THE FITNESS CONSEQUENCES OF KIN RECOGNITION RESPONSES

DETERMINING THE FITNESS CONSEQUENCES OF KIN RECOGNITION RESPONSES IN ALLOCATION AND MORPHOLOGICAL TRAITS

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ABSTRACT

Many plant species recognize kin and respond with changes in functional traits. Researchers hypothesize that siblings compete less than strangers. However, no study has directly tested whether siblings are less competitive. Measuring natural selection on kin recognition responses in root allocation and other destructively measured traits is challenging, since trait and fitness cannot be measured on the same individual. Here, a methodology using family-level selection is developed, measuring the trait on one individual and measuring its fitness value using another related individual. Three greenhouse pot experiments were conducted using six *Brassica oleracea* cultivars at two nutrient levels. We investigated whether root allocation and morphological traits were under natural selection. We tested whether or not there was cultivar recognition or resource partitioning in *B. oleracea*. We found that putative competitive traits (size, height, emergence and root allocation) had expected patterns of individual selection for an increase in each trait and group selection for a reduction of each trait. There was no indication that resource partitioning was occurring or that *B. oleracea* could recognize cultivars. However, plants were experiencing competitive interactions within pots. In conclusion, we demonstrate that using family-level selection estimates the fitness consequences of root allocation and morphological traits.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Neighbouring plants often compete for access to aboveground and belowground resources (Casper and Jackson 1997; Smith 1982; Smith 1995). Some plants have limited dispersal (reviewed in Cain et al. 2000), thus offspring are often surrounded by, and therefore competing with closely related individuals (Silvertown and Charlesworth 2009). These are conditions in which kin recognition can develop. Kin recognition is most likely to occur when relatives frequently overlap spatially and temporally (Waldman 1988). This kin recognition can facilitate the evolution of cooperation among relatives (Waldman 1988). Kin recognition responses are hypothesized to prevent costly competitive behaviour towards relatives (Murphy and Dudley 2009) by directing altruistic behaviours or reducing competitive behaviours towards relatives. Behaving altruistically increases the inclusive fitness of the focal individual (Waldman 1988). Many species of plants are plastic to the relatedness of neighbours (Dudley and File 2007; Murphy and Dudley 2009, Biedrzycki et al. 2010; Bhatt et al. 2011; Biernaskie 2011; Lepik et al. 2012; Fang et al. 2013; Marler 2013; Mercer and Eppley 2014; Crepy and Casal 2015). Plants recognise kin through root exudates (Biedrzycki et al. 2010), volatiles (Karban et al. 2013) and photosensory receptors (Crepy and Casal 2015). However, we do not know if kin recognition responses increase fitness. Rather than measuring the fitness consequences of kin recognition responses by comparing the outcome of fitness of sibling and strangers, we argue that to demonstrate kin selection, researchers have to show that the kin recognition responses affect competitive ability. Though we see kin recognition

responses in some plant species, we do not know the competitive value of these morphological and root allocation responses.

As the majority of plants interact socially through resource competition, plant kin recognition studies measure phenotypic plasticity of competitive traits between kin and strangers (Marler 2013; Crepy and Casal 2015; reviewed in Dudley et al. 2013). Plants allocate to different competitive traits when grown under different environmental conditions. In low water or nutrient environments, plants have shown increased root allocation (Dudley and File 2007; Biernaskie 2011). Alternately, in adequate water and nutrient environments, plants have shown increased stem elongation (Dudley and Schmitt 1996; Murphy and Dudley 2009), increased branchiness and allocation to leaves (Murphy and Dudley 2009; File et al. 2012). Stem elongation allows plant leaves to be positioned higher up in the canopy, enabling them to acquire more light (Smith 1995), while increased root proliferation in low nutrient environments allows plants to better forage for nutrients (Casper and Jackson 1997). Depending on the competitive trait expressed by the focal plant and the competitive traits expressed by neighbours, there may be different fitness consequences for the focal plant.

There are two ways to measure the fitness consequences of kin recognition responses. One approach to measuring the fitness consequences of kin recognition responses is to use a fitness-based approach (File et al. 2012). Plants are grown in groups of siblings and groups of strangers and the fitness outcome of the two groups are compared. If kin selection is acting, the group of siblings should have higher fitness than the group of strangers. The problem with the fitness-based approach is that there may be

processes acting in opposition to kin selection. One such process is resource partitioning. Resource partitioning predicts that related individuals will compete more than unrelated individuals because of the increased overlap in resource use (Cheplick and Kane 2004). Thus in competition, unrelated individuals are predicted to have higher fitness than related individuals. A second approach to studying the fitness consequences of kin recognition is to use the trait-based approach. In this approach, natural selection is measured on the trait (Lande and Arnold 1983). An altruistic trait will have a positive effect on the fitness of the individuals in a group (Goodnight et al. 1992), whereas a competitive trait is a selfish trait that will have a positive effect on fitness of an individual.

The evolutionary approach to measuring competitive traits in plants is to measure multilevel selection (Stevens et al. 1995; Aspi et al. 2003; Donohue 2003; Donohue 2004; Weinig et al. 2007; Boege 2010). Multilevel selection considers how the focal plant's fitness is affected by its own phenotype and the phenotype of the group with which the focal plant associates. Utilizing multilevel selection, we can measure how the putative competitive traits that showed kin recognition responses affect the fitness of individuals and the fitness of their neighbours. There are two types of multilevel selection studies: cross-sectional and longitudinal. Performing a cross-sectional study in plants is problematic. One of the consequences of competition in plants is that competition leads to size inequality (Weiner 1985). Thus measuring competitive traits and fitness at the same time can lead to misinterpretation of the results (i.e. it is hard to determine if a plant was tall because it had high fitness or if the plant had high fitness because it was tall).

Unfortunately, using a longitudinal study to measure multilevel selection also poses a problem in plants. Many of the responses to neighbour relatedness have been in root allocation (Dudley and File 2007; Biedrzycki et al. 2010; Bhatt et al. 2011; Biernaskie 2011; Mercer and Eppley 2014), which requires the sacrifice of the plant in order to measure. Therefore, one cannot measure the trait on an individual plant early in life and determine the fitness value later in life. However, a proposed method using family-level selection succeeds in overcoming these challenges through the use of cultivars. Cultivars have been bred to have uniform phenotypes (Brown et al. 2014), therefore we can measure a potential competitive trait early in life on one individual and measure the fitness value later in life on another related individual.

In the following sections, I outline a methodology using family-level selection to measure the fitness consequences of traits that show kin recognition responses. Using this method, I can measure selection on allocation and morphological traits which have been shown to respond to neighbour relatedness.

Aboveground and belowground competition and competitive ability

Plants are sessile organisms that do not choose their growing environment. Plants modify their growth and development based on cues they receive from their competitive environment including light quality (Ballaré 1999; Franklin and Whitelam 2005), presence/absence of roots (Gersani et al. 2001) and volatiles (Karban and Maron 2002; Heil and Karban 2010). Competition between neighbours due to a shared limiting resource triggers phenotypic changes in traits that help acquire those resources. With neighbours, plants allocate resources to leaves, stems and roots to better capture light,

water and nutrients during a competitive encounter (Trinder et al. 2013). Even without neighbours, plants allocate more biomass to leaves when light is limited and more biomass to roots when water and nutrients are limited (McCarthy and Enquist 2007), because plants allocate biomass to organs used in acquiring limiting resources (Freschet et al. 2015).

Aboveground, plants compete for access to light, a source of energy to produce sugars, but light also provides information to a plant about the local environment. Photoreceptors in the leaves perceive the light by absorbing red (R) and blue wavelengths and reflecting far-red (FR) wavelengths. Plants can predict light competition through the R:FR ratio. Neighbours reduce R:FR as they absorb red and reflect far red wavelengths (Ballaré et al. 1990). The focal plant perceives the reduced R:FR and this triggers morphological changes such as stem, internode and petiole elongation (Ballaré et al. 1990, Franklin and Whitelam 2005) to avoid being shaded (Ballaré et al. 1990). Plants also respond to low R:FR by increasing their specific leaf area (SLA), leaf area divided by leaf biomass (Rijkers et al. 2000, Evans and Poorter 2001). These phenotypic changes in the presence of neighbours allow plants to capture more light than their neighbours.

Belowground, plants are competing for resources including water and nutrients. Plants acquire nutrients through their roots, thereby reducing nutrient availability in the surrounding soil (McNickle et al. 2014; Wright et al. 2014) leading to decreased growth and performance of a focal plant (Lamb and Cahill 2008; Wright et al. 2014). However, plants have mechanisms in their roots to anticipate changes in resource availability imposed by surrounding neighbours (Gersani et al. 2001; Maina et al. 2002; O'Brien et al.

2005) and respond by increasing allocation to fine roots (Poorter et al. 2012) to capture more resources. This is an example of a tragedy of the commons. Tragedy of the commons denotes a situation in which one individual gains at the expense of others (Hardin 1968; Gersani et al. 2001). The focal plant has greater access to belowground resources through increased root growth at the expense of neighbouring plant's ability to acquire those same resources.

Competition directly results in one plant negatively affecting the performance or fitness of a neighbouring plant (Fowler 1986). The degree to which the fitness of a neighbouring plant is reduced depends on its competitive ability. Competitive ability can be broken down into two elements: competitive response and competitive effect (Goldberg and Fleetwood 1987; Goldberg 1990; Goldberg and Landa 1991; Wang et al. 2010). Competitive response is the ability of a plant to tolerate competitors and to perform well in their presence. Measuring competitive response is done by comparing the fitness of a focal plant grown with the competitor relative to the fitness of a focal plant grown alone. Competitive effect is the ability of the focal plant to decrease the fitness of competitors and is measured as the fitness of the competitor grown in competition with a focal plant relative to the fitness of the competitor when grown alone. Differences in individual competitive ability, like all traits, are caused by variation in genes, the environment and interactions between genes and the environment (Aarssen 1992). Depending on resource availability and social environment, we may see different outcomes of competition.

Kin recognition responses are potential competitive traits

Traits that show plasticity responses to relatedness are potentially competitive. If a plant recognizes kin, it is hypothesized that traits expressed in plants grown with strangers are competitive, while traits expressed in plants grown with siblings are altruistic (Murphy and Dudley 2009; File et al. 2012) although this is not always the case (see Lepik et al. 2012). The competitive traits that strangers express depend on the competitive environment of the species.

Some of the variation in kin recognition responses has been attributed to the ecology of the species being studied (Dudley et al. 2013). In a high light, low water and nutrient environment, related *Cakile edentula* plants had lower root allocation compared to when grown with unrelated plants (Dudley and File 2007). *Arabidopsis thaliana* grows in disturbed sites, rocky areas and in forest openings where light is not limiting (Mitchell-Olds 2001). When *A. thaliana* was exposed to the root exudates of a stranger, more lateral roots were produced than when exposed to the exudates of a sibling or its own secretions (Biedrzycki et al. 2010). *Ipomoea hederacea* which normally grows in environments with high light availability, had lower root mass when grown with siblings compared to when grown with non-siblings (Biernaskie 2011). As these three species are naturally found in environments in which light is not limiting, belowground competition will have an important effect on competitive outcome. Only the group of strangers increased root allocation, a trait that likely give the plant a competitive advantage. Conversely, when light was limiting and nutrients and water were plentiful, *Impatiens pallida*, a forest understory plant, had greater leaf allocation, greater stem elongation and greater

branching when neighbours were strangers compared to siblings (Murphy and Dudley 2009). In this case, strangers changed their aboveground morphology, arguably to increase competitive ability to capture more light. The traits expressed with relatives are hypothesized to be less competitive, as they reduced the negative effect on the fitness of the neighbour. However, the fitness outcomes of these competitive traits depend on the different processes operating during sibling competition.

Kin selection and resource partitioning predict different outcomes of sibling competition

There are two processes that can affect the outcome of sibling competition: resource partitioning and kin selection. Resource partitioning predicts that related individuals will compete more because of the overlap in resource use compared to unrelated individuals (Cheplick and Kane 2004). Kin selection predicts that relatives cooperate (Eberhard 1975). These processes predict opposite fitness outcomes for sibling competition and empirical plant studies have yielded inconsistent results (Donohue 2003; Cheplick and Kane 2004; Karban and Shiojiri 2009; Milla et al. 2009; Masclaux et al. 2010; Biernaskie 2011). Depending on the direction of the fitness outcome, the results from the studies were interpreted as either kin selection or resource partitioning.

Relatives of the same species interacting within an environment can lead to cooperative behaviour through kin selection. As siblings share genes, they can gain indirect fitness by increasing the fitness of a relative (Van Baalen and Rand 1998). According to Hamilton's rule, an altruistic behaviour will evolve if $rB > C$, where r is the relatedness between the actor and the relative, B is the benefit to the relative and C is the

cost to actor (Hamilton 1964). For example, female ground squirrels produce alarm calls to warn relatives that predators are nearby (Sherman 1977; Waldman 1988). These female squirrels are increasing their inclusive fitness by improving the likelihood of survival of related individuals. The male squirrels rarely produced alarm calls as males were rarely surrounded by relatives. In plants, the hypothesis is that kin selection explains cooperation among relatives through competitive behaviour avoidance (File et al. 2012) to increase ones indirect fitness. Thus, groups of relatives should have higher fitness compared to groups of strangers.

Resource partitioning predicts a different outcome than kin selection. Each species has their own niche which allows them to access different limiting resources (Silvertown 2004; Finke and Snyder 2008). The greater the niche overlap between two individuals, the more competition there will be for access to resources. Individuals with different genotypes can have different phenotypes that allow them to access resources in diverse ways (File et al. 2012). In plants, resource partitioning is more complex as plants require the same resources to survive and most plant species acquire these resources in analogous ways (Silvertown 2004). One study suggests that plants partition along niche axes, such as rooting depth in grassland herbs (Mamolos et al. 1995). This means that related individuals that share genes are more likely to compete along the same axis. Therefore, relatives growing together will have relatively lower fitness due to niche overlap and increased competition compared to strangers growing together. Niche partitioning has been known to lead to negative frequency dependence, where the rare genotype performs better than the common genotype in competition (Antonovics & Kareiva 1988).

Confounding results of sibling and stranger competition have been found. Higher reproductive success was seen when *C. edentula* was grown with siblings compared to non-siblings or mixed neighbour groups (Donohue 2003). This provides evidence for kin selection as sibling groups had higher reproductive success. Nonetheless, evidence has also been found for resource partitioning. Sibling competition between sandgrass (*Triplasis purpurea*) plants resulted in reduced growth compared to competition between unrelated plants (Cheplick and Kane 2004). Another species, *Lupinus angustifolius* had lower fitness, produced fewer flowers and as a pot, produced less vegetative biomass when pots contained related individuals compared to pots with strangers (Milla et al. 2009). Both these studies found that groups of strangers performed better in competition, attributing the higher fitness to differential resource use. Although studies looking at the fitness outcomes of sibling and stranger competition have been mixed, to provide support for kin selection, we must show that relatives reduce competitiveness. This is done through multilevel selection, where we can determine if the traits expressed with strangers are competitive traits while traits expressed with siblings are altruistic.

Traits under multilevel selection

A common approach to determine how competitive traits affect fitness is through the use of multilevel selection. Multilevel selection analysis is a variation of Lande and Arnold's (1983) phenotypic selection analysis that evaluates how an individual's phenotype affects its fitness. Phenotypic selection analysis involves regressing relative fitness on phenotypic traits using multivariate regression. Yet plant fitness is not only defined by the phenotype of an individual, but by the phenotype of the group that

individual interacts with (Heisler and Damuth 1987; Goodnight et al. 1992). This distinction means that we can look at natural selection on a trait at multiple levels: at the level of the individual and at the group level (Stevens et al. 1995; Aspi et al. 2003; Donohue 2003; Donohue 2004; Weinig et al. 2007). Individual and group level selection can be determined by using multilevel selection (contextual analysis) where an individual's relative fitness is regressed on the individual's phenotype and the group's mean phenotype. The covariance between the trait and relative fitness gives the strength of selection acting on that trait (Price 1970), broken down to the individual and group levels.

Traits will be selected on differently at the individual and group level depending on whether it is a selfish or altruistic trait. In accordance with kin selection, an altruistic trait should be selected against at the individual level, but selected for at the group level (Goodnight et al. 1992). Since a competitive trait is a selfish trait, it should be favoured at the individual level, but selected against at the group level. Multilevel selection analyses have found that plant size appears to be a competitive trait, as it is favoured at the individual level but not at the group level (Stevens et al. 1995; Aspi et al. 2003; Donohue 2004; Weinig et al. 2007; Boege 2010). As previously discussed, plant height and elongation are known competitive traits. In three studies, height and elongation were selected to increase at the individual level, but decrease at the group level (Donohue 2003; Donohue 2004; Weinig et al. 2007), while another study found that height and elongation were selected to increase only at the individual level (Boege 2010), and yet another study found that height was selected to increase at both the individual and group

level in *Silene tatarica* as to appear more attractive to pollinators (Aspi et al. 2003). These studies all measured selection using phenotypic traits. However, selection can be measured another way using genotypic values (Rausher 1992). Through the use of genotypic selection analysis (family-level selection), one can measure the traits of one individual and determine the fitness value of another individual of the same genotype. This methodology can be applied to putative competitive traits that are measured destructively. Previous multilevel selection studies have looked at the fitness consequences of aboveground morphological traits using multilevel selection analyses, but no one has used family-level selection analyses to look at the fitness consequences of allocation and morphological traits, responses seen in many kin recognition studies.

Outline of this study

The general objective of this work is to better understand the fitness consequences of kin recognition by looking at various traits under selection during intraspecific competition. Kin recognition is a process by which relatives cooperate rather than compete. Although plants grown with kin have different phenotypes to plants grown with strangers, studies have shown mixed fitness outcomes with sibling and stranger competition. However, no kin recognition studies have looked at how individual plant traits and the plant traits of its neighbours affect plant fitness.

To study the fitness consequences of kin recognition we used six cultivars of a highly domesticated species, *Brassica oleracea* (wild field cabbage). No kin recognition studies have yet used *B. oleracea.* However a related plant, rapid cycling *Brassica rapa,* in a preliminary study showed kin recognition responses with two genotypes (S. Dudley,

personal communication, September 2, 2015). Using different *B. oleracea* cultivars with exaggerated plant traits increases the variation to get a more accurate measure of natural selection. *B. oleracea* has high phenotypic variation between cultivars, but little phenotypic variation within each cultivar (Brown et al. 2014), making *B. oleracea* an ideal study species.

