants surrounded by non-kin plants produced more flowers than focal plants neighboured by either self-sibs

Table 1. Model of the effect of neighbour relatedness on (A) flowering allocation, (B) stolon allocation, (C) focal plant flower allocation in response to neighbour flower number and (D) stolon allocation in response to neighbour biomass. Models use maximum likelihood GLMMs, with a random effect for family. (A) and (B) show the fixed effects of treatment and plant size (number of nodes at week 6), pairwise comparisons among treatments (*p*-values adjusted for multiple testing) and random effects of family and its interaction with treatment. (C) and (D) show the fixed effects of treatment and neighbour flower or stolon production, their interaction and a random effect of family. Bold *p*-values indicate significant effects.

		condition	F/X^2	d.f.	*p*-value
(A)	flowering allocation				
		treatment flowering allocation	4.88	2, 181.07	**0.009**
		self versus out	0.316	183	0.947
		self versus non-kin	−2.520	186	**0.034**
		out versus non-kin	−2.874	182	**0.013**
		number of nodes	708.71	1, 139.53	**<0.001**
		family	338.43	1	**<0.001**
		family × treatment	6.42	1	0.267
(B)	stolon allocation				
		treatment	5.36	2, 191.42	**0.005**
		self versus out	−0.462	191	0.889
		self versus non-kin	−3.046	191	**0.007**
		out versus non-kin	−2.564	192	**0.029**
		number of nodes	158.19	1, 176.01	**<0.001**
		family	144.24	1	**<0.001**
		family x treatment	7.52	1	0.185
(C)	flowering response				
		treatment	3.68	2, 182	**0.027**
		neighbour flowers	66.48	1, 182	**<0.001**
		treatment × neighbour flowers	5.76	2, 182	**0.004**
		number of nodes	37.10	1, 182	**<0.001**
		family	27.38	1	**<0.001**
(D)	stolon response				
		treatment	3.22	2, 200.97	**0.042**
		neighbour biomass	13.23	1, 141.94	**<0.001**
		treatment × neighbour biomass	5.77	2, 201.52	**0.004**
		number of nodes	85.35	1, 196.47	**<0.001**
		family	2.74	1	**0.049**

or outcross-sibs (figure 2A). Similarly, when we compared the clonal biomass of the focal plant to the total biomass of their neighbours, we found a significant interaction between treatment and neighbour biomass (table 1B). Focal plants responded to the presence of high-biomass non-kin neighbours by increasing their own clonal biomass more relative to those surrounded by either type of kin neighbours (figure 2B).

(c) Potential contributors shaping allocation

(i) Niche partitioning

It is possible that the increase in allocation to flowers and stolons of focal plants in the presence of non-kin neighbours is due to lower niche overlap and, therefore, greater resource access for non-kin plants. We tested this by comparing the total above-ground biomass of all plants in a pot between treatments. We found that pots in the three treatments had very similar biomass (figure 3) and that there was no significant difference between treatments (treatment effect: $F_{2,189.3} = 0.57$, $p = 0.56$). Similarly, there was no difference in the productivity of the neighbours (i.e. excluding focal plants) between treatments for either the number of flowers on neighbours (self-sib mean = 2.59, 95% CI = 2.40–2.78; outcross-sib mean = 2.86, 95% CI = 2.67–3.05; non-kin mean = 2.80, 95% CI = 2.60–2.99; treatment effect: $F_{2,222}= 2.10$, $p = 0.13$) or biomass of neighbours (self-sib mean = 3.39, 95% CI = 3.21–3.57; outcross-sib mean = 3.44, 95% CI = 3.26–3.61; non-kin mean = 3.27, 95% CI = 3.10–3.45; treatment effect: $F_{2,220}= 0.89$, $p = 0.41$). Thus, we find no support for niche partitioning as an explanation for our results.