To understand better the impact of kin recognition responses on fitness, three experiments were performed using six different *B. oleracea* cultivars. In the first experiment which tested for cultivar recognition, cultivars were grown either alone or with neighbours in soilless mixture in both high and low nutrients. We looked at eight potentially competitive morphological and allocation traits: natural height, meristem elongation, aboveground biomass, specific leaf area, leaf shape, total biomass, stem to leaf allocation and root allocation. To conduct a longitudinal competitive selection analysis of the *B. oleracea* cultivars, we carried out two experiments. Since measuring the biomass of certain above and belowground structures results in the death of the plant, in experiment two, phenotyping, groups of cultivars were grown to the seedling stage in order to phenotype . We obtained for each cultivar the average value of the traits listed previously for the genetic analysis. In experiment three, fitness and competition, groups of cultivars were grown in soil to the juvenile stage to measure fitness. Since the plants had not yet reached reproduction, we measured aboveground biomass as fitness as it is highly correlated with total seed production (Grundy et al. 2004; Soltani et al. 2011; Cheplick 2015). We tested 1) if seedling and juvenile plants of the cultivar have varying phenotypes, 2) if nutrients had an effect on morphological and allocation traits, 3) if *B.*

oleracea were experiencing competition, if there was an effect of neighbour identity and if cultivars differed in competitive ability, 4) whether there was selection acting on functional traits and whether selection differed with nutrient availability, 5) if cultivar recognition, here-on referred to as kin recognition, is observed in *B. oleracea* and 6) if there was frequency dependence due to resource partitioning in *B. oleracea*.

MATERIAL AND METHODS

Study Species

Brassica oleracea subspecies *oleracea* (Brassicaceae) is a perennial wild field cabbage found on limestone and grassy slopes near coastlines (Snogerup et al. 1990). Its feral form is native to the northern coast of Spain, western and northern France, the British Isles and the Helgoland of Germany (Snogerup et al. 1990). *B. oleracea* seeds are heavy and therefore dispersal is limited, although seeds can sometimes be transported by the wind (Snogerup et al. 1990). Artificial selection for exaggerated plant traits has led to high morphological diversity between domesticated *B. oleracea* cultivars (Fig. 1). *B. oleracea* cultivars include many important crops such as brussel sprouts, kai-lan (chinese broccoli), cabbage, cauliflower, collards, broccoli, kale and kohlrabi. We selected six different cultivars for which seeds could be obtained locally and which had exaggerated leaves and stems, traits that might be competitive. The specific modified structures of the six cultivars can be found in Table 1.1. All experimental plants were grown from seed purchased from Ontario Seed Co. Limited (Waterloo, Ontario, Canada).

Figure 1. Examples of artificial selection for leaf, stem, bud and flower traits in *B. oleracea*. The arrow origin indicates what part of the plant has been modified. Figure has been modified from Stromberg (2015).

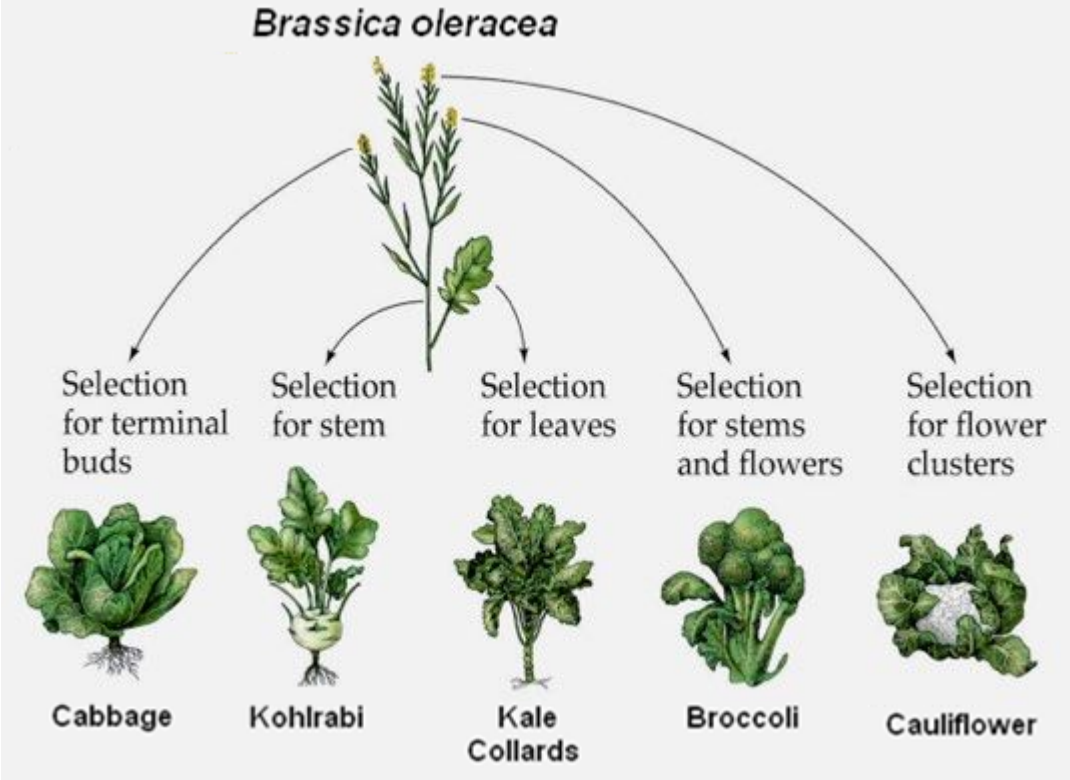

Brassica oleracea
Selection for terminal buds
Selection for stem
Selection for leaves
Selection for stems and flowers
Selection for flower clusters
Cabbage
Kohlrabi
Kale
Collards
Broccoli
Cauliflower

Table 1.1. Summary of the modified structures of the *B. oleracea* cultivars used in all experiments.

Cultivar	**Scientific name**	**Modified structure**
Broccoli	*B. oleracea* var. *italica*	stem, inflorescence and flowering shoots
Cabbage	*B. oleracea* var. *sabauda*	large terminal buds
Cauliflower	*B. oleracea* var. *botrytis*	inflorescence and flowering shoots
Collards	*B. oleracea* var. *viridis*	increased allocation to leaves
Kale	*B. oleracea* var. *sabellica*	increased allocation to leaves
Kohlrabi	*B. oleracea* var. *gongylodes*	enlarged stems

Experiment 1 – Phenotyping seedlings with and without a neighbour

Experimental Design

To determine the phenotypic plasticity responses of six *Brassica oleracea* cultivars, we grew plants either in the presence or absence of neighbours and in either high or low nutrient environments. Between June and July, 2014 under ambient light conditions, cultivars were grown in 8.5 x 8.5 x 8 cm pots in the Biology Greenhouse at McMaster University Hamilton, Ontario, Canada. We tested for effects of the nutrient and neighbour treatments.

Nutrient treatment: We tested if nutrient availability changed whether competition was occurring above or belowground. Half of all pots were treated with high nutrients while the other half was treated with low nutrients. On a weekly basis, the high nutrient treatment received 1250 ppm of 20-20-20 NPK water soluble fertilizer (Plant Products Co. Ltd., Brampton, Ontario) while the low nutrient treatment received 125 ppm of water soluble 20-20-20 NPK fertilizer (1/10 that of the high treatment). There were three replicates of each neighbour treatment per nutrient level and plants in both high and low nutrient treatments were watered daily. The first application of fertilizer was applied a week after seeds were sown and continued until plants were harvested.

Neighbour treatment: We tested to see the phenotypic response to the presence or absence of neighbours, identity of neighbour and social environment. Pots contained either a single plant or pairs of plants in all possible cultivar pair combinations (e.g. kale-kale, kale-cauliflower, kale-broccoli). There were three replicates of each pot. The total

sample size was 36 alone pots and 126 paired pots ([6 individual + 21 paired combinations] x 3 replicates x 2 nutrient levels).

Soil: Seeds were sown directly into pots in a soil mix of 3:1 fine granulated play sand (Pefferlaw Peat Products Inc., Pefferlaw, Ontario and All Treat Farms Limited, Arthur, Ontario) and turface (Profile Products LLC, Buffalo Grove, IL, USA) by volume. The bottom interior of each pot contained a layer of landscape fabric to prevent soil loss.

Planting: Planting dates and seed depth followed Ontario Seed Company recommendations in an effort to obtain similar emergence times between cultivars. Cabbage and cauliflower were planted on June 5th and 6th, 2014, collards were planted on June 6th, broccoli were planted on June 9th, and kale and kohlrabi were planted on June 10th. The first seedlings emerged on June 7th and date of emergence was recorded daily. Cabbage had low germination and therefore many of the pots with pairs of plants only had one plant germinate. Overall, many plants failed to emergence and also, there were many plants that died before harvest. Of the 288 seeds planted, only 172 plants emerged. Single plants were planted in the centre of the pot, while pairs were planted 2.5 cm apart and arranged around the middle of the pot.

Setup: Pots were permanently designated to a greenhouse bench. Once a week, all pots were rearranged on the bench to avoid location effects due to being placed near a window or being on the edge of the bench. Plants were sprayed once with 1.2 mL/L of Thiodan 4EC insecticide (AgrEvo, Regina, SK, Canada) to reduce the white fly population that was feeding on the plants.

Data collection: Plants were harvested from July 7 to July 10, 2014. The plants were harvested at an early stage so that allocation to leaf, stem and roots during vegetative growth could be determined. After 5-6 weeks of growth, plants from both nutrient levels were still in the initial stages of seedling growth due to the lack of nutrients in the soil, even with the additional application of fertilizer. All traits, except leaf area and dry mass, were measured with a ruler to the closest 0.1 mm. Leaf area was measured as the average of three reads to 0.1 cm using a leaf area meter (Area Meter AM100, *Analytical Development Co. Ltd*, Hoddesdon, England). We noted that kale was the most difficult to flatten because of the curled leaves and we took the value from the best reading with the most leaf area. Dry mass was measured to 4 decimal places. Just prior to harvest, we measured the natural height of the plant from the base of the soil to the highest point of the plant. Of the 172 plants that emerged, we harvested 168 plants due to seedling mortality. If plants were extremely small (i.e. had no leaves), then they were excluded from analysis.

Aboveground: Meristem height was measured for all bolted plants as the length from the base of the plant at soil level to the shoot apical meristem. The largest leaf of each plant was identified and the length, width and area of that leaf were measured. Leaf length was defined as the length along the midvein, from the base to the apex. Leaf width was defined as the longest width perpendicular to the midvein. Aboveground biomass was partitioned into the largest leaf and all other leaves with petioles, cotyledons and stem, which were all dried at 40 °C for 24 hours and weighed separately to obtain dry mass.

Belowground: We collected root mass as a pot due to the difficulty of assigning roots to an individual plant. Roots were collected by first washing and separating roots from the landscape fabric with tweezers. The roots were then dried at 40 °C for 24 hours and all soil and debris were removed to obtain dry root mass.

Experiment 2 – Phenotyping seedlings grown in groups

Experimental Design

We conducted this experiment to determine the phenotype of the six *B. oleracea* cultivars grown in different group combinations in high and low nutrient environments. Between June and July, 2014 under ambient light conditions, cultivars were grown in 14 x 20 x 14 cm pots in the Biology Greenhouse at McMaster University Hamilton, Ontario, Canada. We tested for effects of the nutrient and group composition treatment.

Nutrient treatment: We tested whether nutrient availability changed which traits were under selection. Half of the pots were given high nutrients and half were given low. On a weekly basis, the high nutrient condition received 1250 ppm of 20-20-20 NPK water soluble fertilizer (Plant Products Co. Ltd., Brampton, Ontario) and the low received 125 ppm (1/10 that of the high treatment). There were three replicates of each group combination per nutrient level and plants in both high and low nutrient treatments were watered daily. The first application of fertilizer was applied a week after seeds were sown and the last application was a week before harvest began.

Group composition treatment: We tested whether the frequency of cultivar in the pot and social environment affected phenotypic plasticity responses of plants grown in groups. Six seeds were planted in each pot in one of the following cultivar proportions:

monoculture (one cultivar) or 3:3 ratio for all possible cultivar pair combinations (e.g. 6 kale, 6 broccoli or 3 kale-3 broccoli, 3 kale-3 cauliflower). The total sample size was 126 pots ([6 monoculture + 15 paired combinations] x 3 replicates x 2 nutrient levels).

Soil: Seeds were sown directly into pots in a soil mix of 3:1 fine granulated play sand (Pefferlaw Peat Products Inc., Pefferlaw, Ontario and All Treat Farms Limited, Arthur, Ontario) and turface (Profile Products LLC, Buffalo Grove, IL, USA) by volume. The bottom interior of each pot contained a layer of landscape fabric to prevent soil loss.

Planting: Planting dates and seed depth followed Ontario Seed Company recommendations in an effort to obtain similar emergence times between cultivars. Cabbage and cauliflower were planted on June 5th and 6th 2014, collards were planted on June 6th, broccoli were planted on June 9th, and kale and kohlrabi were planted on June 10th. The first seedlings emerged on June 7th and date of emergence was recorded daily. Cabbage had low germination and therefore many of the pots did not have all 6 plants germinate. Overall, many plants failed to emerge and many plants died before harvest. Of the 756 seeds planted, only 563 plants emerged. Five of the seeds were planted in a circle, with each seed approximately 3 cm from the edge of the pot and approximately 7 cm between them. The sixth seed was placed in the center of the pot, approximately 6 cm from each of the other five seeds. For each paired cultivar replicate we randomized seed position in the pots as the center plant might be experiencing a varying amount of competition compared to the plants around the edge.

Setup: Pots were permanently designated to a greenhouse bench, with equal numbers of both high and low nutrient levels on each bench, but not group composition treatment.

We pooled two of the three benches together due to the lack of pots on one of the benches. Once a week, all pots were rearranged on the bench to avoid location effects due to being placed near a window or being on the edge of the bench. Plants were sprayed once with 1.2 mL/L of Thiodan 4EC insecticide (AgrEvo, Regina, SK, Canada) to reduce the white fly population that was living on the plants.

Data collection: Plants were harvested starting July 10, 2014 over an eight day period. The plants were harvested at an early stage so that allocation to leaf, stem and roots during vegetative growth could be determined. After 5-6 weeks of growth, plants from both nutrient levels were still in the initial stages of seedling growth due to the lack of nutrients in the soil even with the additional application of fertilizer. All traits, except leaf area and dry mass, were measured with a ruler to the closest 0.1 mm. Leaf area was measured as the average of three reads to 0.1 cm using a leaf area meter (Area Meter AM100, *Analytical Development Co. Ltd*, Hoddesdon, England). As much as possible, leaves were flattened before leaf area was measured. We noted that kale was the most difficult to flatten because of the curled leaves and we took the value from the best reading with the most leaf area. Dry mass was measured to 4 decimal places. Just prior to harvest, we determined the natural height of the plant from the base of the soil to the highest point of the plant. Of the 563 plants that emerged, we harvested 547 plants due to seedling mortality. If plants were extremely small (e.g. had no leaves), then they were excluded from analysis.

Aboveground: Meristem height was measured for all bolted (elongation of stem to produce flowers and seeds) plants as the length from the base of the plant at soil level to

the shoot apical meristem. The largest leaf of each plant was identified and the length, width and area of that leaf were measured. Leaf length was defined as the length along the midvein, from the base to the apex. Leaf width was the defined as the longest width perpendicular to the midvein. Aboveground biomass was partitioned into the largest leaf and all other leaves with petioles, cotyledons and stem, which were all dried at 40 °C for 24 hours and weighed separately to obtain dry mass.

Belowground: We collected the roots as a pot due to the difficulty of assigning roots to an individual plant. There was root growth through the landscape fabric thus removing roots was time consuming. We collected roots by two methods, as method changed to increase harvesting efficiency. Method one: roots were collected by first washing and picking off roots from landscape fabric with tweezers, then drying roots at 40 °C for 24 hours and weighing them to obtain dry mass. Method two: roots were collected by washing roots and landscape fabric, then both were dried together at 40 °C for 24 hours and all soil and debris were removed to obtain dry root mass.

Experiment 3 – Cage Match – determining juvenile fitness

Experimental Design

We conducted this experiment to test whether selection was acting on various allocation and morphological traits and whether there was resource partitioning occurring in high and low nutrient environments. Between June and July, 2014 under ambient light conditions, cultivars were grown in 14 x 20 x 14 cm pots in the Biology Greenhouse at McMaster University Hamilton, Ontario, Canada. We tested for effects of the nutrient and group composition treatment.

Nutrient treatment: We tested whether nutrient availability changed which traits were under selection. Half of the pots were given high nutrients and half were given low. On a weekly basis, the high nutrient condition received 1250 ppm of 20-20-20 NPK water soluble fertilizer (Plant Products Co. Ltd., Brampton, Ontario) and the low received 125 ppm (1/10 that of the high treatment). There were four replicates of each group combination per nutrient level and plants in both high and low nutrient treatments were watered daily. The first application of fertilizer was applied a week after seeds were sown and the last application was 12 days before harvesting commenced. Fertilization stopped because of leaf damage sustained during movement of plants for fertilizer application as high and low nutrient treatment pots were mixed on benches.

Group composition treatment: We tested which traits were under selection in competition and to see if the rare cultivar in the pot had higher fitness than the common cultivar in the pot due to resource partitioning. We chose several group combinations that were as follows: monoculture (one cultivar), 5:1 for all cultivar pair combinations (e.g. 6 kale, 6 cabbage or 5 kale-1 cabbage, 5 kale-1 cauliflower), one of each cultivar, less leafy cultivars of plants with more leafy cultivars of plants and shorter cultivars of plants with taller cultivars of plants (see Table 1.2). These were a priori cultivar groups that increased expected variation in competitive traits (i.e. leafy vs. non-leafy cultivars and tall vs. short). The total sample size was 360 pots (45 combinations x 4 replicates x 2 nutrient levels).

Soil: Seeds were sown directly into pots in a soil mix of 4:2 Pro Mix Bx mycorrhizae (Premier Horticulture Inc., Quakertown, PA, USA) and fine granulated play sand

Table 1.2. Group combinations present in pots that had leafy vs. non-leafy cultivars and tall vs. short cultivars.

Planting combination	**Tall vs. short**					
1	Kale	Kale	Collards	Broccoli	Cauliflower	Cabbage
2	Kale	Collards	Collards	Broccoli	Cauliflower	Cabbage
3	Kale	Collards	Broccoli	Broccoli	Cauliflower	Cabbage
4	Kale	Collards	Broccoli	Cauliflower	Cauliflower	Cabbage
Planting combination	**Leafy vs. non-leafy**					
5	Kale	Kale	Collards	Broccoli	Cauliflower	Kohlrabi
6	Kale	Collards	Collards	Broccoli	Cauliflower	Kohlrabi
7	Kale	Collards	Broccoli	Broccoli	Cauliflower	Kohlrabi
8	Kale	Collards	Broccoli	Cauliflower	Cauliflower	Kohlrabi

Notes: Kale and collards were expected to be leafy and broccoli and cauliflower were expected to be tall.

(Pefferlaw Peat Products Inc., Pefferlaw, Ontario and All Treat Farms Limited, Arthur, Ontario) by volume.

Planting: Planting dates and seed depth followed Ontario Seed Company recommendations in an effort to obtain similar emergence times between cultivars. Cabbage and cauliflower were planted on June 5th and 6th 2014, collards were planted on June 6th, broccoli were planted on June 9th, and kale and kohlrabi were planted on June 10th. The first seedlings emerged on June 7th and date of emergence was recorded daily. Cabbage had low germination and therefore many of the pots did not have all 6 plants germinate. Overall, many plants failed to emergence and also, there were many plants that died before harvest. 2160 seeds were planted and 1957 of them germinated. Five of the seeds were planted in a circle, with each seed approximately 3 cm from the edge of the pot and approximately 7 cm between them. The last seed was placed in the center, approximately 6 cm from each of the other five seeds. For each paired cultivar replicate we randomized seed position in the pots as the center plant might be experiencing a varying amount of competition compared to the plants around the edge.

Setup: Pots were permanently designated to a greenhouse bench, with equal numbers of both high and low nutrient levels on each bench, but not group composition treatment. Once a week, all pots were rearranged on the bench to avoid location effects due to being placed near a window or being on the edge of the bench. Plants were sprayed once with 1.2 mL/L of Thiodan 4EC insecticide (AgrEvo, Regina, SK, Canada) to reduce the white fly population that was living and feeding on the plants.

Data collection: Aboveground harvest began on July 21, 2014 and continued over 5 days. We chose this time as plants had many leaves but no flowers. Plants were cut at the base of the stem and placed in paper bags for drying. All bags were dried in an oven at 65°C for 36 hours and when the oven was full, plants were stored in paper bags in a fridge at 2°C for up to 3 weeks until they were able to be dried. Some plants in bags, however, became moldy before they were placed in the oven and dried. We recorded which plants were moldy and tested for a significant effect of mold weight on plant biomass. Plants were weighed to obtain aboveground dry mass to 4 decimal places. No belowground harvesting occurred as we only needed the aboveground biomass of plants for a measure of fitness. Of the 1956 plants that emerged, we harvested 1917 plants due to seedling mortality. If plants were extremely small (had no true leaves), they were excluded from analysis.

Statistical Analysis

The data was analyzed using SAS statistical software (version 9.3 for Windows (English); SAD Cary, North Carolina, USA). PROC GLM was used to perform analysis of variance (ANOVA) and analysis of covariance (ANCOVA) to compare the least mean square (LSMEANS option) of morphological and allocation traits between the different treatments of each experiment (Coleman et al. 1994; Cahill 2003). If necessary, the natural logarithm ($\log_e$) or the square root transformation of raw data was taken to satisfy the assumptions of GLM. For the two seedling experiments, each individual in a pot was used as both the focal and neighbouring plant. All aboveground traits from seedling and juvenile experiments are observations at the individual plant level. Leaf mass is the sum

of the largest leaf mass and all other leaves excluding cotyledons. Aboveground biomass is the sum of stem mass, and leaf and cotyledon mass. We defined bolted plants as 1 and unbolted plants as 0. Plants with a neighbour were assigned the value of 1 and plants grown alone were assigned the value of 0. Due to the difficulty of separating the roots of individual plants sharing a pot, roots from the seedling experiment were collected and analysed on a per pot basis. Total pot biomass is the sum of root mass and all aboveground biomass in a pot. There was possible variation in traits caused by differing emergence and harvest dates and the variation in belowground biomass due to changing of root collection methods. Thus harvest date and emergence date were included in all models, and root collection method was added to root allocation and total biomass models, but variables were only kept if $p<0.1$. Because the play sand used was from two different manufacturers in group seedling and juvenile experiment, we tested to see if there was an effect of play sand brand on aboveground biomass and found no significant difference (data not shown). Pots where only one of the two plants germinated were treated as alone pot treatments as there was no difference in aboveground biomass found between pots with one plant and pots where only one of the two plants germinated (data not shown).We tested to see if plants were experiencing different levels of competition due to different positions in the pot, but found no difference in aboveground biomass between the 6 positions in the pot (data not shown). To test if there was size inequality within a single pot, we checked for differences in aboveground biomass by comparing the unbiased Gini coefficient of each pot (Weiner 1985). No differences were found between

any of the treatments, except in the juvenile experiment there was an effect of bench location within the greenhouse (data not shown).

Phenotyping neighbour seedlings experiment: To investigate what factors led to the bolting of seedlings, we used a generalized linear model (Proc GENMOD). In the model, bolting was the dependent variable and nutrients and cultivar were the independent variables and number of plants in the pot was the covariate. We used ANOVAs and ANCOVAs to test for effects of neighbour presence, cultivar of neighbour, social environment, nutrient and cultivar of focal plant on all plants traits. Due to the collinearity of neighbour presence, identity of neighbour and social environment, separate ANCOVAs were used to investigate these effects.

To investigate the effects of neighbour presence on each plant trait, we conducted multiple ANOVAs and ANCOVAs. For aboveground biomass an ANCOVA was used with aboveground biomass as the dependent variable, cultivar and nutrient as independent variables and emergence date, harvest date and neighbour presence as covariates. For natural height an ANCOVA was used with natural height as the dependent variable, cultivar and nutrient as independent variables and emergence date, neighbour presence and stem mass as covariates. For meristem elongation, an ANCOVA was used with meristem height as the dependent variable, cultivar and nutrient as independent variables and neighbour presence and stem mass as covariates. For specific leaf area, an ANCOVA was used with largest leaf area as the dependent variable, cultivar and nutrient as independent variables and neighbour presence and largest leaf mass as covariates. For leaf shape, an ANCOVA was used with largest leaf length as the dependent variable,

cultivar and nutrient as independent variables and emergence date, neighbour presence and largest leaf width as covariates. For stem to leaf allocation, an ANCOVA was used with stem mass as the dependent variable, cultivar and nutrient as independent variables and neighbour presence and leaf mass as covariates. For root allocation, an ANCOVA was used with average root mass of a pot as the dependent variable, nutrient as the independent variable and neighbour presence and average leaf mass of a pot as covariates. For total pot biomass, an ANCOVA was used with average total biomass of a pot as the dependent variable, nutrient as the independent variable and neighbour presence as the covariate. To estimate the effects of cultivar on root allocation and total biomass, we had to use alone plants because of the difficulty of identifying individual plant roots in pots with paired plants. For root allocation, an ANCOVA was used with root mass of a pot as the dependent variable, nutrient and cultivar as independent variables and leaf mass of a pot as the covariate. For total biomass, an ANOVA was used with total biomass of a pot as the dependent variable and nutrient and cultivar as independent variables.

To investigate the effects of neighbour identity on each plant trait, we conducted multiple ANCOVAs. For aboveground biomass an ANCOVA was used with aboveground biomass as the dependent variable, cultivar, identity of neighbour and nutrient as independent variables and emergence date as the covariate. All interactions were dropped in the model because lsmeans were not estimable because of plant death. For natural height an ANCOVA was used with natural height as the dependent variable, cultivar, identity of neighbour and nutrient as independent variables and emergence date and stem mass as covariates. All interactions were dropped in the model because lsmeans

were not estimable because of plant death. For meristem elongation, an ANCOVA was used with meristem height as the dependent variable, cultivar, identity of neighbour and nutrient as independent variables and stem mass as the covariate. For specific leaf area, an ANCOVA was used with largest leaf area as the dependent variable, cultivar, identity of neighbour and nutrient as independent variables and largest leaf mass as the covariate. For leaf shape, an ANCOVA was used with largest leaf length as the dependent variable, cultivar, identity of neighbour and nutrient as independent variables and emergence date and largest leaf width as covariates. For stem to leaf allocation, an ANCOVA was used with stem mass as the dependent variable, cultivar, identity of neighbour and nutrient as independent variables and leaf mass as the covariate. For root allocation, an ANCOVA was used with average pot root mass as the dependent variable, nutrient as the independent variable and frequency of broccoli, cabbage, cauliflower, collards, kale, and kohlrabi and average leaf mass of a pot as covariates. For total biomass, an ANCOVA was used with average total biomass of a pot as the dependent variable, nutrient as the independent variable and frequency of broccoli, cabbage, cauliflower, collards, kale and kohlrabi as covariates.

To investigate the effects of social environment on each plant trait, we conducted multiple ANOVAs and ANCOVAs. For aboveground biomass an ANCOVA was used with aboveground biomass as the dependent variable, cultivar, social environment and nutrient as independent variables and emergence date as the covariate. All interactions were dropped in the model because lsmeans were not estimable because of plant death. For natural height an ANCOVA was used with natural height as the dependent variable,

cultivar, social environment and nutrient as independent variables and stem mass as the covariate. All interactions were dropped in the model because lsmeans were not estimable because of plant death. For meristem elongation, an ANCOVA was used with meristem height as the dependent variable, cultivar, social environment and nutrient as independent variables and stem mass as the covariate. For specific leaf area, an ANCOVA was used with largest leaf area as the dependent variable, cultivar, social environment and nutrient as independent variables and harvest date and largest leaf mass as covariates. All interactions were dropped in the model because lsmeans were not estimable because of plant death. For leaf shape, an ANCOVA was used with largest leaf length as the dependent variable, cultivar, social environment and nutrient as independent variables and emergence date and largest leaf width as covariates. For stem to leaf allocation, an ANCOVA was used with stem mass as the dependent variable, cultivar, social environment and nutrient as independent variables and leaf mass as the covariate. All interactions were dropped in the model because lsmeans were not estimable because of plant death. For root allocation, an ANCOVA was used with average root mass of a pot as the dependent variable, nutrient and social environment as independent variable and average leaf mass of a pot as the covariate. For total biomass, an ANOVA was used with average total biomass of a pot as the dependent variable, and nutrient and social environment as independent variables.

Phenotyping seedling groups experiment: To test the effect of the number of plants in the pot on juvenile aboveground biomass, we explored both a linear and quadratic relationship. Aboveground biomass was used as the dependent variable, nutrients as the

independent variable and the linear as well as the quadratic term of number of plants as covariates.

To investigate the effect of social environment and the number of plants in pots due to varying germination on plant traits, we conducted ANCOVAs. The ANCOVAs for natural height, meristem elongation, aboveground biomass, SLA, leaf shape, stem to leaf allocation, root allocation and total biomass were the same as in the phenotyping neighbour seedlings experiment, except that we included bench as an independent variable. To test the effect of the number of plants in the pot on seedling aboveground biomass, we explored both a linear and quadratic relationship. Aboveground biomass was used as the dependent variable and nutrients, the linear as well as the quadratic term of number of plants as independent variables.

To investigate the effect of cultivar frequency in the pot on plant traits, we conducted ANCOVAs. The ANCOVAs for natural height, meristem elongation, aboveground biomass, SLA, leaf shape, stem to leaf allocation, root allocation and total biomass were the same as in the phenotyping neighbour seedlings experiment, except that we included bench as an independent variable and the frequency of broccoli, cabbage, cauliflower, collards, kale and kohlrabi as covariates.

Juvenile fitness experiment: We tested for an effect of mold presence on aboveground biomass and found no significant difference between plants with and without mold (data not shown). To test the effect of the number of plants in the pot on juvenile aboveground biomass, we explored both a linear and quadratic relationship. Aboveground biomass was used as the dependent variable, bench as the independent variable and the linear as well as

the quadratic term of number of plants as covariates. Neither the linear plants term nor quadratic plants term was significant (data not shown). Nutrient level was not included in the model as there was no significant difference in aboveground biomass based on nutrient level (data not shown).

As there can be an environmental bias in selection analysis with phenotype and fitness, we used a family-level selection as advocated by Rausher (1992) in which selection is measured as the covariance between fitness and the mean trait of each genotype or family. Thus we used cultivar means instead of individual traits for the phenotypic traits measured before selection. To estimate multilevel selection, we used a modified Lande and Arnold (1983) analysis using multiple linear regression of fitness on cultivar trait means and group traits (Heisler and Damuth 1987; Goodnight et al. 1992; Rausher 1992). Due to differences in the number of plants per pot, we conducted a posthoc analysis of covariance to determine if density in the pot affected selection. We found that there were no differences in results with density included therefore for simplicity, results without density are shown. A significant nutrient effect in seedlings grown in groups led us to separate high and low nutrient levels to conduct selection analyses. Individual fitness (aboveground biomass) of juveniles was relativized to the average fitness of all pots on the same bench from the same nutrient level (average fitness of the population) as both bench and nutrients had a significant effect on aboveground biomass (data not shown). Harvest date did not have a significant effect on aboveground biomass, therefore was not included in the analyses.

A principal components analysis (PCA) was performed to condense the seedling data due to the number of traits and the correlation between traits. Root allocation was not included in the PCA because we did not have a value for each individual. Before performing the PCA, all traits except bolting were corrected for bench by nutrient level. The PROC PRINCOMP procedure was used to identify significant components at both high and low nutrients that described at least > 5% of the variance in the data. All seedling and adult traits were standardized before selection analysis, to provide a method of comparison between traits. The principal components were then standardized at both high and low nutrients to mean=0 and a standard deviation =1 using PROC STANDARD. The mean of each component was calculated at high and low nutrients for each cultivar using PROC MEANS to estimate individual selection. Because seedling root allocation did not differ by social environment, we used the average root allocation of single cultivar pots to get the standardized value for each cultivar. Seedling root allocation was corrected for bench by nutrient level using leaf mass as a covariate and then was standardized to mean=0 and standard deviation=1 using an ANCOVA to estimate individual selection. The mean of the population was calculated using the mean of the population and the root mean square error was the estimator of the standard deviation based on my model. The lsmeans of each cultivar was standardized by subtracting the mean of the population and dividing by the root mean square error. Emergence date of juvenile plants was corrected for bench by nutrient level and then was standardized to mean=0 and standard deviation=1 using an ANCOVA to estimate individual selection. The mean of the population was calculated using the mean of the population and the root mean square

error was the estimator of the standard deviation based on my model. The lsmeans of each cultivar was standardized by subtracting the mean of the population and dividing by the root mean square error. To estimate group selection, the average root allocation, emergence and principal component was calculated per pot. The regressions for the selection analysis were run using PROC GLM.

The residuals of the multilevel selection analyses were not homoscedastic but the traits could not be transformed as were standardized. This violates one of the assumptions of the regression analyses therefore the data was resampled using bootstrapping in R. First, we used the robust linear model function in the MASS package, available through the Companion to Applied Regression (car) package, to re-run the regressions. The Boot function from the boot package was used to resample the data 10 000 times. The boot.ci function was used to calculate the BCa adjusted 95% confidence intervals for the coefficients of the model to see if they were significant, ie. if 0 did not fall within the confidence interval.

To test if the rare cultivar in a pot was experiencing less competition than the common cultivar due to resource partitioning, we selected pairs of cultivars with the most replicates and did ANCOVAs with aboveground biomass of plant as the dependent variable, bench and cultivar as independent variables and the frequency of one of the cultivars as the covariate. We selected kohlrabi and kale, collards and kale, kohlrabi and cabbage, kale and broccoli, kohlrabi and collards, broccoli and cauliflower and broccoli and kohlrabi. If the rare cultivar always performed better, we would see a significant cultivar x frequency effect effects where the rare cultivar had higher aboveground

biomass compared to when it is common. This would indicate that the common cultivars were competing more than the rare cultivar because the common cultivar had reduced aboveground biomass.

RESULTS

Phenotypic variation between cultivars

Cultivars in neighbour seedling experiment differed in aboveground biomass (Table 3.1, 3.2, 3.3), specific leaf area (Table 4.1, 4.2, 4.3), leaf shape (Table 5.1, 5.2, 5.3), stem to leaf allocation (Table 6.1, 6.2, 6.3), and likelihood to bolt (Table 9.1). Cabbage had significantly lower aboveground biomass than the other cultivars (Fig. 2A). Specific leaf area was lowest with cauliflower (Fig. 2B). Leaf shape was greatest with kohlrabi, where leaf length was greater than leaf width (Fig. 2C). On average, broccoli had the greatest stem to leaf allocation, whereas kale had the lowest (Fig. 2D). Cauliflower and collards were more likely to bolt compared to other cultivars (Fig. 6A). Natural height and meristem elongation did not vary between cultivar ($p<0.1638$, $p<0.0648$, $p<0.6483$ and $p<0.0939$, $p<0.0784$, $p<0.1944$, respectively). When plants were grown alone, root allocation and total biomass differed between the cultivars (Table 8.4). Root to leaf allocation was greatest in cauliflower and kohlrabi (Fig. 3A). Total biomass of alone plants was greatest in collards (Fig. 3B).

In the group seedling experiment, cultivar phenotypes were similar to those of the neighbour seedling experiment. Cultivars differed in aboveground biomass (Table 12.1, 12.2), SLA (Table 13.1, 13.2), leaf shape (Table 14.1, 14.2), stem to leaf allocation (Table

11.1, 11.2), natural height (Table 15.1, 15.2), meristem elongation (Table 10.1, 10.2) and likelihood to bolt (Table 9.2). Cabbage had the lowest aboveground biomass, while kale had the highest aboveground biomass (Fig. 4A). Specific leaf area was highest in kale and lowest in cauliflower (Fig. 4B). Again, kohlrabi had the longest leaves compared to width, while broccoli and kale had the shortest leaves compared to width (Fig. 4C). As well, broccoli allocated more to stem mass than to leaf mass compared to other cultivars, whereas kale allocated the least to stem mass than to leaf mass (Fig. 4D). The cultivars differed in natural height (Fig. 4E). Broccoli and cauliflower were more likely to bolt compared to the other cultivars (Fig. 6B). For the subset of plants that bolted, meristem elongation was greatest in broccoli and collards, while meristem elongation was lowest in kohlrabi (Fig. 4F). When pots contained a single cultivar, there was no difference in average root allocation of a pot between cultivars ($p<0.5836$). However, average total biomass of pot was lowest when pots contained just broccoli or just cabbage (Table 16.3; Fig. 5).

The differences of meristem elongation (Table 10.1, 10.2), stem to leaf allocation (Table 11.1, 11.2) and aboveground biomass (Table 12.1, 12.2) among cultivars were affected by nutrients. In low nutrients, all cultivars were less elongated, had less stem to leaf allocation and overall had less aboveground biomass than plants in high nutrients.

Effect of nutrients on morphological and allocation traits

As expected, plants in both the neighbour and group seedling experiments in high nutrients had higher specific leaf area (Table 4.1-4.3, 13.1, 13.2), greater leaf length than width (Table 5.1-5.3, 14.1, 14.2), higher aboveground biomass (Table 3.1-3.3, 12.1, 12.2)

and higher average total biomass of a pot (Table 8.1-8.3, 16.1, 16.2) compared to low nutrients. In the neighbour seedling experiment, plants were more likely to bolt in high nutrients (Table 9.1) and had more variable aboveground biomass (Fig. 6A) compared to plants in low nutrients. There was no nutrient effect on stem to leaf allocation ($p<0.4942$, $p<0.6545$, $p<0.1502$), meristem elongation ($p<0.7841$, $p<0.3584$, $p<0.4349$), natural height ($p<0.6109$, $p<0.6838$, $p<0.1840$) or average root allocation of a pot ($p<0.5313$, $p<0.4906$, $p<0.6651$). In group seedling experiment (Table 9.2), at low nutrients the likelihood of cultivars to bolt varied among cultivars, but the cultivars had similar aboveground biomass (Fig. 6B). At high nutrients, aboveground biomass varied, but likelihood of cultivars to bolt were similar (Fig. 6B). Also, at high nutrients, plants had allocated more to stem than to leaf (Tables 11.1, 11.2), had greater meristem elongation (Tables 10.1, 10.2), had greater natural height (Tables 15.1, 15.2) and had decreased the average root allocation of the pot (Tables 16.1-16.3).