Table 2. Trait mean values (min, max) for floral, stolon and vegetative traits for focal plants of *M. guttatus* grown in neighbour treatments in the greenhouse.

trait	neighbour treatment		
	self sibs	outcross sibs	non-kin
floral traits—sample size	67	70	66
corolla length (second flower)	34.8 (19, 45.5)	36.5 (21, 49)	37 (28, 47)
corolla width (second flower)	26.5 (12.3, 38.9)	28.8 (15.5, 43)	29 (19.1, 41)
number flowers (week 6)	3.6 (0, 15)	4.2 (0, 16)	6 (0, 51)
number flowers (week 9)	15.7 (0, 93)	14.9 (0, 52)	18.5 (0, 124)
first flowering (Julian day)	78.6 (73, 84)	78.0 (72, 84)	77.7 (71, 84)
stolon traits—sample size	73	73	74
number stolons (week 6)	3.4 (0, 6)	3.3 (0, 6)	3.7 (0, 7)
stolon width (week 6)	1.3 (0.5, 2.8)	1.3 (0.5, 2.6)	1.4 (0.4, 2.9)
number stolons (week 9)	4 (0, 8)	4 (0, 7)	4.3 (0, 8)
stolon length (week 9)	69.9 (5.4, 345)	83.8 (2, 460)	89.4 (12.1, 430)
stolon biomass	0.3 (0, 2.2)	0.3 (0, 1.8)	0.5 (0, 2.7)
vegetative traits—sample size	75	75	75
stem thickness (week 6)	2.79 (0.97, 7.11)	2.88 (0.66, 6.84)	2.89 (0.94, 6.87)
number nodes (week 6)	10.07 (4, 16)	10.19 (3, 15)	9.88 (3, 15)
leaf length (week 6)	42.25 (11, 96.5)	43.93 (10.5, 87)	45.45 (11.5, 100)
number branches (week 6)	2.51 (0, 8)	2.68 (0, 9)	2.35 (0, 7)
rosette biomass	0.4 (0, 3.0)	0.4 (0, 1.5)	0.4 (0, 2.4)

(ii) Inbreeding depression

In line with our predictions, we found substantial evidence for a decline in fitness components due to inbreeding. Using only plants grown in the solitary treatment, we found that selfed plants were smaller than their outcrossed counterparts for almost all phenotypic traits measured, and many of these differences were significant (electronic supplementary material, table S2).

4. Discussion

Competitive interactions among plants within a neighbourhood are a major feature of plant ecology, physiology and evolution. Within-neighbourhood competition can reduce individual fitness because increased competitive allocation frequently comes at the cost of reproductive output [48]. Yet, individuals who reduce their own competitive measures cede resources to their neighbours, incurring even larger fitness costs (a 'tragedy of the commons' [21]). However, when neighbours are kin, reducing competitive measures can increase indirect fitness, resulting in selection for cooperative strategies [17,49]. Consistent with this, we found that individuals of *M. guttatus* reduced floral and clonal allocation in the presence of kin compared with when they were surrounded by non-kin neighbours.

Flowers are expensive structures to produce and maintain [26,50], but their costs are typically balanced by increased fitness through pollinator attraction and visitation [25]. In general, plants that invest in larger floral displays increase their share of visits from pollinators and have greater seed set and pollen transfer success [51–53]. One of our main results was that focal plants increased floral advertisement when surrounded by non-kin. We further found that the degree of increasing floral display differed depending on the neighbourhood: focal flowers increased their own floral display in high-flowering, non-kin pots, while those surrounded by kin showed a more muted response to the advertisement of their neighbours. This contrasts with results in the self-incompatible annual *Moricandia moricandioides*, where focal individuals increased floral advertisement in the presence of kin [18]. In their study, increased flowering suggested a cooperative 'magnet effect' to increase the attractiveness of a patch with related individuals to pollinators. Although neither their study nor our present study examines the mechanism behind the pattern of flowering, the contrasting results may be due to differences in pollinator behaviour, spatial genetic structure, life history or mating systems.

Patches with a high incidence of relatives and local pollen dispersal experience biparental inbreeding (mating between relatives). Both geitonogamy (selfing between flowers on the same plant) and biparental inbreeding increase with long visitation sequences encouraged by large displays of attractive flowers [54,55], and floral display size and selfing correlate positively [30,56–58]. Biparental inbreeding requires localized pollinator movements and spatial genetic structure [59]. The species we have studied here (*M. guttatus*) is one of a handful of species where the incidence of biparental inbreeding has been investigated in natural conditions. In two very large annual populations, no evidence of spatial genetic structure and biparental inbreeding was found [60], while in perennial populations there was evidence for spatial genetic structure and biparental inbreeding

[39,61]. The consequences of biparental inbreeding will depend on the expression of inbreeding depression, which is substantial in *M. guttatus* [36,62], and also documented here in differences between traits in selfed versus outcrossed plants. Together, this lends support for the interpretation that plants growing in dense patches with kin experience less benefit from increasing their floral display compared with plants growing with non-kin when inbreeding depression and competition are influential social forces.