Effect of density on morphological and allocation traits

In the two seedling experiments, there was low plant emergence due to the soilless mixture used. Many of the pots in the neighbour seedling experiment had only one plant emerge of the two that were planted, while in the group seedling experiment, not all six plants emerged. Therefore, density in the pot had to be accounted for. Overall, many traits were affected by the density of plants in pots and showed that plants were experiencing competition. In the neighbour and group experiment, an increase in density decreased specific leaf area (Table 4.1, 13.2; Fig. 7B), increased stem to leaf allocation (Table 6.1, 11.2; Fig. 7C) and decreased leaf length compared to width (Table 5.1, 14.2). In addition,

an increase in density decreased aboveground biomass (Table 3.1, 12.2, 17; Fig.7A) and decreased the average total biomass of the pot (Table 8.1, 16.2). Natural height and meristem height did not change with density of plants in the pot (Table 7.1, 15.2 and 2.1, 10.2, respectively).

Interestingly, in the neighbour seedling experiment density had no effect on the likelihood to bolt in neighbour seedling experiment ($p<0.1566$). However, density did increase the average root allocation of the pot (Table 8.1; Fig. 7D).

In the group seedling experiment, density increased the likelihood of bolting (Table 9.2), but density had no effect on average root allocation of the pot ($p<0.4603$). Aboveground biomass was affected by density and nutrients (Table 17). At low nutrients, the more plants there were in the pot, the more a plant's aboveground biomass decreased due to the increase in competition (Fig. 8A). At high nutrients, there was a significant quadratic relationship in individual aboveground biomass, where plants with moderate competition had the greatest individual aboveground biomass (Fig. 8B).

Effect of competitive ability, neighbour identity and frequency of cultivars in pot on morphological and allocation traits

In the neighbour seedling experiment, the aboveground biomass of the focal plant was affected by the competitive ability of its neighbour (Table 3.2). If the focal plant had a neighbour that was a cauliflower, collards or broccoli, the aboveground biomass of the focal plant was less than if it was grown alone (Fig. 9). However, when the neighbour was a cabbage, kale or kohlrabi the aboveground biomass of the focal plant was not significantly different than when grown alone (Fig. 9). The natural height, meristem

elongation, specific leaf area, leaf shape and stem to leaf allocation was not affected by neighbour identity ($p<0.8311$, $p<0.2700$, $p<0.1481$, $p<0.7208$ and $p<0.1236$, respectively). As there was difficulty in assigning roots to a specific individual, roots were collected as a pot. Compared to plants grown alone, the addition of a cauliflower or kohlrabi increased the average root to leaf allocation of the pot (Table 8.2). However, the addition of a broccoli, cabbage, kale or kohlrabi decreased average total biomass of the pot (Table 8.2).

In the group seedling experiment, the frequency of cultivars in the pot had a significant effect on many traits. An increase in the numbers of any cultivar other than cabbage in the pot significantly decreased the aboveground biomass of the focal plant (Table 12.1). The greater the number of any cultivar in the pot significantly decreased the specific leaf area of the focal plant (Table 13.1). The more collards, kale or kohlrabi in the pot significantly increased stem to leaf allocation of the focal plant (Table 11.1), whereas the more broccoli, cauliflower or kale decreased leaf length compared to width of the focal plant (Table 14.1). Adding more broccolis increased average root to leaf allocation of the pot, while more cabbage or kohlrabi decreased the average total biomass of the pot (Table 16.1). These results are consistent with results the density results and are further evidence that plants are experiencing competition in experiment. Overall, there was no effect of cultivar frequency in natural height (Table 15.1) or meristem elongation (Table 10.1).

Selection on morphological and allocation traits

Principal component analysis was used to reduce a number of traits measured in the group seedling experiment. The traits included in the PCA were largest leaf length, largest leaf area, leaf mass, stem mass, natural height and bolting. Root allocation was not included because there was no root allocation value for each individual plant, only a pot average. At each nutrient level, the first three components, which each accounted for greater than 5% of the variation of the variables were used (Table 18.1, 18.2). The mean of each component was calculated at high and low nutrients for each cultivar. At both high and low nutrients, component 1 had positive loading for all variables, including leaf mass and stem mass and is referred to as "size" and component 2 had a large positive loading of likelihood to bolt and is referred to as "bolting". Component 3 had different loadings at high and low nutrients. Component 3 was heavily weighted by short height and long leaves at low nutrients and is referred to as "rosette". At high nutrients, component 3 was heavily weighted by natural height and is referred to as "height".

At both nutrient levels, individual and group level selection were acting in opposing directions on emergence date (Table 19.1, 19.2, 19.3). Selection on the individual favoured earlier emergence, while selection on the group favoured delayed emergence (Fig. 12C-17C).

In all three low nutrient models, root allocation was only under selection at the individual level (Table 19.1, 19.2, 19.3). Root allocation was selected to increase at the individual level, but there was no group selection (Fig. 13B, 15B, 17B). However at high nutrients, root allocation was only under selection in the model that included bolting and

emergence date (Table 19.2). Root allocation was favoured to increase at the individual level, but favoured to decrease at the group level (Fig. 14B).

Of the two models that included "size", there was only selection acting on plant "size" at high nutrients (Table 19.1). A larger size was favoured at the individual level, while a smaller mean size was favoured at the group level (Fig. 12A). In the two "bolting" models, "bolting" was also only under selection at high nutrients (Table 19.2). Selection favoured bolting at the individual level, but there was no group selection (Fig. 14A). At high nutrients, component 3 "height" was favoured to increase at the individual level, but a group with smaller mean height was selected at the group level (Table 19.3; Fig. 16A). At low nutrients, component 3 "rosette" was selected against at the individual level, in other words selection was against a plant that had heavier leaves but a light stem (Table 19.3; Fig. 17A). In effect, selection was acting to increase the height and reduce the leaf mass.

Morphological and allocation responses to social environment

In the neighbour seedling experiment, *B. oleracea* responded differently depending on the social environment. Aboveground biomass was greater when plants were grown alone compared to plants grown with same or different cultivar (Table 3.3; Fig. 7A). SLA was greater when plants were grown alone compared to plants grown with same or different cultivar (Table 4.3; Fig. 7B). Stem to leaf allocation was greater when plants were grown with same or different cultivar, compared to plants that were grown alone (Table 6.3; Fig. 7C). The average root to leaf allocation of a pot did not differ between pots with same cultivar and different cultivar, but root allocation was

significantly more than alone plants (Table 8.3; Fig. 7D). The average total biomass of the pot did not differ significantly between plants grown with same cultivar and plants grown with a different cultivar (Table 8.3; Fig. 7E). However, the average total biomass of the pot with same cultivar was not significant different from plants that were grown alone (Fig. 7E). Natural height, meristem elongation and leaf shape were not affected by social environment ($p<0.1094$, $p<0.9658$ and $p<0.1874$, respectively). There was a significant social environment by nutrient effect on stem to leaf allocation, in which at high nutrients both plants grown with the same and different cultivar had higher stem to leaf allocation compared to low nutrients plants.

In the group seedling experiment, there was significant effect of social environment on aboveground biomass (Table 12.2). Plants grown with the same cultivar had more aboveground biomass than plants grown with mixed cultivars (Fig. 10). There was a significant social environment by nutrient interaction with stem to leaf allocation (Table 11.2) and specific leaf area (Table 13.2). Same and mixed cultivar pots did not differ in stem to leaf allocation or SLA, but high nutrients plants had greater SLA and greater stem to leaf allocation compared to low nutrients plants.

Outcome of rare vs. common cultivar in the pot

Overall, no evidence of resource partitioning was found in the juvenile experiment. Resource partitioning predicts that the rare cultivar in a pot would outperform the common cultivar. In an analysis with pairs of cultivars, a significant cultivar by frequency of cultivar effect might indicate resource partitioning. Nonetheless, there was no difference in aboveground biomass based on frequency of the second

cultivar between cauliflower and broccoli (Table 20.1), collards and kohlrabi (Table 20.2), kale and kohlrabi, collards and kale, cabbage and kohlrabi, and kale and broccoli (data not shown). With the broccoli and kohlrabi pair, there was a significant frequency of cultivars effect (Table 20.3; Fig. 11). Both broccoli and kohlrabi had higher aboveground biomass when there was a high frequency of kohlrabi in the pot.

Figure 2. Average aboveground biomass, SLA, leaf shape and stem to leaf allocation of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). (A) The aboveground biomass is derived from the least squares means (lsmeans) of an analysis of covariance with natural logarithm aboveground as the dependent variable, nutrient and cultivar as independent variables and emergence date and harvest date as covariates. (B) The specific leaf area is derived from the lsmeans of an analysis of covariance with natural logarithm largest leaf area as the dependent variable, nutrient and cultivar as independent variables and emergence date and natural logarithm largest leaf mass as covariates. (C) Leaf shape is derived from the lsmeans of an analysis of covariance with natural logarithm largest leaf length as the dependent variable, nutrient and cultivar as independent variables and natural logarithm largest leaf width as the covariate (D) Stem to leaf allocation is derived from the lsmeans of an analysis of covariance with natural logarithm stem mass as the dependent variable, nutrient and cultivar as independent variables and natural logarithm leaf mass as the covariate. Lsmeans with same letter do not significant differ at the 0.05 level. Lsmeans and standard errors were back-transformed for clarity. Bars indicate ± 1 S.E.

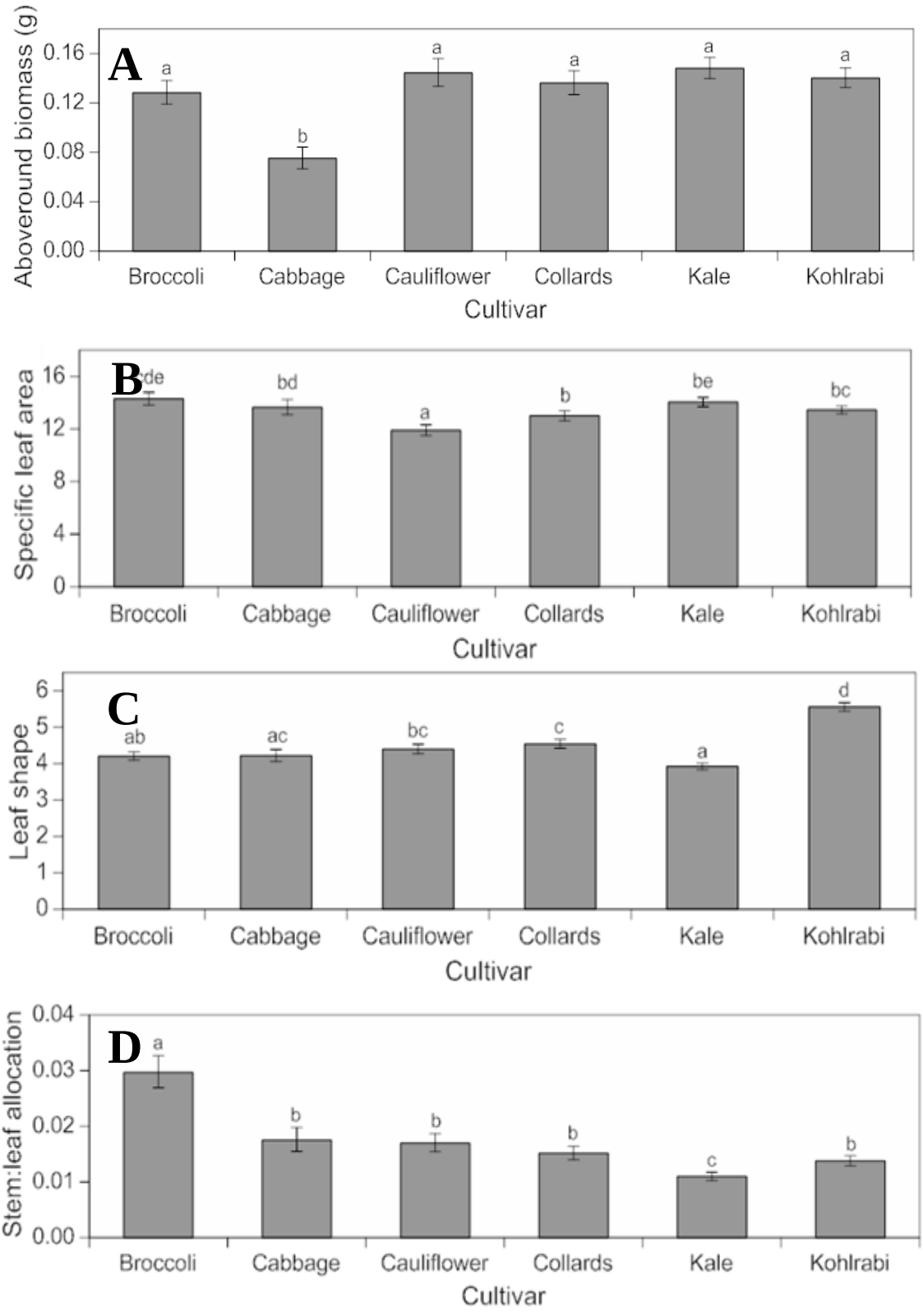

A
Aboveround biomass (g)
0.16
0.12
0.08
0.04
0.00
a
b
a
a
a
a
Broccoli
Cabbage
Cauliflower
Collards
Kale
Kohlrabi
Cultivar
B
Specific leaf area
16
12
8
4
0
de
bd
a
b
be
bc
Broccoli
Cabbage
Cauliflower
Collards
Kale
Kohlrabi
Cultivar
C
Leaf shape
6
5
4
3
2
1
0
ab
ac
bc
c
a
d
Broccoli
Cabbage
Cauliflower
Collards
Kale
Kohlrabi
Cultivar
D
Stem:leaf allocation
0.04
0.03
0.02
0.01
0.00
a
b
b
b
c
b
Broccoli
Cabbage
Cauliflower
Collards
Kale
Kohlrabi
Cultivar

Figure 3. Average root allocation and total biomass of *B. oleracea* cultivars grown alone in a greenhouse (Experiment 1). (A) The root allocation is derived from the lsmeans of an analysis of covariance with natural logarithm average root mass of a pot as the dependent variable, nutrient and cultivar as independent variables and natural logarithm average leaf mass of a pot as covariates. (B) The total pot biomass is derived from the lsmeans of an analysis of variance with natural logarithm average total biomass of a pot as the dependent variable and nutrient and cultivar as independent variables. Lsmeans with same letter do not significant differ at the 0.05 level. Lsmeans and standard errors were back-transformed for clarity. Bars indicate ± 1 S.E.

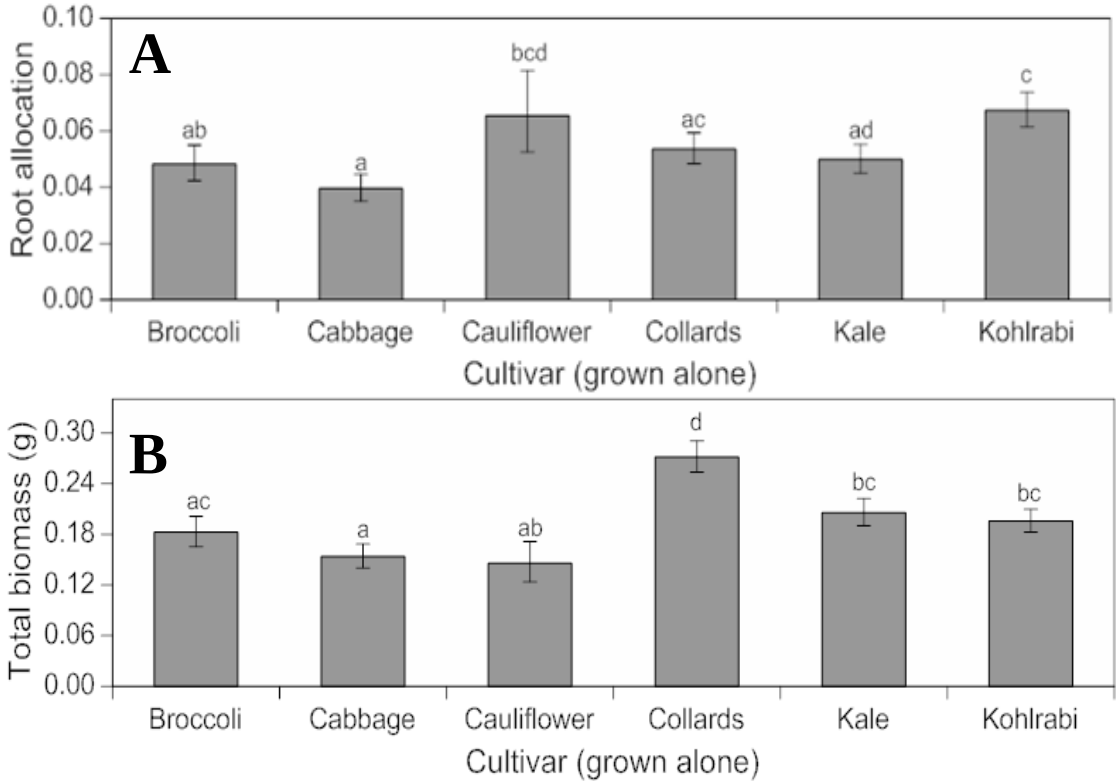

A
Root allocation
0.10
0.08
0.06
0.04
0.02
0.00
ab
a
bcd
ac
ad
c
Broccoli
Cabbage
Cauliflower
Collards
Kale
Kohlrabi
Cultivar (grown alone)
B
Total biomass (g)
0.30
0.24
0.18
0.12
0.06
0.00
ac
a
ab
d
bc
bc
Broccoli
Cabbage
Cauliflower
Collards
Kale
Kohlrabi
Cultivar (grown alone)

Figure 4. Average of various morphological and allocation traits of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). (A) The aboveground biomass is derived from the lsmeans of an ANCOVA with natural logarithm aboveground as the dependent variable, nutrient, kin, bench and cultivar as independent variables and number of neighbour, emergence date and harvest date as covariates. (B) The specific leaf area is derived from the lsmeans of an ANCOVA with natural logarithm largest leaf area as the dependent variable, nutrient, kin, bench and cultivar as independent variables and number of neighbours and natural logarithm largest leaf mass as covariates. (C) Leaf shape is derived from the lsmeans of an ANCOVA with natural logarithm largest leaf length as the dependent variable, nutrient, kin, bench and cultivar as independent variables and emergence date, number of neighbours and largest leaf width as the covariate. (D) Stem to leaf allocation is derived from the lsmeans of an ANCOVA with natural logarithm stem mass as the dependent variable, nutrient, kin, bench and cultivar as independent variables and emergence date, number of neighbours and natural logarithm leaf mass as covariates. (E) The natural height is derived from the lsmeans of an ANCOVA with natural logarithm natural height as the dependent variable, nutrient, kin, bench and cultivar as independent variables and number of neighbours and $\log_e$ stem mass as covariates. (F) The meristem elongation is derived from the lsmeans of an ANCOVA with natural logarithm meristem height as the dependent variable, nutrient, kin, bench and cultivar as independent variables and number of neighbours and natural logarithm stem mass as covariates. Lsmeans with same letter do not significant differ at the 0.05 level. Lsmeans and standard errors were back-transformed for clarity. Bars indicate ± 1 S.E.

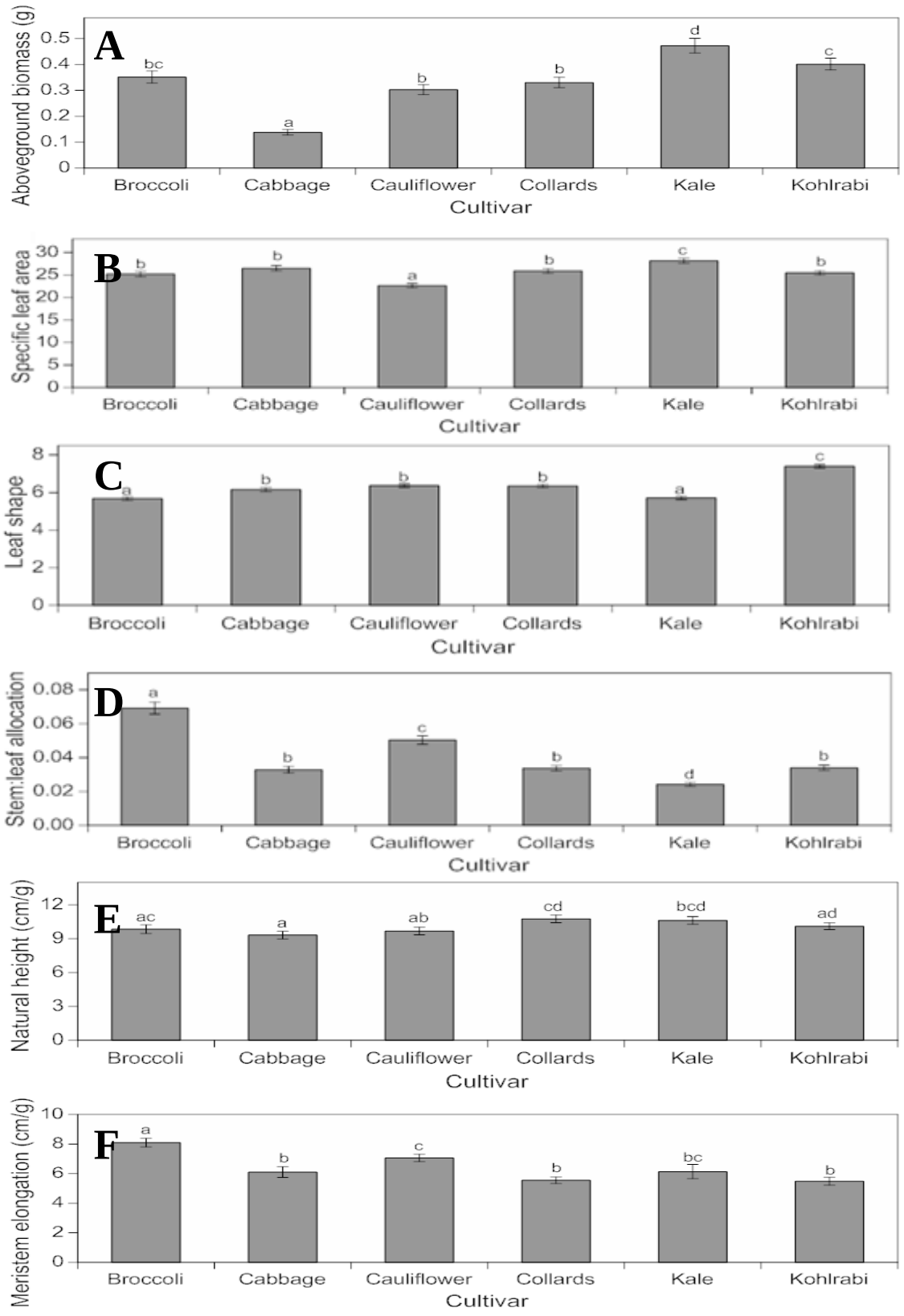

A
Aboveground biomass (g)
0
0.1
0.2
0.3
0.4
0.5
bc
a
b
b
d
c
B
Specific leaf area
0
5
10
15
20
25
30
b
b
a
b
c
b
C
Leaf shape
0
2
4
6
8
a
b
b
b
a
c
D
Stem:leaf allocation
0.00
0.02
0.04
0.06
0.08
a
b
c
b
d
b
E
Natural height (cm/g)
0
3
6
9
12
ac
a
ab
cd
bcd
ad
F
Meristem elongation (cm/g)
0
2
4
6
8
10
a
b
c
b
bc
b
Broccoli
Cabbage
Cauliflower
Collards
Kale
Kohlrabi
Cultivar

Figure 5. Average total biomass of *B. oleracea* cultivars grown in single cultivar groups of 6 plants in a greenhouse (Experiment 2). The total pot biomass is derived from the lsmeans of an analysis of variance with natural logarithm of the average total biomass of a pot as the dependent variable and nutrient, bench and cultivar as independent variables. Lsmeans with same letter do not significant differ at the 0.05 level. Lsmeans and standard errors were back-transformed for clarity. Bars indicate ± 1 S.E.

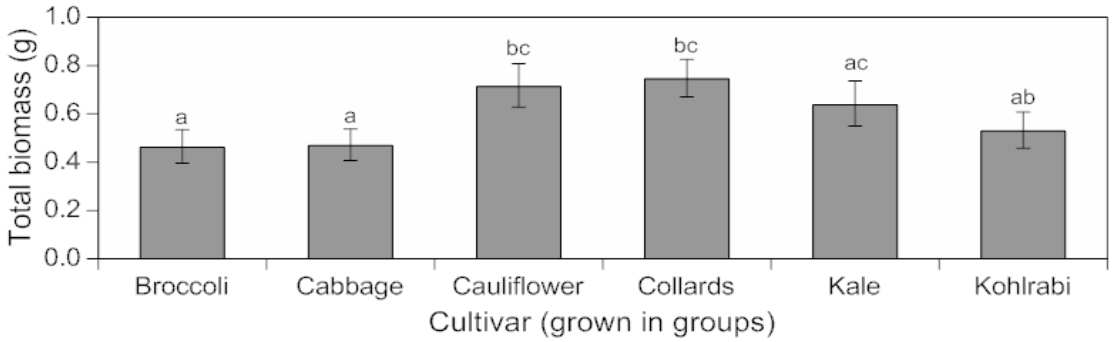

Total biomass (g)
1.0
0.8
0.6
0.4
0.2
0.0
a
a
bc
bc
ac
ab
Broccoli
Cabbage
Cauliflower
Collards
Kale
Kohlrabi
Cultivar (grown in groups)

Figure 6. Comparing average aboveground biomass of *B. oleracea* cultivars grown in the presence or absence of a neighbour and in groups of 6 plants in a greenhouse to the likelihood of bolting (Experiment 1 and 2). (A) Experiment 1 - the likelihood to bolt as the dependent variable, cultivar and nutrients as independent variables and neighbour presence as the covariate and (B) experiment 2 - the likelihood to bolt as the dependent variable, cultivar and nutrients as independent variables and the number of plants in the pot as the covariate. The solid line is the linear trendline of the cultivar lsmeans from a GENMOD at high nutrients. The dashed line is the linear trendline of lsmeans cultivar from a GENMOD at low nutrients. B refers to broccoli, cab refers to cabbage, cau refers to cauliflower, co refers to collards, ka refers to kale and ko refers to kohlrabi. Aboveground biomass lsmeans were back-transformed for clarity.

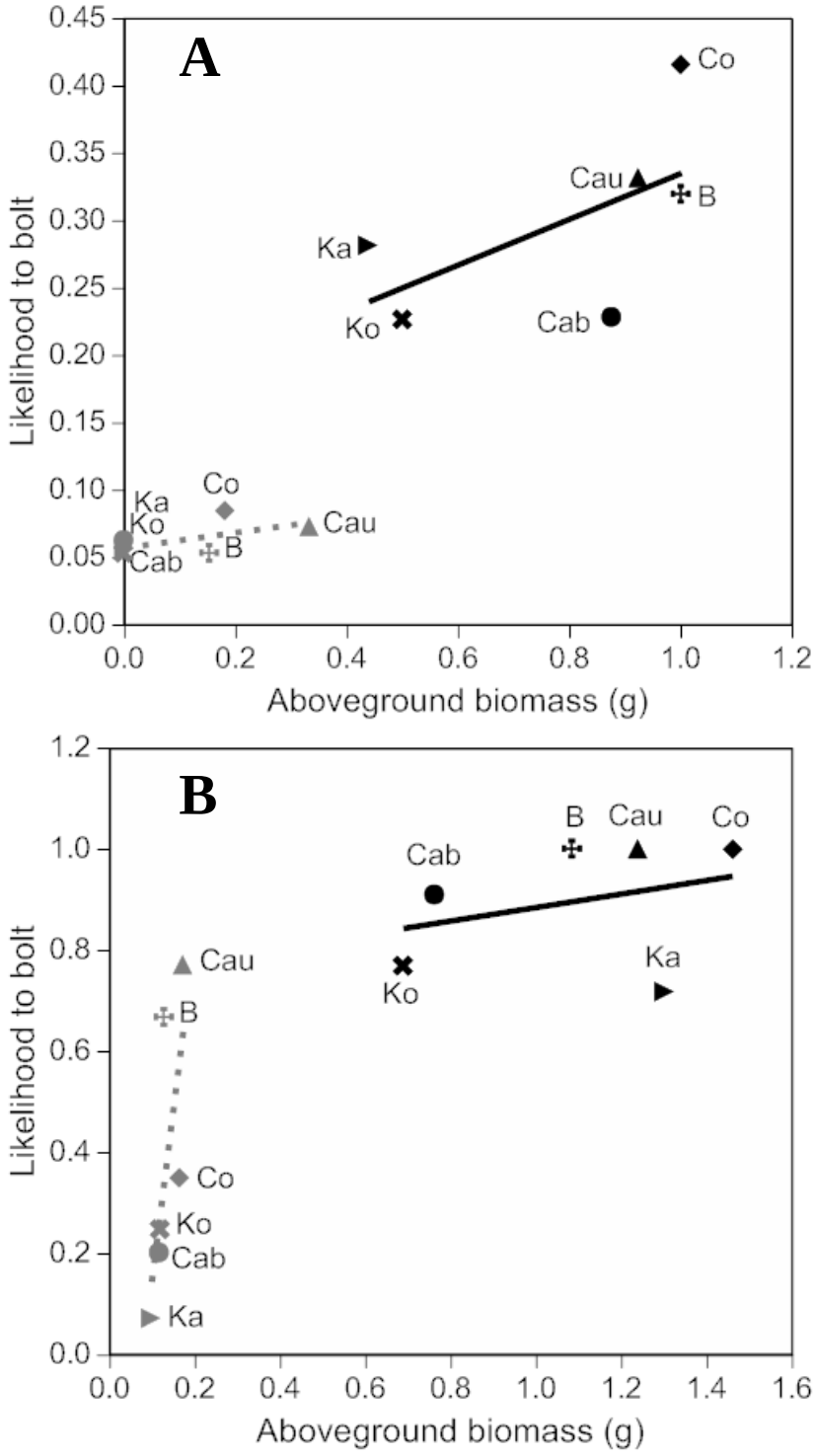

A
Likelihood to bolt
Aboveground biomass (g)
Co
Cau
B
Ka
Ko
Cab
B
Co
Cau
Ka
Ko
Cab
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0.45
0.0
0.2
0.4
0.6
0.8
1.0
1.2
B
Likelihood to bolt
Aboveground biomass (g)
B
Cau
Co
Cab
Ka
Ko
Cau
B
Co
Ko
Cab
Ka
0.0
0.2
0.4
0.6
0.8
1.0
1.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6

Figure 7. Effect of social environment on the average of various allocation and morphological traits of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). (A) The aboveground biomass is derived from the lsmeans of an analysis of covariance with natural logarithm aboveground as the dependent variable, nutrient, cultivar and kin as independent variables and emergence date as the covariate. (B) The specific leaf area is derived from the lsmeans of an analysis of covariance with natural logarithm largest leaf area as the dependent variable, nutrient, kin and cultivar as independent variables and harvest date and natural logarithm largest leaf mass as covariates. (C) Stem to leaf allocation is derived from the lsmeans of an analysis of covariance with natural logarithm stem mass as the dependent variable, nutrient, kin and cultivar as independent variables and natural logarithm leaf mass as the covariate. (D) The average root allocation is derived from the lsmeans of an analysis of covariance with natural logarithm root mass as the dependent variable, nutrient, cultivar and kin as independent variables and leaf mass as the covariate. (E) The total pot biomass is derived from the lsmeans of an analysis of variance with natural logarithm average total biomass as the dependent variable and nutrient and kin as independent variables. Lsmeans with same letter do not significant differ at the 0.05 level. Lsmeans and standard errors were back-transformed for clarity. Bars indicate ± 1 S.E.

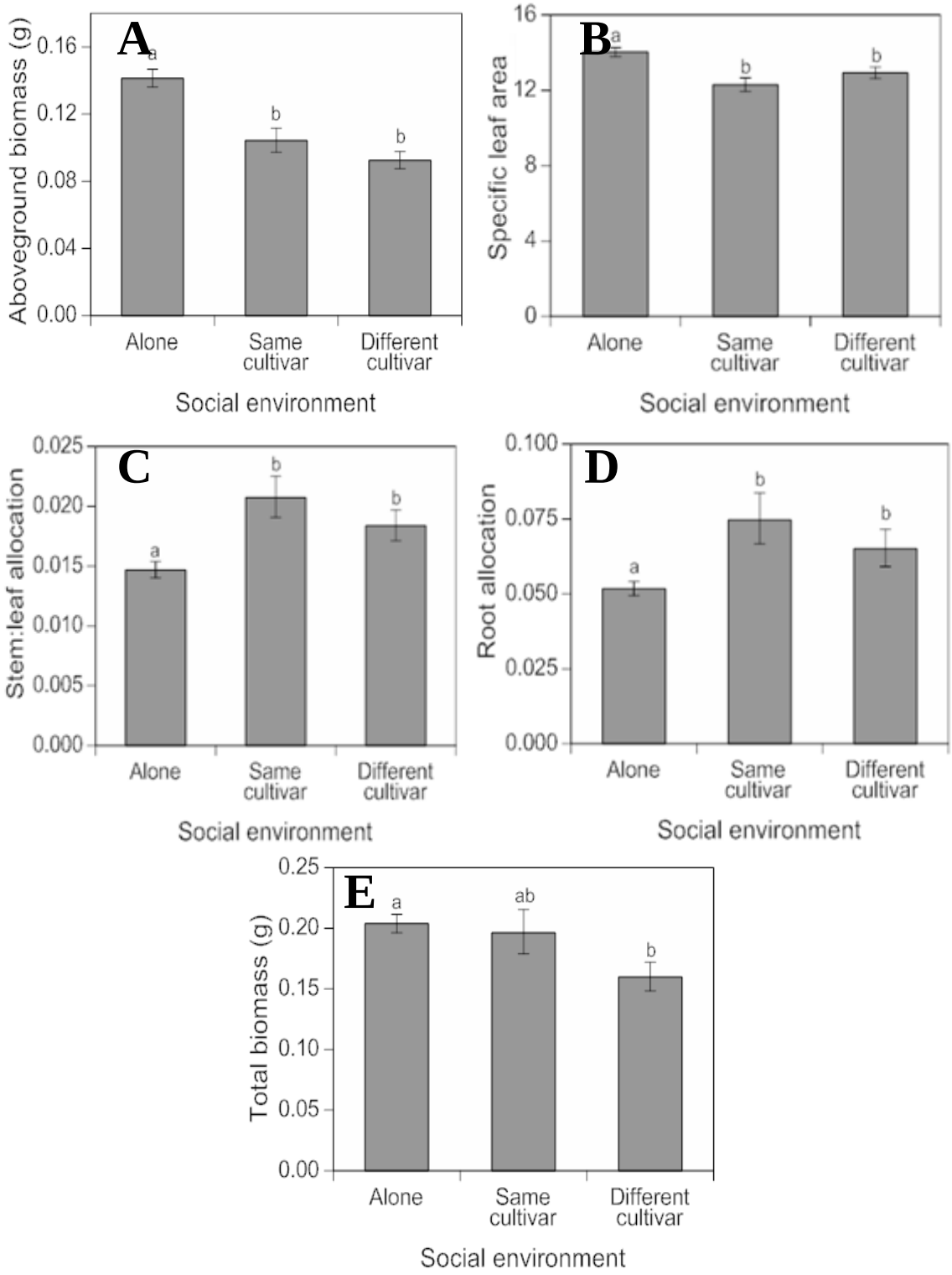

A
Aboveground biomass (g)
0.16
0.12
0.08
0.04
0.00
a
b
b
Alone
Same cultivar
Different cultivar
Social environment
B
Specific leaf area
16
12
8
4
0
a
b
b
Alone
Same cultivar
Different cultivar
Social environment
C
Stem:leaf allocation
0.025
0.020
0.015
0.010
0.005
0.000
a
b
b
Alone
Same cultivar
Different cultivar
Social environment
D
Root allocation
0.100
0.075
0.050
0.025
0.000
a
b
b
Alone
Same cultivar
Different cultivar
Social environment
E
Total biomass (g)
0.25
0.20
0.15
0.10
0.05
0.00
a
ab
b
Alone
Same cultivar
Different cultivar
Social environment

Figure 8. Scatter plot of the natural logarithm of aboveground biomass of *B. oleracea* cultivars grown in groups based on the number of plants in the pot (Experiment 2). The natural logarithm of aboveground biomass is derived from an analysis of covariance with the natural logarithm of aboveground biomass as the dependent variable, nutrients as the independent variable and the number of plants in the pot and quadratic number of plants in the pot as covariates. (a) Linear trendline at low nutrients and (B) quadratic trendline at high nutrients.