The study of spatial aggregation in populations goes back to the early days of plant ecology [63], and spatial aggregation of ramets belonging to the same genet is ubiquitous in clonal plants [64]. Ramets of clonal plants are able to discriminate between ramets that are physiologically connected to them and other ramets that are detached from them [65] and alter their growth in response [66]. In a study on wild strawberries, the physical connection between clones induced them to segregate their roots, significantly increasing performance [67]. Our results here provide evidence that plants may adjust their stolon growth in response to whether their neighbours are kin or non-kin. In line with expectations from previous studies on ramet growth (e.g. [68]), plants surrounded by non-kin had significantly greater stolon allocation. Furthermore, focal individuals surrounded by non-kin increased the degree of their own stolon size as their neighbours did, but plants surrounded by kin showed no such response. The ability to recognize and avoid competition between relatives may have consequences for the allocation of resources within individuals and for the emerging spatial structure in populations.

Our main results provide evidence of kin recognition, but without measuring the fitness consequences of the change in allocation, it does not necessarily imply cooperation. Because we examined focal plant responses under greenhouse conditions, we could not track the resulting fruit and seed set. Our measurements of competitive outcomes were restricted to traits that are components of fitness, whereas for kin selection the responses must ultimately increase a focal individual's inclusive fitness [69]. Here, we used a perennial population because we expected spatial structuring in clonal populations to promote kin-discriminatory behaviour, and we were interested in plasticity in clonality. The limitation of using a perennial is that there could be trade-offs between allocation in one year and future survival and reproduction [70]. Although we found that the presence of kin affected floral and clonal investment at multiple life stages (i.e. early life, peak flowering and post-reproduction), ultimately we only looked at a single growing season. Greater floral and clonal allocation in non-kin treatments may be exacerbated by a longer growing season or balanced by future reproductive costs; future work in perennial *M. guttatus* on demographics and long-term survival would be necessary to establish the fitness consequences of adjusting allocation. It is also possible that kin discrimination, resource competition and competitive asymmetry are co-occurring processes, the exact outcomes of which will depend on an individual's resulting inclusive fitness [9,69] and life-history strategy.

A pattern where competitive asymmetry between dissimilar genotypes leads to reduced productivity can occur through a mathematical expectation known as Jensen's inequality [71]. When there are saturating nonlinear relations between a trait and fitness, greater trait variance will inevitably result in lower fitness. Previous studies are equivocal: in one case, this phenomenon explained a pattern of lower fitness in non-kin groups [72]; in another, no difference between non-kin and kin may be due to a lack of nonlinearity [73], or this phenomenon may not be involved [74]. Likewise, we do not believe this explanation accounts for our findings here. For our two primary traits of interest—flowering and clonal investment—we find linear relations with plant size (number of nodes measured at either four weeks or six weeks, or final biomass). For the latter measures of plant size, focal plants growing with non-kin neighbours were slightly smaller than when growing with kin, and yet they invested more in competitive traits of flower display and stolon colonization (table 2). Thus, it is unlikely that differences in allocation between kin treatments are because non-kin groups included inferior or superior neighbour genotypes.

Ecological niche partitioning theory proposes that a reduction in the degree of niche overlap between unrelated individuals reduces competition by maximizing resource use, leading to increased growth in patches with unrelated genotypes [22,75]. Our results do not provide support for this phenomenon—the total biomass of non-kin pots did not differ from that of kin pots. Because we wanted to replicate possible interactions in nature, our experiment used families of plants created from a single source population and so even our 'unrelated' plants may not be too distantly related. It is possible that with more dissimilar genotypes we may have found support for niche partitioning.

The effects of kin discrimination within related patches can have widespread implications for the genetic structuring of populations, for instance leading to spatial structuring and reducing heterogeneity of patches within a population [9]. Even with this, the resulting phenotypic outcomes of kin discrimination may change across species, environmental contexts [18] or levels of resource availability [76–78]. Despite the complex consequences of neighbour associations on the fitness of individual plants, few studies have investigated how within-patch interactions may be shaped by kin responses in nature. We look forward to future work in the field that investigates these processes and measures the inclusive fitness of individuals in natural conditions.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The doi for our data is: https://doi.org/10.5061/dryad.ns1rn8q3f. [79].

Supplementary material is available online [80].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. I.L.: data curation, formal analysis, funding acquisition, investigation, writing—original draft, writing—review and editing; J.F.: conceptualization, data curation, formal analysis, funding acquisition, investigation, project administration, supervision, writing—original draft, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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References

1. Callaway RM, Pennings SC, Richards CL. 2003 Phenotypic plasticity and interactions among plants. *Ecology* **84**, 1115–1128. (doi:10.1890/0012-9658(2003)084[1115:ppaiap]2.0.co;2)
2. Bell DL, Galloway LF. 2007 Plasticity to neighbour shade: fitness consequences and allometry. *Funct. Ecol*. **21**, 1146–1153. (doi:10.1111/j.1365-2435.2007.01327.x)
3. Gruntman M, Groß D, Májeková M, Tielbörger K. 2017 Decision-making in plants under competition. *Nat. Commun*. **8**, 2235. (doi:10.1038/s41467-017-02147-2)
4. Brunet J. 1996 Male reproductive success and variation in fruit and seed set in *Aquilegia caerulea* (Ranunculaceae). *Ecology* **77**, 2458–2471. (doi:10.2307/2265746)
5. Lundholm JT, Aarssen LW. 1994 Neighbour effects on gender variation in *Ambrosia artemisiifolia*. *Can. J. Bot*. **72**, 794–800. (doi:10.1139/b94-101)
6. Ballaré CL, Scopel AL, Sánchez RA. 1990 Far-red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. *Science* **247**, 329–332. (doi:10.1126/science.247.4940.329)
7. Schmitt J, Stinchcombe JR, Heschel MS, Huber H. 2003 The adaptive evolution of plasticity: phytochrome-mediated shade avoidance responses. *Integr. Comp. Biol.* **43**, 459–469. (doi:10.1093/icb/43.3.459)
8. Levin DA, Kerster HW. 1971 Neighborhood structure in plants under diverse reproductive methods. *Am. Nat*. **105**, 345–354. (doi:10.1086/282729)
9. Anten NPR, Chen BJW. 2021 Detect thy family: mechanisms, ecology and agricultural aspects of kin recognition in plants. *Plant Cell Environ*. **44**, 1059–1071. (doi:10.1111/pce.14011)
10. Hamilton WD. 1964 The genetical evolution of social behaviour. I. *J. Theor. Biol*. **7**, 1–16. (doi:10.1016/0022-5193(64)90038-4)
11. Lehmann L, Keller L. 2006 The evolution of cooperation and altruism: a general framework and a classification of models. *J. Evol. Biol*. **19**, 1365–1376. (doi:10.1111/j.1420-9101.2006.01119.x)
12. Dudley SA. 2015 Plant cooperation. *AoB Plants* **7**, plv113. (doi:10.1093/aobpla/plv113)
13. Kelly JK. 1996 Kin selection in the annual plant *Impatiens capensis*. *Am. Nat*. **147**, 899–918. (doi:10.1086/285885)
14. Biedrzycki ML, Jilany TA, Dudley SA, Bais HP. 2010 Root exudates mediate kin recognition in plants. *Commun. Integr. Biol*. **3**, 28–35. (doi:10.4161/cib.3.1.10118)
15. Crepy MA, Casal JJ. 2015 Photoreceptor-mediated kin recognition in plants. *New Phytol*. **205**, 329–338. (doi:10.1111/nph.13040)
16. Dudley SA, File AL. 2007 Kin recognition in an annual plant. *Biol. Lett*. **3**, 435–438. (doi:10.1098/rsbl.2007.0232)
17. Murphy GP, Dudley SA. 2009 Kin recognition: competition and cooperation in *Impatiens* (*Balsaminaceae*). *Am. J. Bot*. **96**, 1990–1996. (doi:10.3732/ajb.0900006)
18. Torices R, Gómez JM, Pannell JR. 2018 Kin discrimination allows plants to modify investment towards pollinator attraction. *Nat. Commun*. **9**. (doi:10.1038/s41467-018-04378-3)
19. Torices R, DeSoto L, Narbona E, Gómez JM, Pannell JR. 2021 Effects of the relatedness of neighbours on floral colour. *Front. Ecol. Evol*. **9**, 589781. (doi:10.3389/fevo.2021.589781)
20. Schoener TW. 1983 Field experiments on interspecific competition. *Am. Nat*. **122**, 240–285. (doi:10.1086/284133)
21. Hardin G. 1968 The tragedy of the commons: the population problem has no technical solution; it requires a fundamental extension in morality. *Science* **162**, 1243–1248.
22. File AL, Murphy GP, Dudley SA. 2012 Fitness consequences of plants growing with siblings: reconciling kin selection, niche partitioning and competitive ability. *Proc. R. Soc. B* **279**, 209–218. (doi:10.1098/rspb.2011.1995)