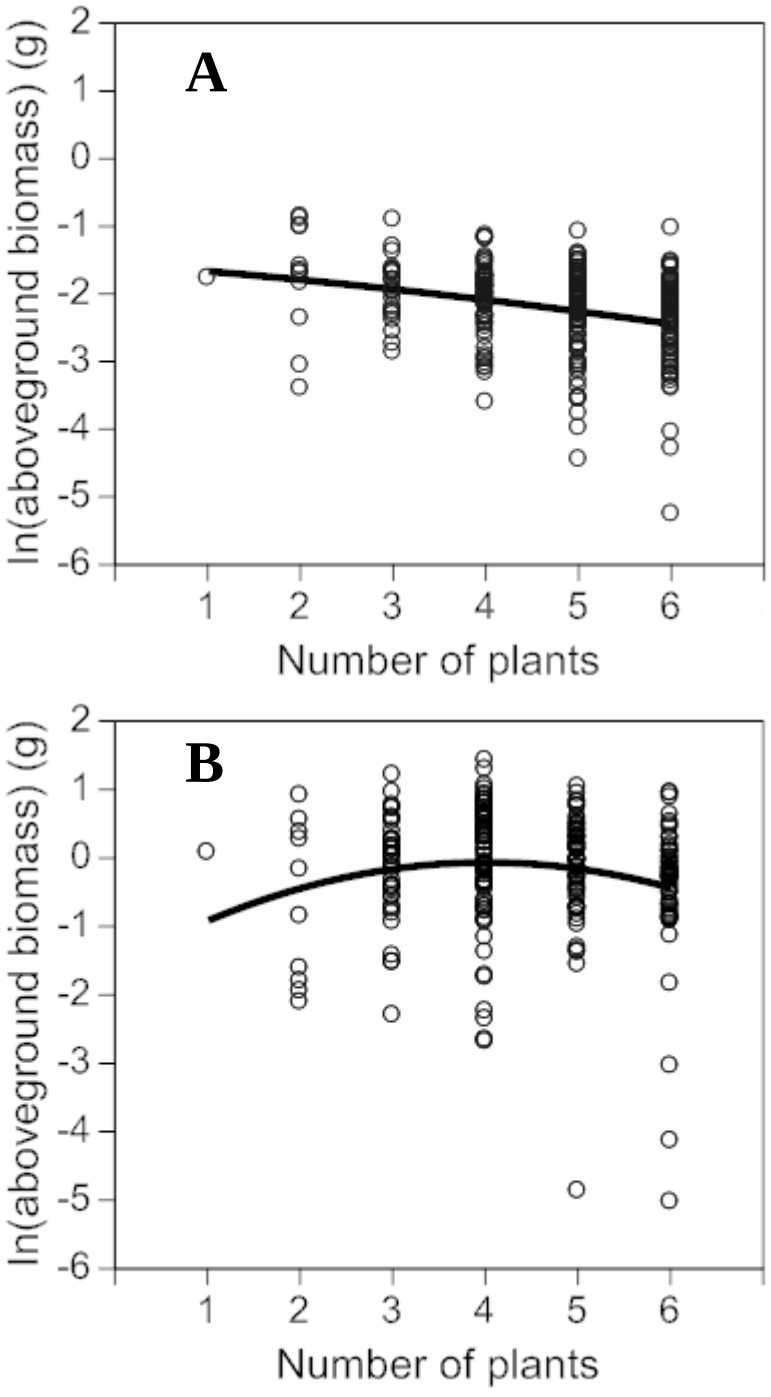

A
ln(aboveground biomass) (g)
2
1
0
-1
-2
-3
-4
-5
-6
1
2
3
4
5
6
Number of plants
B
ln(aboveground biomass) (g)
2
1
0
-1
-2
-3
-4
-5
-6
1
2
3
4
5
6
Number of plants

Figure 9. Average aboveground biomass of focal plant of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse based on the identity of its neighbour (Experiment 1). The aboveground biomass is derived from the lsmeans of an analysis of covariance with natural logarithm aboveground biomass as the dependent variable, nutrient, opponent and cultivar as independent variables and emergence date and natural logarithm leaf mass as covariates. Lsmeans with same letter do not significant differ at the 0.05 level. Lsmeans and standard errors were back-transformed for clarity. Bars indicate ± 1 S.E.

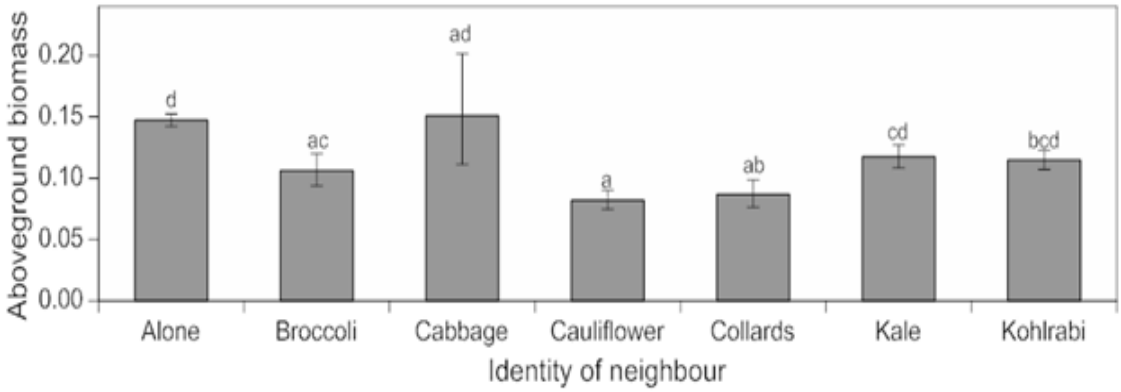

Aboveground biomass
0.20
0.15
0.10
0.05
0.00
d
ac
ad
a
ab
cd
bcd
Alone
Broccoli
Cabbage
Cauliflower
Collards
Kale
Kohlrabi
Identity of neighbour

Figure 10. Effect of social environment on the average aboveground biomass of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). The aboveground biomass is derived from the lsmeans of an analysis of covariance with natural logarithm aboveground mass as the dependent variable and nutrient, bench and kin as independent variables and number of neighbours as the covariate. Lsmeans with same letter do not significant differ at the 0.05 level. Lsmeans and standard errors were back-transformed for clarity. Bars indicate ± 1 S.E.


Aboveground biomass
0.4
0.3
0.2
0.1
0.0
a
b
Same cultivar
Mixed cultivars
Social environment

Figure 11. Average aboveground biomass of broccoli and kohlrabi, *B. oleracea* plants, grown in groups of 6 plants in a greenhouse based on frequency of kohlrabi in the pot (Experiment 3). An analysis of variance of the natural logarithm of aboveground biomass of broccoli and kohlrabi was used as the dependent variable, bench, cultivar and frequency of kohlrabi as independent variable. Lsmeans with same letter do not significant differ at the 0.05 level. Lsmeans and standard errors were back-transformed for clarity. Bars indicate ± 1 S.E.

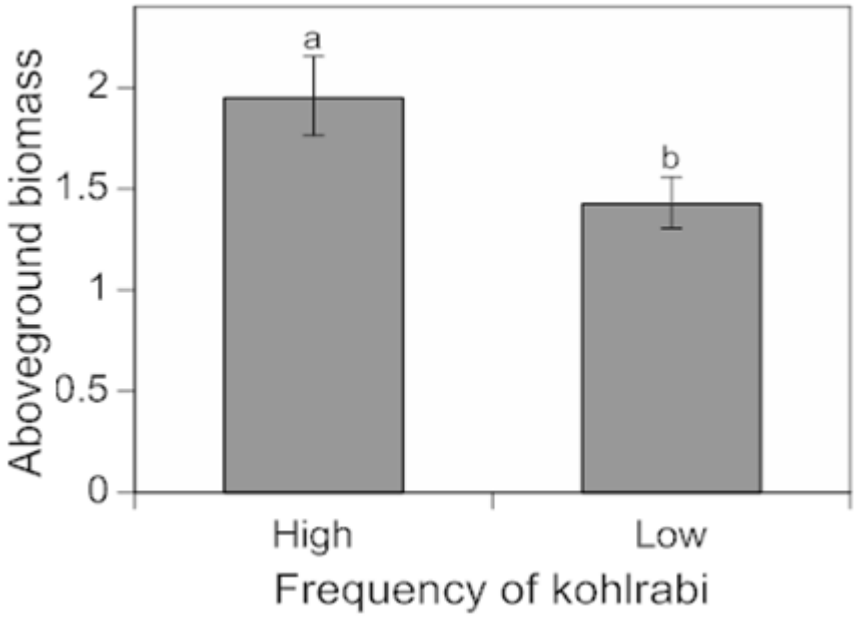
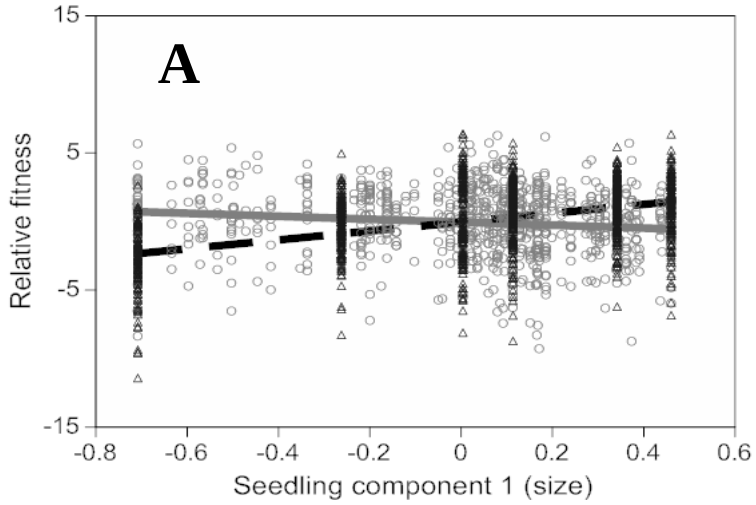
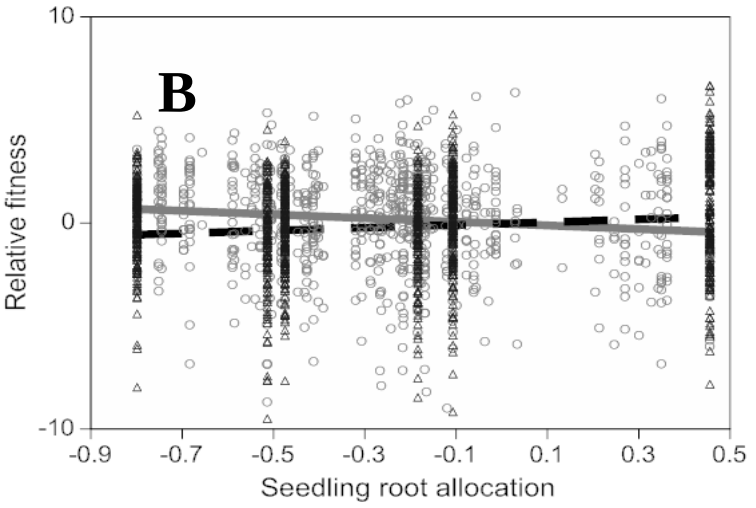

Aboveground biomass
2
1.5
1
0.5
0
a
b
High
Low
Frequency of kohlrabi

Figure 12. Selection acting on component 1, root allocation and emergence date at high nutrients. Partial regression of relative fitness on (A) seedling component 1 (size), (B) average seedling root allocation and (C) emergence date. The black dashed line indicates directional selection on the individual trait and the grey solid line indicates directional selection on the group trait. Aboveground biomass, the measure of fitness, was relativized and component 1, root allocation and emergence were standardized. *P<0.05, **P<0.01, ***P<0.001


A
Relative fitness
15
5
-5
-15
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
Seedling component 1 (size)


B
Relative fitness
10
0
-10
-0.9
-0.7
-0.5
-0.3
-0.1
0.1
0.3
0.5
Seedling root allocation

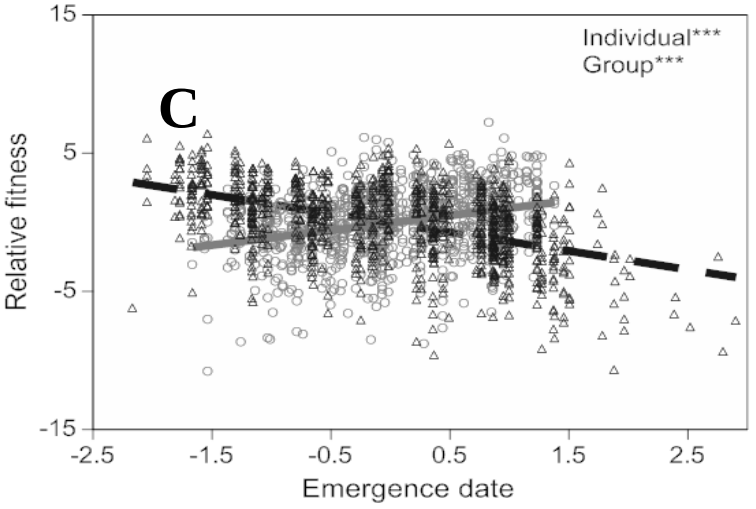

C
Individual***
Group***
Relative fitness
15
5
-5
-15
-2.5
-1.5
-0.5
0.5
1.5
2.5
Emergence date

Figure 13. Selection acting on component 1, root allocation and emergence date at low nutrients. Partial regression of relative fitness on (A) seedling component 1 (size), (B) average seedling root allocation and (C) emergence date. The black dashed line indicates directional selection on the individual trait and the grey solid line indicates directional selection on the group trait. Aboveground biomass, the measure of fitness, was relativized and component 1, root allocation and emergence were standardized. *P<0.05, **P<0.01, ***P<0.001

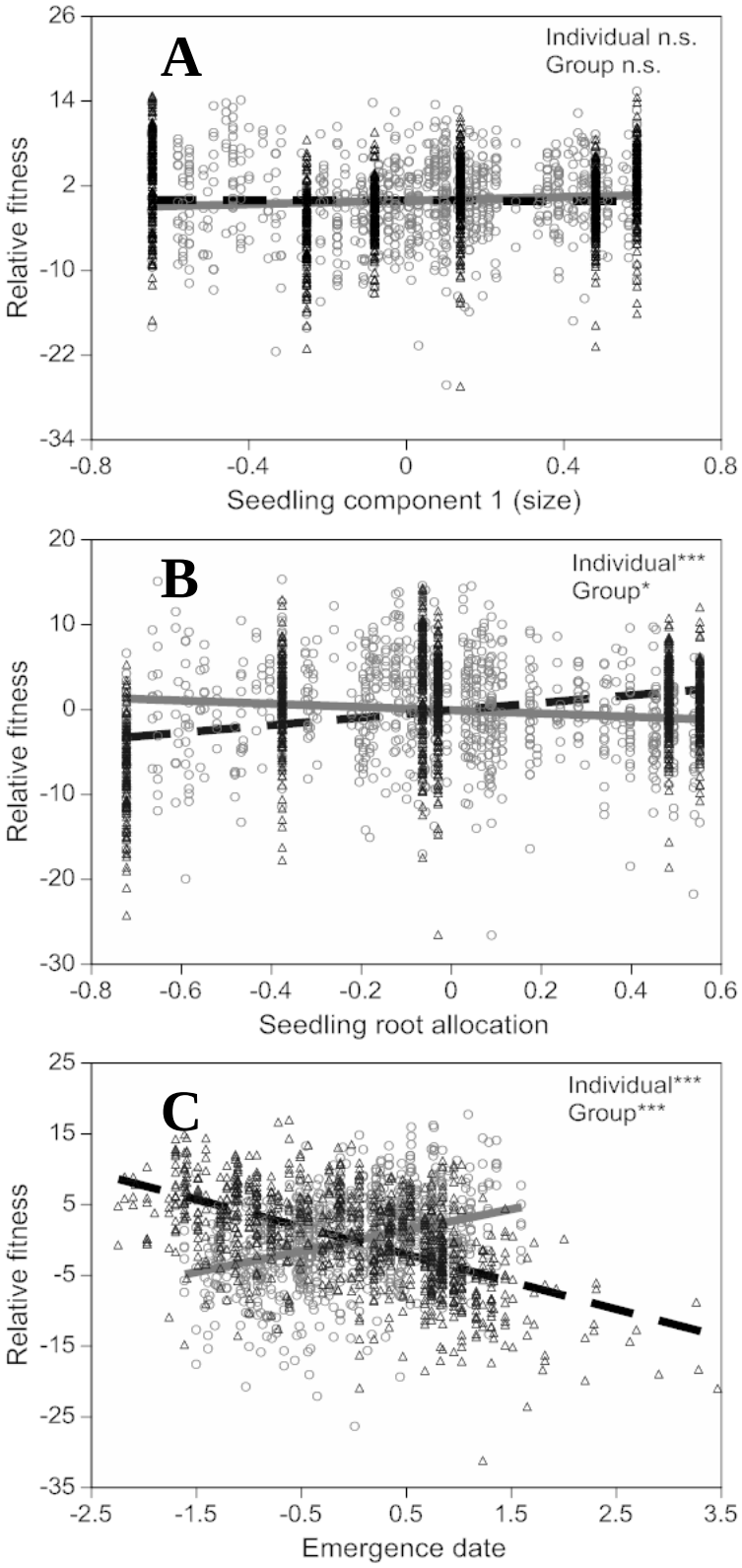

A
Individual n.s.
Group n.s.
Relative fitness
Seedling component 1 (size)
B
Individual***
Group*
Relative fitness
Seedling root allocation
C
Individual***
Group***
Relative fitness
Emergence date

Figure 14. Selection acting on component 2, root allocation and emergence date at high nutrients. Partial regression of relative fitness on (A) seedling component 2 (bolting), (B) average seedling root allocation and (C) emergence date. The black dashed line indicates directional selection on the individual trait and the grey solid line indicates directional selection on the group trait. Aboveground biomass, the measure of fitness, was relativized and component 2, root allocation and emergence were standardized. *P<0.05, **P<0.01, ***P<0.001

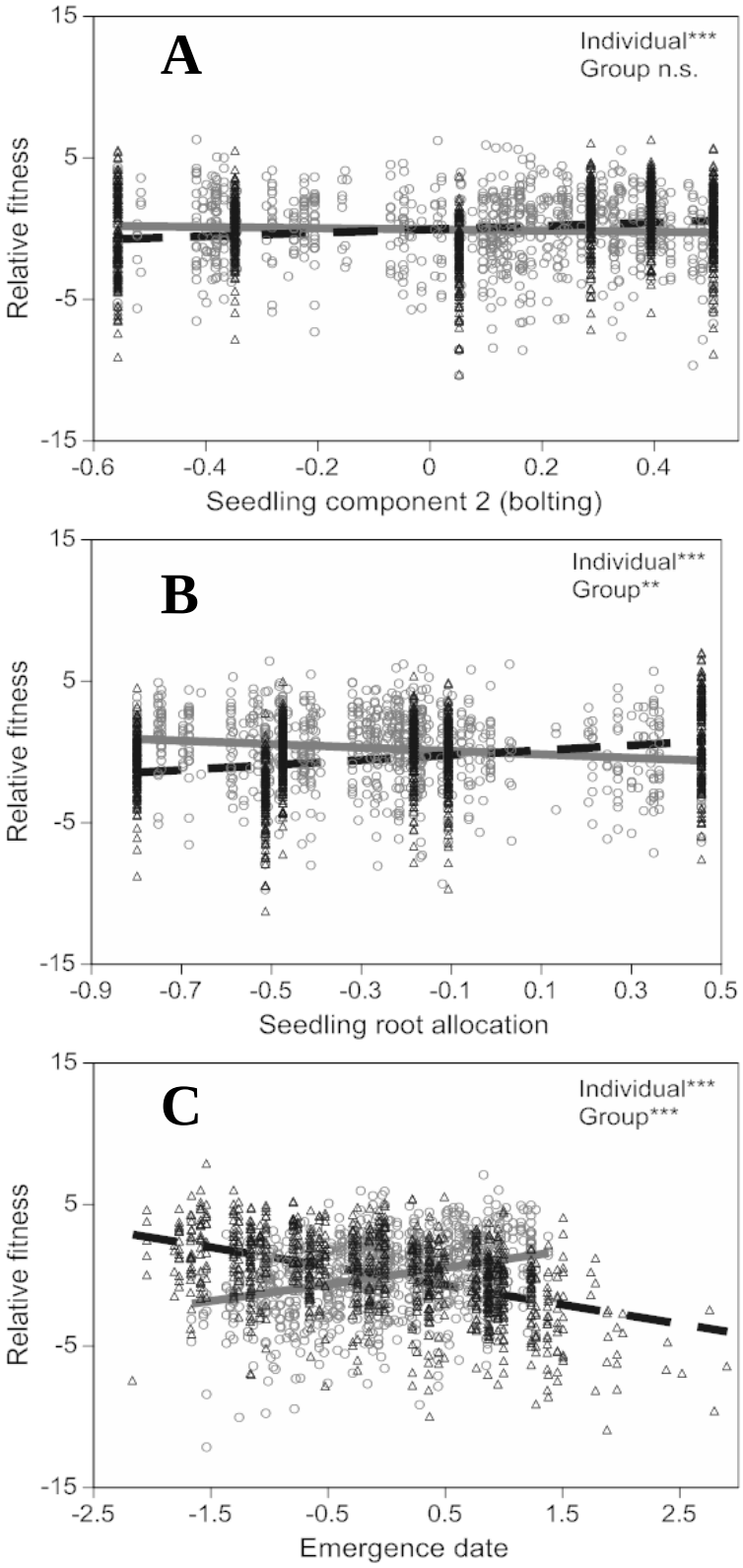

A
Individual***
Group n.s.
Relative fitness
15
5
-5
-15
-0.6
-0.4
-0.2
0
0.2
0.4
Seedling component 2 (bolting)
B
Individual***
Group**
Relative fitness
15
5
-5
-15
-0.9
-0.7
-0.5
-0.3
-0.1
0.1
0.3
0.5
Seedling root allocation
C
Individual***
Group***
Relative fitness
15
5
-5
-15
-2.5
-1.5
-0.5
0.5
1.5
2.5
Emergence date

Figure 15. Selection acting on component 2, root allocation and emergence date at low nutrients. Partial regression of relative fitness on (A) seedling component 2 (bolting), (B) average seedling root allocation and (C) emergence date. The black dashed line indicates directional selection on the individual trait and the grey solid line indicates directional selection on the group trait. Aboveground biomass, the measure of fitness, was relativized and component 2, root allocation and emergence were standardized. *P<0.05, **P<0.01, ***P<0.001

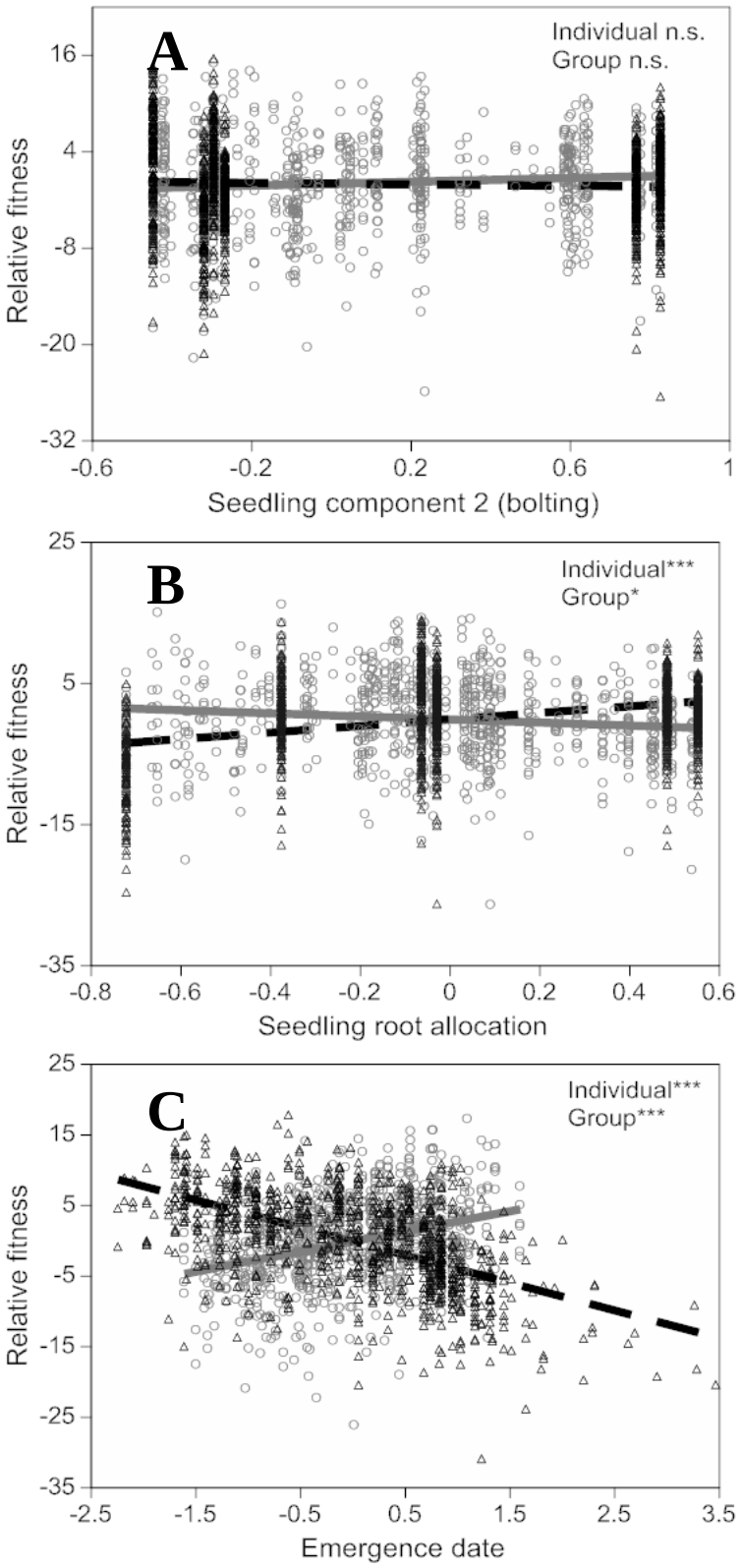

A
Individual n.s.
Group n.s.
Relative fitness
16
4
-8
-20
-32
-0.6
-0.2
0.2
0.6
1
Seedling component 2 (bolting)
B
Individual***
Group*
Relative fitness
25
5
-15
-35
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
Seedling root allocation
C
Individual***
Group***
Relative fitness
25
15
5
-5
-15
-25
-35
-2.5
-1.5
-0.5
0.5
1.5
2.5
3.5
Emergence date

Figure 16. Selection acting on component 3, root allocation and emergence date at high nutrients. Partial regression of relative fitness on (A) seedling component 3 (height), (B) average seedling root allocation and (C) emergence date. The black dashed line indicates directional selection on the individual trait and the grey solid line indicates directional selection on the group trait. Aboveground biomass, the measure of fitness, was relativized and component 3, root allocation and emergence were standardized. *P<0.05, **P<0.01, ***P<0.001

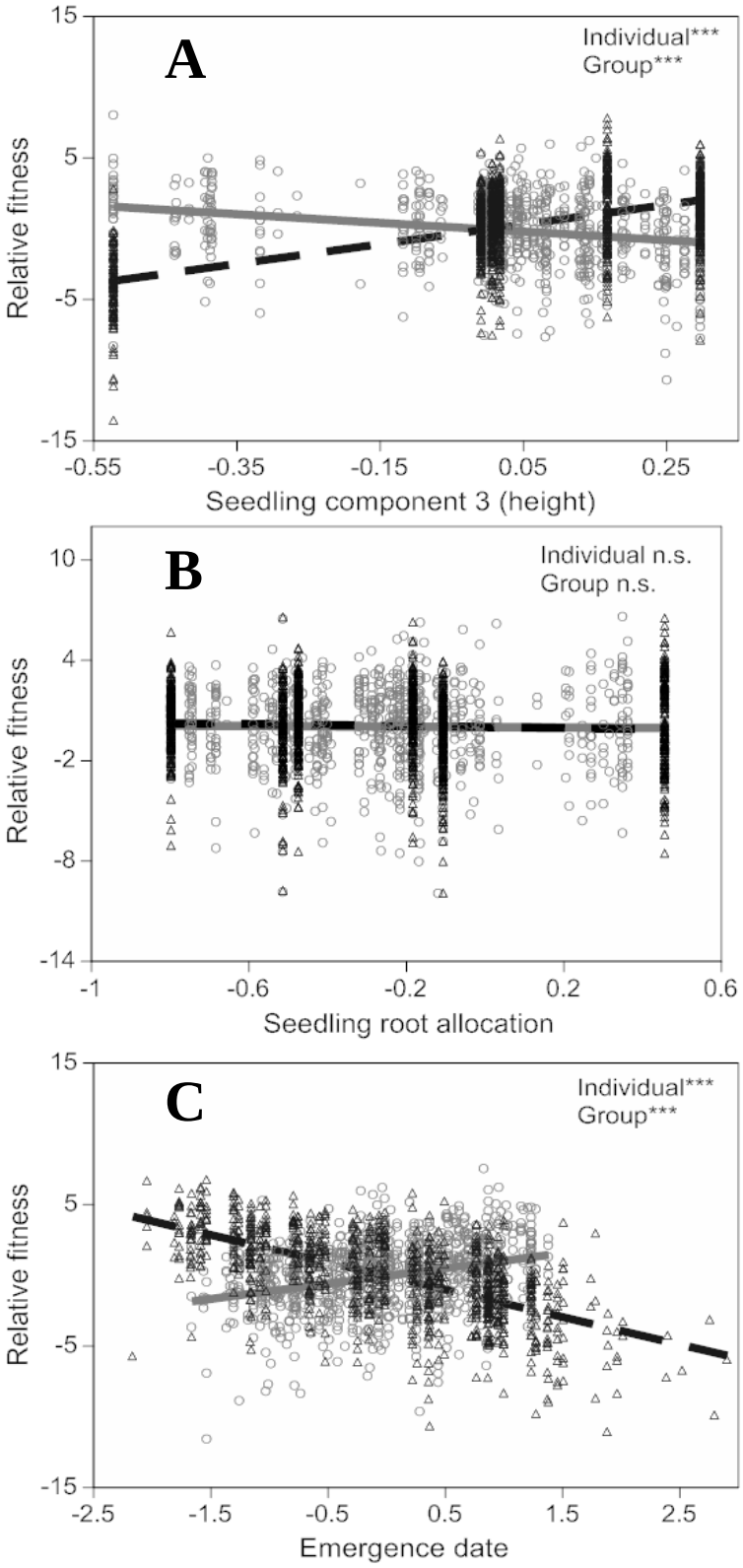

A
Individual***
Group***
Relative fitness
15
5
-5
-15
-0.55
-0.35
-0.15
0.05
0.25
Seedling component 3 (height)
B
Individual n.s.
Group n.s.
Relative fitness
10
4
-2
-8
-14
-1
-0.6
-0.2
0.2
0.6
Seedling root allocation
C
Individual***
Group***
Relative fitness
15
5
-5
-15
-2.5
-1.5
-0.5
0.5
1.5
2.5
Emergence date

Figure 17. Selection acting on component 3, root allocation and emergence date at low nutrients. Partial regression of relative fitness on (A) seedling component 3 (rosette), (B) average seedling root allocation and (C) emergence date. The black dashed line indicates directional selection on the individual trait and the grey solid line indicates directional selection on the group trait. Aboveground biomass, the measure of fitness, was relativized and component 3, root allocation and emergence were standardized. *P<0.05, **P<0.01, ***P<0.001

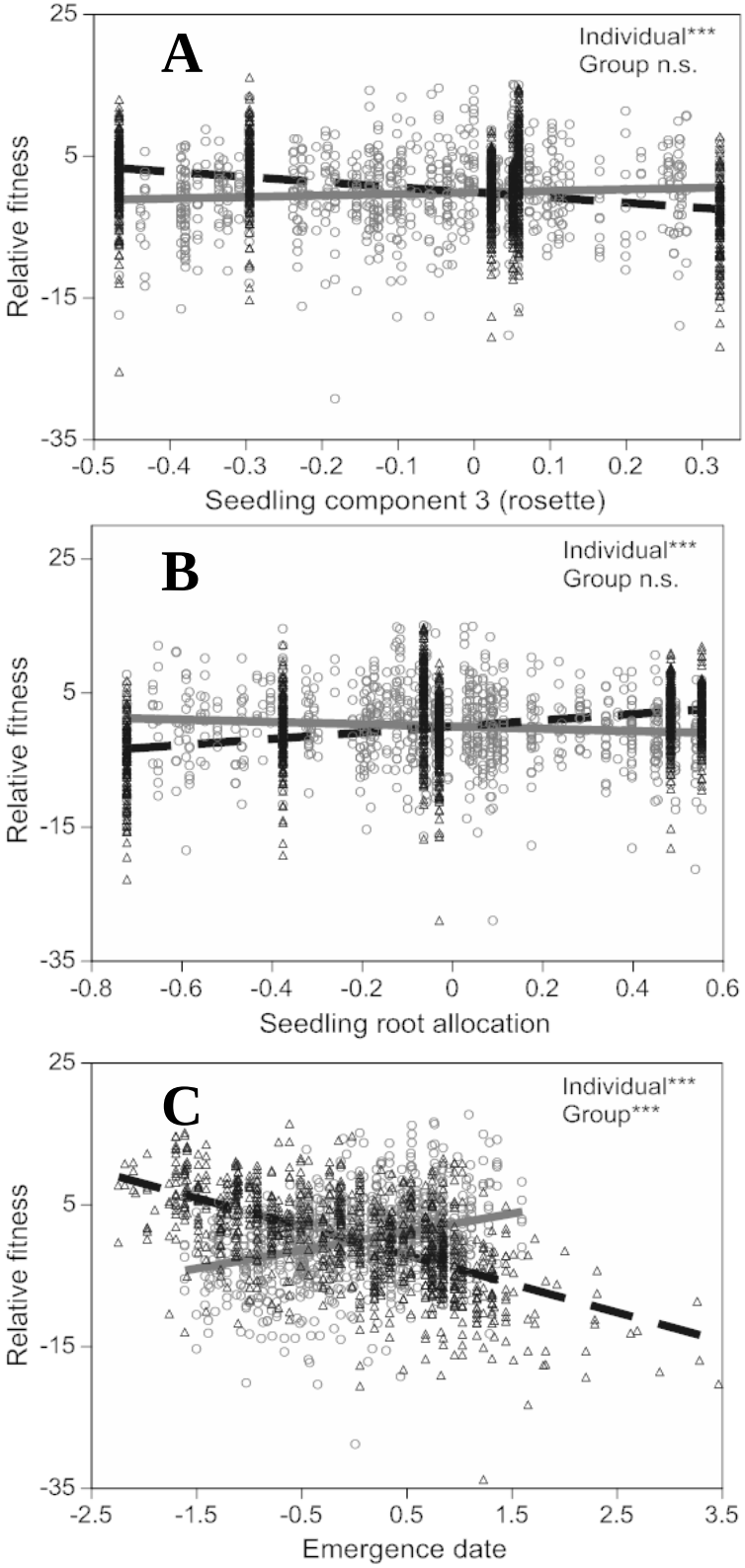

A
Individual***
Group n.s.
Relative fitness
25
5
-15
-35
-0.5 -0.4 -0.3 -0.2 -0.1 0 0.1 0.2 0.3
Seedling component 3 (rosette)
B
Individual***
Group n.s.
Relative fitness
25
5
-15
-35
-0.8 -0.6 -0.4 -0.2 0 0.2 0.4 0.6
Seedling root allocation
C
Individual***
Group***
Relative fitness
25
5
-15
-35
-2.5 -1.5 -0.5 0.5 1.5 2.5 3.5
Emergence date

Table 2.1. Effect of neighbour presence on meristem elongation for bolted *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of meristem height was used as the dependent variable. Nutrients and cultivar and their interactions were independent discrete variables and natural logarithm of stem mass and neighbour presence were covariates. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low. Error d.f. was 51. N=62. Overall model significances was P<0.0001.

Source		$\log_e$ meristem height	
	d.f.	*F*-ratio	*P*-value
Log_e stem mass	1	65.21	**<.0001**
Cultivar	5	2.00	0.0939
Nutrients	1	0.08	0.7841
Cultivar x nutrients	2	0.48	0.6245
Neighbour	1	1.98	0.1656

Notes: P-value <0.05 are bolded.

Table 2.2. Effect of neighbour identity on meristem elongation for bolted *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of meristem height was used as the dependent variable. nutrients, cultivar and identity of neighbour (opponent) and their interactions as independent discrete variables and natural logarithm of stem mass as the covariate. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low; Opponent treatments are alone, broccoli, cabbage, cauliflower, collards, kale or kohlrabi. Error d.f. was 35. N=62. Overall model significances was P<0.0001.

Source		$\log_e$ meristem height	
	d.f.	*F*-ratio	*P*-value
Log_e stem mass	1	37.38	**<.0001**
Cultivar	5	2.18	0.0784
Nutrients	1	0.87	0.3584
Cultivar x nutrients	2	2.33	0.1122
Opponent	6	1.33	0.2700
Cultivar x opponent	10	1.41	0.2183
Nutrients x opponent	1	3.23	0.0811

Notes: P-value <0.05 are bolded.

Table 2.3. Effect of social environment on meristem elongation for bolted *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of meristem height was used as the dependent variable. Nutrients, cultivar and social environment (kin) and their interactions were independent discrete variables and natural logarithm of stem mass as the covariate. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low; Kin treatments are alone, same cultivar or different cultivar. Error d.f. was 40. N=62. Overall model significances was P<0.0001.