23. Goddard EL, Varga S, John EA, Soulsbury CD. 2020 Evidence for root kin recognition in the clonal plant species *Glechoma hederacea*. *Front. Ecol. Evol*. **8**. (doi:10.3389/fevo.2020.578141)
24. Rautiainen P, Koivula K, Hyvärinen M. 2004 The effect of within-genet and between-genet competition on sexual reproduction and vegetative spread in *Potentilla anserina* ssp. *egedii*. *J. Ecol*. **92**, 505–511. (doi:10.1111/j.0022-0477.2004.00878.x)
25. Klinkhamer PGL, de Jong TJ, de Bruyn GJ. 1989 Plant size and pollinator visitation in *Cynoglossum officinale*. *Oikos* **54**, 201. (doi:10.2307/3565267)
26. Andersson S. 2000 The cost of flowers in *Nigella degenii* inferred from flower and perianth removal experiments. *Int. J. Plant Sci*. **161**, 903–908. (doi:10.1086/317558)
27. Moeller DA. 2004 Facilitative interactions among plants via shared pollinators. *Ecology* **85**, 3289–3301. (doi:10.1890/03-0810)
28. Hegland SJ. 2014 Floral neighbourhood effects on pollination success in red clover are scale-dependent. *Funct. Ecol*. **28**, 561–568. (doi:10.1111/1365-2435.12223)
29. Sun S, Broom M, Johanis M, Rychtář J. 2021 A mathematical model of kin selection in floral displays. *J. Theor. Biol*. **509**, 110470. (doi:10.1016/j.jtbi.2020.110470)
30. Harder LD, Barrett SCH. 1995 Mating cost of large floral displays in hermaphrodite plants. *Nature* **373**, 512–515. (doi:10.1038/373512a0)
31. Harder LD, Richards SA, Routley MB. 2008 Effects of reproductive compensation, gamete discounting and reproductive assurance on mating-system diversity in hermaphrodites. *Evolution* **62**, 157–172. (doi:10.1111/j.1558-5646.2007.00272.x)
32. Ritland K. 1989 Correlated Matings in the Partial Selfer *Mimulus guttatus*. *Evolution* **43**, 848. (doi:10.2307/2409312)
33. Twyford AD, Wong ELY, Friedman J. 2020 Multi-level patterns of genetic structure and isolation by distance in the widespread plant *Mimulus guttatus*. *Heredity* **125**, 227–239. (doi:10.1038/s41437-020-0335-7)
34. Waser NM, Vickery RK, Price MV. 1982 Patterns of seed dispersal and population differentiation in *Mimulus guttatus*. *Evol. N. Y*. **36**, 753. (doi:10.2307/2407888)
35. Willis JH. 1993 Partial self-fertilization and inbreeding depression in two populations of *Mimulus guttatus*. *Heredity* **71**, 145–154. (doi:10.1038/hdy.1993.118)
36. Willis JH. 1993 Effects of different levels of inbreeding on fitness components in *Mimulus guttatus*. *Evolution* **47**, 864. (doi:10.2307/2410190)
37. Carr DE, Dudash MR. 1995 Inbreeding depression under a competitive regime in *Mimulus guttatus*: consequences for potential male and female function. *Heredity* **75**, 437–445. (doi:10.1038/hdy.1995.159)
38. Brown KE, Kelly JK. 2020 Severe inbreeding depression is predicted by the ‘rare allele load’ in *Mimulus guttatus*. *Evolution (N Y)* **74**, 587–596. (doi:10.1111/evo.13876)
39. Leclerc-Potvin C, Ritland K. 1994 Modes of self-fertilization in *Mimulus guttatus* (Scrophulariaceae): a field experiment. *Am. J. Bot*. **81**, 199. (doi:10.2307/2445634)
40. Carr DE, Fenster CB, Dudash MR. 1997 The relationship between mating-system characters and inbreeding depression in *Mimulus guttatus*. *Evol. N. Y*. **51**, 363. (doi:10.2307/2411108)
41. Steinecke CM. 2023 Selection and genetic constraints on clonal investment in a perennial plant. Master’s thesis, Queen’s University.
42. Cahill JF, Kembel SW, Gustafson DJ. 2005 Differential genetic influences on competitive effect and response in *Arabidopsis thaliana*. *J. Ecol.* **93**, 958–967. (doi:10.1111/j.1365-2745.2005.01013.x)
43. Wadgymar SM, Sheth S, Josephs E, DeMarche M, Anderson J. 2024 Defining fitness in evolutionary ecology. *IJPS*. **185**, 218–227. (doi:10.1086/729360)
44. Douglas Bates MM, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *Stat. Softw*. (doi:10.18637/jss.v067.i01)
45. R Core Team. 2021 R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
46. Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009 *Mixed effects models and extensions in ecology with R*. New York, NY: Springer.
47. Lenth R, Singmann H, Love J, Buerkner P, Herve M. 2021 Emmeans: estimated marginal means, aka least-squares means R package version 1.5.1

48. Rankin DJ, Bargum K, Kokko H. 2007 The tragedy of the commons in evolutionary biology. *Trends Ecol. Evol*. **22**, 643–651. (doi:10.1016/j.tree.2007.07.009)
49. Zea-Cabrera E, Iwasa Y, Levin S, Rodríguez-Iturbe I. 2006 Tragedy of the commons in plant water use. *Water Resour. Res*. **42**. (doi:10.1029/2005wr004514)
50. Teixido AL, Valladares F. 2014 Large flowers tend to be short-lived in Mediterranean ecosystems: Insights from three *Cistus* species. *Plant Biosyst. Int. J. Deal. All Asp. Plant Biol*. **148**, 1211–1220. (doi:10.1080/11263504.2014.948095)
51. Mitchell RJ. 1994 Effects of floral traits, pollinator visitation, and plant size on *Ipomopsis aggregata* fruit production. *Am. Nat*. **143**, 870–889. (doi:10.1086/285637)
52. Vaughton G, Ramsey M. 1998 Floral display, pollinator visitation and reproductive success in the dioecious perennial herb *Wurmbea dioica* (*Liliaceae*). *Oecologia* **115**, 93–101. (doi:10.1007/s004420050495)
53. Thompson JD. 2001 How do visitation patterns vary among pollinators in relation to floral display and floral design in a generalist pollination system? *Oecologia* **126**, 386–394. (doi:10.1007/s004420000531)
54. de Jong TJ, Waser NM, Klinkhamer PG. 1993 Geitonogamy: the neglected side of selfing. *Trends Ecol. Evol.* **8**, 321–325. (doi:10.1016/0169-5347(93)90239-L)
55. Snow AA, Spira TP, Simpson R, Klips RA. 1996 The ecology of geitonogamous pollination. In *Floral biology: studies on floral evolution in animal-pollinated plants* (eds DG Lloyd, SCH Barrett), pp. 191–216. Boston, MA: Springer US. (doi:10.1007/978-1-4613-1165-2_7)
56. Crawford TJ. 1984 The estimation of neighbourhood parameters for plant populations. *Heredity* **52**, 273–283. (doi:10.1038/hdy.1984.29)
57. Barrett SCH, Harder LD, Cole WW. 1994 Effects of flower number and position on self-fertilization in experimental populations of *Eichhornia paniculata* (Pontederiaceae). Funct. Ecol. **8**, 526. (doi:10.2307/2390078)
58. Vrieling K, Saumitou- Laprade P, Cuguen J, Van Dijk H, De Jong TJ, Klinkhamer PGL. 1999 Direct and indirect estimates of the selfing rate in small and large individuals of the bumblebee pollinated *Cynoglossum officinale* L (*Boraginaceae*). *Ecol. Lett*. **2**, 331–337. (doi:10.1046/j.1461-0248.1999.00093.x)
59. Griffin CAM, Eckert CG. 2003 Experimental analysis of biparental inbreeding in a self-fertilizing plant. *Evolution (N. Y.)* **57**, 1513–1519. (doi:10.1554/02-649)
60. Kelly JK, Willis JH. 2002 A manipulative experiment to estimate biparental inbreeding in monkeyflowers. *Int. J. Plant Sci*. **163**, 575–579. (doi:10.1086/340735)
61. Ritland K, Ganders FR. 1987 Covariation of selfing rates with parental gene fixation indices within populations of *Mimulus guttatus*. *Evolution* **41**, 760. (doi:10.2307/2408886)
62. Carr DE, Dudash MR. 1996 Inbreeding depression in two species of *Mimulus* (Scrophulariaceae) with contrasting mating systems. *Am. J. Bot*. **83**, 586. (doi:10.2307/2445917)
63. Greig-Smith P. 1964 *Quantitative plant ecology*. Berkeley, CA: University of California Press.
64. Wilhalm T. 1995 A comparative study of clonal fragmentation in tussock-forming grasses. *Abstr Bot* **19**, 51–60.
65. Gruntman M, Novoplansky A. 2004 Physiologically mediated self/non-self discrimination in roots. *Proc. Natl. Acad. Sci*. **101**, 3863–3867. (doi:10.1073/pnas.0306604101)
66. Novoplansky A, Cohen D, Sachs T. 1990 How *portulaca* seedlings avoid their neighbours. *Oecologia* **82**, 490–493. (doi:10.1007/bf00319791)
67. Holzapfel C, Alpert P. 2003 Root cooperation in a clonal plant: connected strawberries segregate roots. *Oecologia* **134**, 72–77. (doi:10.1007/s00442-002-1062-x)
68. Herben T, Novoplansky A. 2008 Implications of self/non-self discrimination for spatial patterning of clonal plants. *Evol. Ecol*. **22**, 337–350. (doi:10.1007/s10682-007-9214-4)
69. Ehlers BK, Bilde T. 2019 Inclusive fitness, asymmetric competition and kin selection in plants. *Oikos* **128**, 765–774. (doi:10.1111/oik.06390)
70. Roach DA, Smith EF. 2020 Life-history trade-offs and senescence in plants. *Funct. Ecol*. **34**, 17–25. (doi:10.1111/1365-2435.13461)
71. Jensen JLWV. 1906 Sur les fonctions convexes et les inégalités entre les valeurs moyennes. *Acta Math*. **30**, 175–193. (doi:10.1007/bf02418571)
72. Simonsen AK, Chow T, Stinchcombe JR. 2014 Reduced plant competition among kin can be explained by Jensen's inequality. *Ecol. Evol.* **4**, 4454–4466. (doi:10.1002/ece3.1312)
73. Masclaux F, Hammond RL, Meunier J, Gouhier-Darimont C, Keller L, Reymond P. 2010 Competitive ability not kinship affects growth of *Arabidopsis thaliana* accessions. *New Phytol*. **185**, 322–331. (doi:10.1111/j.1469-8137.2009.03057.x)
74. Biernaskie JM. 2011 Evidence for competition and cooperation among climbing plants. *Proc. Biol. Sci. B* **278**, 1989–1996. (doi:10.1098/rspb.2010.1771)
75. Milla R, Forero DM, Escudero A, Iriondo JM. 2009 Growing with siblings: a common ground for cooperation or for fiercer competition among plants? *Proc. Biol. Sci.* **276**, 2531–2540. (doi:10.1098/rspb.2009.0369)
76. Fan Y, Zhang R, Zhang Y, Yue M. 2022 The effects of genetic distance, nutrient conditions, and recognition ways on outcomes of kin recognition in *Glechoma longituba*. *Front. Plant Sci*. **13**, 950758. (doi:10.3389/fpls.2022.950758)
77. Fang S, Clark RT, Zheng Y, Iyer-Pascuzzi AS, Weitz JS, Kochian LV, Edelsbrunner H, Liao H, Benfey PN. 2013 Genotypic recognition and spatial responses by rice roots. *Proc. Natl. Acad. Sci*. **110**, 2670–2675. (doi:10.1073/pnas.1222821110)
78. Palmer AG *et al*. 2016 Kin recognition is a nutrient-dependent inducible phenomenon. *Plant Signal. Behav*. **11**, e1224045. (doi:10.1080/15592324.2016.1224045)
79. Lewis I, Friedman J. 2024 Kin discrimination causes plastic responses in floral and clonal allocation. (doi:10.5061/dryad.ns1rn8q3f)
80. Lewis I, Friedman J. 2025 Supplementary material from: Kin discrimination causes plastic responses in floral and clonal allocation. Figshare. (doi:10.6084/m9.figshare.c.7611378)