Source		$\log_e$ meristem height	
	d.f.	*F*-ratio	*P*-value
Log_e stem mass	1	39.35	**<.0001**
Cultivar	5	1.56	0.1944
Nutrients	1	0.62	0.4349
Cultivar x nutrients	2	0.28	0.7574
Kin	2	0.03	0.9658
Cultivar x kin	8	1.92	0.0830
Nutrients x kin	1	0.02	0.8998
Cultivar x kin x nutrients	1	1.58	0.2167

Notes: P-value <0.05 are bolded.

Table 3.1. Effect of neighbour presence on aboveground biomass of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of aboveground biomass was used as the dependent variable. Nutrients and cultivar and their interactions were independent discrete variables and emergence date, harvest date and neighbour presence were covariates. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low. Error d.f. was 132. N=147. Overall model significances was P<0.0001.

Source		$\log_e$ aboveground biomass	
	d.f.	*F*-ratio	*P*-value
Cultivar	5	6.85	**<.0001**
Nutrients	1	630.55	**<.0001**
Cultivar x nutrients	5	1.19	0.3165
Neighbour	1	46.54	**<.0001**
Emergence date	1	45.23	**<.0001**
Harvest date	1	5.15	**0.0249**

Notes: P-value <0.05 are bolded.

Table 3.2. Effect of neighbour identity on aboveground biomass of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of aboveground biomass was used as the dependent variable. Nutrients, cultivar and identity of neighbour (opponent) and their interactions were independent discrete variables and emergence date as the covariate. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low; Opponent treatments are alone, broccoli, cabbage, cauliflower, collards, kale or kohlrabi. Error d.f. was 133. N=147. Overall model significances was P<0.0001.

Source	d.f.	$\log_e$ aboveground biomass	
		F-ratio	*P*-value
Cultivar	5	9.22	**<.0001**
Nutrients	1	787.97	**<.0001**
Opponent	6	9.56	**<.0001**
Emergence date	1	61.46	**<.0001**

Notes: P-value <0.05 are bolded.

Table 3.3. Effect of social environment on aboveground biomass of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of aboveground biomass was used as the dependent variable. Nutrients, cultivar and social environment (kin) and their interactions were independent discrete variables and emergence date as the covariate. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low; Kin treatments are alone, same cultivar or different cultivar. Error d.f. was 137. N=147. Overall model significances was P<0.0001.

Source		$\log_e$ aboveground biomass	
	d.f.	*F*-ratio	*P*-value
Cultivar	5	7.96	**<.0001**
Nutrients	1	709.39	**<.0001**
Kin	2	23.21	**<.0001**
Emergence date	1	59.61	**<.0001**

Notes: P-value <0.05 are bolded.

Table 4.1. Effect of neighbour presence on specific leaf area of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of largest leaf area was used as the dependent variable. Nutrients and cultivar and their interactions were independent discrete variables and the natural logarithm of largest leaf mass and neighbour presence were covariates. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low. Error d.f. was 131. N=145. Overall model significances was P<0.0001.

Source		$\log_e$ largest leaf area	
	d.f.	*F*-ratio	*P*-value
Log_e largest leaf mass	1	812.84	**<.0001**
Cultivar	5	4.00	**0.0021**
Nutrients	1	66.82	**<.0001**
Cultivar x nutrients	5	1.05	0.3928
Neighbour	1	8.36	**0.0045**

Notes: P-value <0.05 are bolded.

Table 4.2. Effect of neighbour identity on specific leaf area of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of largest leaf area was used as the dependent variable. Nutrients, cultivar and identity of neighbour (opponent) and their interactions were independent discrete variables and the natural logarithm of largest leaf mass as the covariate. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low; Opponent treatments are alone, broccoli, cabbage, cauliflower, collards, kale or kohlrabi. Error d.f. was 101. N=145. Overall model significances was P<0.0001.

Source		log_e largest leaf area	
	d.f.	*F*-ratio	*P*-value
Log_e largest leaf mass	1	523.35	**<.0001**
Cultivar	5	2.88	**0.0179**
Nutrients	1	45.87	**<.0001**
Cultivar x nutrients	5	0.76	0.5803
Opponent	6	1.62	0.1481
Cultivar x opponent	14	1.15	0.3281
Nutrients x opponent	5	0.69	0.6309
Cultivar x nutrients x opponent	6	0.89	0.5033

Notes: P-value <0.05 are bolded.

Table 4.3. Effect of social environment on specific leaf area of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of largest leaf area was used as the dependent variable. Nutrients, cultivar and social environment (kin) and their interactions were independent discrete variables and the natural logarithm of largest leaf mass and harvest date were covariates. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low; Kin treatments are alone, same cultivar or different cultivar. Error d.f. was 134. N=145. Overall model significances was P<0.0001.

Source		$\log_e$ largest leaf area	
	d.f.	*F*-ratio	*P*-value
Log_e largest leaf mass	1	815.75	**<.0001**
Cultivar	5	3.74	**0.0033**
Nutrients	1	78.82	**<.0001**
Kin	2	7.44	**0.0009**
Harvest date	1	2.48	0.1173

Notes: P-value <0.05 are bolded.

Table 5.1. Effect of neighbour presence on leaf shape of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of largest leaf length was used as the dependent variable. Nutrients and cultivar and their interactions were independent discrete variables and the natural logarithm of largest leaf width, emergence date and neighbour presence were covariates. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low. Error d.f. was 132. N=147. Overall model significances was P<0.0001.

Source		$\log_e$ largest leaf length	
	d.f.	*F*-ratio	*P*-value
Log_e largest leaf width	1	149.75	**<.0001**
Cultivar	5	35.41	**<.0001**
Nutrients	1	27.10	**<.0001**
Cultivar x nutrients	5	0.88	0.4967
Neighbour	1	3.28	0.0725
Emergence date	1	9.07	**0.0031**

Notes: P-value <0.05 are bolded.

Table 5.2. Effect of neighbour identity on leaf shape of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of largest leaf length was used as the dependent variable. Nutrients, cultivar and identity of neighbour (opponent) and their interactions were independent discrete variables and the natural logarithm of largest leaf width and emergence date were covariates. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low; Opponent treatments are alone, broccoli, cabbage, cauliflower, collards, kale or kohlrabi. Error d.f. was 103. N=147. Overall model significances was P<0.0001.

Source		$\log_e$ largest leaf length	
	d.f.	*F*-ratio	*P*-value
Log_e largest leaf width	1	90.81	**<.0001**
Cultivar	5	18.63	**<.0001**
Nutrients	1	21.25	**<.0001**
Cultivar x nutrients	5	0.94	0.4610
Opponent	6	0.61	0.7208
Cultivar x opponent	14	0.50	0.9255
Nutrients x opponent	5	0.56	0.7268
Cultivar x nutrients x opponent	6	1.93	0.0837
Emergence date	1	10.13	**0.0019**

Notes: P-value <0.05 are bolded.

Table 5.3. Effect of social environment on leaf shape of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of largest leaf length was used as the dependent variable. Nutrients, cultivar and social environment (kin) and their interactions were independent discrete variables and the natural logarithm of largest leaf width and emergence date were covariates. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low; Kin treatments are alone, same cultivar or different cultivar. Error d.f. was 115. N=147. Overall model significances was P<0.0001.

Source		$\log_e$ largest leaf length	
	d.f.	*F*-ratio	*P*-value
Log_e largest leaf width	1	128.12	**<.0001**
Cultivar	5	33.09	**<.0001**
Nutrients	1	26.34	**<.0001**
Cultivar x nutrients	5	0.47	0.7986
Kin	2	1.70	0.1874
Cultivar x kin	8	0.83	0.5795
Nutrients x kin	2	1.29	0.2784
Cultivar x kin x nutrients	6	1.06	0.3879
Emergence date	1	7.53	**0.0070**

Notes: P-value <0.05 are bolded.

Table 6.1. Effect of neighbour presence on stem to leaf allocation of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of stem mass was used as the dependent variable. Nutrients and cultivar and their interactions were independent discrete variables and the natural logarithm of leaf mass and neighbour presence were covariates. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low. Error d.f. was 131. N=145. Overall model significances was P<0.0001.

Source		$\log_e$ stem mass	
	d.f.	*F*-ratio	*P*-value
Log_e leaf mass	1	192.13	**<.0001**
Cultivar	5	15.16	**<.0001**
Nutrients	1	0.47	0.4942
Cultivar x nutrients	5	1.13	0.3459
Neighbour	1	12.33	**0.0006**

Notes: P-value <0.05 are bolded.

Table 6.2. Effect of neighbour identity on stem to leaf allocation of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of stem mass was used as the dependent variable. Nutrients, cultivar and identity of neighbour (opponent) and their interactions were independent discrete variables and the natural logarithm of leaf mass as the covariate. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low; Opponent treatments are alone, broccoli, cabbage, cauliflower, collards, kale or kohlrabi. Error d.f. was 103. N=147. Overall model significances was P<0.0001.

Source		$\log_e$ stem mass	
	d.f.	*F*-ratio	*P*-value
Log_e leaf mass	1	97.86	**<.0001**
Cultivar	5	8.07	**<.0001**
Nutrients	1	0.20	0.6545
Cultivar x nutrients	5	1.64	0.1554
Opponent	6	1.72	0.1236
Cultivar x opponent	14	1.03	0.4259
Nutrients x opponent	5	0.92	0.4690
Cultivar x nutrients x opponent	6	1.40	0.2233

Notes: P-value <0.05 are bolded.

Table 6.3. Effect of social environment on stem to leaf allocation of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of stem mass was used as the dependent variable. Nutrients, cultivar and social environment (kin) and their interactions were independent discrete variables and the natural logarithm of leaf mass as the covariate. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low; Kin treatments are alone, same cultivar or different cultivar. Error d.f. was 136. N=146. Overall model significances was P<0.0001.

Source		$\log_e$ stem mass	
	d.f.	*F*-ratio	*P*-Value
Log_e leaf mass	1	193.30	**<.0001**
Cultivar	5	17.01	**<.0001**
Nutrients	1	2.09	0.1502
Kin	2	7.06	**0.0012**

Notes: P-value <0.05 are bolded.

Table 7.1. Effect of neighbour presence on natural height of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of natural height was used as the dependent variable. Nutrients and cultivar and their interactions were independent discrete variables and the natural logarithm of stem mass, emergence date and neighbour presence were covariates. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low. Error d.f. was 132. N=147. Overall model significances was P<0.0001.

Source		$\log_e$ natural height	
	d.f.	*F*-ratio	*P*-value
Log_e stem mass	1	4.69	**0.0321**
Cultivar	5	1.60	0.1638
Nutrients	1	0.26	0.6109
Cultivar x nutrients	5	0.83	0.5329
Neighbour	1	0.75	0.3867
Emergence date	1	7.42	**0.0073**

Notes: P-value <0.05 are bolded.

Table 7.2. Effect of neighbour identity on natural height of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of natural height was used as the dependent variable. Nutrients, cultivar and identity of neighbour (opponent) and their interactions were independent discrete variables and the natural logarithm of stem mass and emergence date were covariates. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low; Opponent treatments are alone, broccoli, cabbage, cauliflower, collards, kale or kohlrabi. Error d.f. was 130. N=145. Overall model significances was P<0.0001.

Source		$\log_e$ natural height	
	d.f.	*F*-ratio	*P*-value
Log_e stem mass	1	18.87	<.0001
Cultivar	5	2.14	0.0648
Nutrients	1	0.17	0.6838
Opponent	6	0.47	0.8311
Emergence date	1	2.87	0.0929

Notes: P-value <0.05 are bolded.

Table 7.3. Effect of social environment on natural height of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of natural height was used as the dependent variable. Nutrients, cultivar and social environment (kin) and their interactions were independent discrete variables and the natural logarithm of stem mass as the covariate. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low; Kin treatments are alone, same cultivar or different cultivar. Error d.f. was 137. N=147. Overall model significances was P<0.0001.

Source		$\log_e$ natural height	
	d.f.	*F*-ratio	*P*-value
Log_e stem mass	1	8.85	**0.0035**
Cultivar	5	0.67	0.6483
Nutrients	1	1.78	0.1840
Kin	2	2.25	0.1094

Notes: P-value <0.05 are bolded.

Table 8.1. Effect of neighbour presence on root allocation and total biomass of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of average total biomass of a pot was used as the dependent variable. Nutrients was an independent discrete variable and neighbour presence was the covariate. In the analysis of covariance, the natural logarithm of average root mass of a pot was used as the dependent variable. Nutrients was an independent discrete variable and natural logarithm of average leaf mass of a pot and neighbour presence were covariates. Nutrient level is high or low. Error d.f. was 109 for $\log_e$ root mass and 110 for $\log_e$ total biomass. N=113. Overall model significances was P<0.0001.

Source		$\log_e$ total biomass		$\log_e$ root mass	
	d.f.	*F*-ratio	*P*-value	*F*-ratio	*P*-value
Log_e leaf mass	1			28.77	**<.0001**
Nutrients	1	501.56	**<.0001**	0.39	0.5313
Neighbour	1	5.00	**0.0273**	10.27	**0.0018**

Notes: P-value <0.05 are bolded.

Table 8.2. Effect of neighbour identity on root allocation and total biomass of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of covariance, the natural logarithm of average total biomass of a pot was used as the dependent variable. Nutrients was an independent discrete variable and the frequency of cultivars were covariates. In the analysis of covariance, the natural logarithm of average root mass of a pot was used as the dependent variable. Nutrients was an independent discrete variable and natural logarithm of average leaf mass of a pot and the frequency of cultivars were covariates. Nutrient level is high or low. Error d.f. was 104 for $\log_e$ root mass and 105 for $\log_e$ total biomass. N=113. Overall model significances was P<0.0001.

Source		$\log_e$ total biomass		$\log_e$ root mass	
	d.f.	*F*-ratio	*P*-value	*F*-ratio	*P*-value
Log_e leaf mass	1			22.28	**<.0001**
Nutrients	1	551.24	**<.0001**	0.48	0.4906
Freq. of broccoli	1	9.82	**0.0022**	0.16	0.6920
Freq. of cabbage	1	13.48	**0.0004**	0.38	0.5399
Freq. of cauliflower	1	1.93	0.1676	6.41	**0.0128**
Freq. of collards	1	0.00	0.9935	0.29	0.5894
Freq. of kale	1	4.68	**0.0328**	3.33	0.0708
Freq. of kohlrabi	1	9.60	**0.0025**	6.33	**0.0134**

Notes: P-value <0.05 are bolded.

Table 8.3. Effect of social environment on root allocation and total biomass of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). In the analysis of variance, the natural logarithm of average total biomass of a pot was used as the dependent variable. Nutrients and social environment (kin) and their interactions were independent discrete variables. In the analysis of covariance, the natural logarithm of average root mass of a pot was used as the dependent variable. Nutrients and social environment (kin) were independent discrete variables and natural logarithm of average leaf mass of a pot as the covariate. Nutrient level is high or low nutrient level; Kin treatment is alone, same cultivar, different cultivar. Error d.f. was 106 for $\log_e$ root mass and 107 for $\log_e$ total biomass. N=113. Overall model significances was P<0.0001.

Source		$\log_e$ total biomass		$\log_e$ root mass	
	d.f.	*F*-ratio	*P*-value	*F*-ratio	*P*-value
Log_e leaf mass	1			26.46	**<.0001**
Nutrients	1	307.06	**<.0001**	0.19	0.6651
Kin	2	4.35	**0.0152**	5.55	**0.0051**
Nutrients x kin	2	0.45	0.6362	0.37	0.6898

Notes: P-value <0.05 are bolded.

Table 8.4. Root allocation and total biomass analysis of *B. oleracea* cultivars grown alone in a greenhouse (Experiment 1). In the analysis of variance, the natural logarithm of average total biomass of a pot was used as the dependent variable and nutrients and cultivar were independent discrete variables. In the analysis of covariance, the natural logarithm of average root mass of a pot was used as the dependent variable, nutrients and cultivar were independent discrete variables and natural logarithm of average leaf mass of a pot as the covariate. Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Nutrient level is high or low. Error d.f. was 67 for $\log_e$ total biomass and 65 for $\log_e$ root mass. N=78 for $\log_e$ total biomass and N=79 for $\log_e$ root mass. Overall model significances was P<0.0001.

Source		$\log_e$ total biomass		$\log_e$ root mass	
	d.f.	*F*-ratio	*P*-value	*F*-ratio	*P*-value
Log_e leaf mass	1			11.10	**0.0014**
Nutrients	1	218.19	**<.0001**	2.31	0.1331
Cultivar	5	6.15	**<.0001**	3.00	**0.0170**
Nutrients x cultivar	5	2.50	**0.0389**	0.29	0.9148

Notes: P-value <0.05 are bolded.

Table 9.1. Generalized linear model (GENMOD) for bolting of *B. oleracea* cultivars grown in the presence or absence of a neighbour in a greenhouse (Experiment 1). The likelihood to bolt was used as the dependent variable, nutrients and cultivar were independent discrete variables and neighbour presence as the covariate. Nutrient level is high or low; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi. N=147.

Source	Bolting *P*
Nutrients	**<.0001**
Cultivar	**0.0097**
Neighbour	0.1566

Notes: P-value <0.05 are bolded.

Table 9.2. Generalized linear model (GENMOD) for bolting of *B. oleracea* grown in groups of 6 plants in a greenhouse (Experiment 2). The likelihood to bolt was used as the dependent variable, nutrients and cultivar were independent discrete variables and the number of plants in the pot as the covariate. Nutrient level is high or low; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi. N=523.

Source	Bolting *P*
Nutrients	**<.0001**
Cultivar	**<.0001**
Number of plants	**0.0122**

Notes: P-value <0.05 are bolded.

Table 10.1. Effect of cultivar frequency on meristem elongation for bolted *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of meristem height was used as the dependent variable, nutrients, bench and cultivar were independent discrete variables and natural logarithm of stem mass and the frequency of cultivars were covariates. Nutrient level is high or low; Bench is 8 or 9; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi. Error d.f. was 289. N=318. Overall model significances was P<0.0001.

Source		$\log_e$ meristem height	
	d.f.	*F*-ratio	*P*-value
Log_e stem mass	1	186.99	**<.0001**
Nutrients	1	6.84	**0.0094**
Bench	1	6.78	**0.0097**
Nutrients x bench	1	5.06	**0.0252**
Cultivar	5	6.89	**<.0001**
Nutrients x cultivar	5	5.03	**0.0002**
Bench x cultivar	5	2.12	0.0634
Nutrients x bench x cultivar	3	1.57	0.1967
Frequency of broccoli	1	0.23	0.6350
Frequency of cabbage	1	0.07	0.7895
Frequency of cauliflower	1	1.73	0.1900
Frequency of collards	1	0.46	0.4963
Frequency of kale	1	3.26	0.0720
Frequency of kohlrabi	1	2.99	0.0848

Notes: P-value <0.05 are bolded.

Table 10.2. Effect of social environment and number of plants in the pot on meristem elongation for bolted *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of meristem height was used as the dependent variable, nutrients, bench, cultivar and social environment (kin) were independent discrete variables and natural logarithm of stem mass and number of plants in the pot were covariates. Nutrient level is high or low; Bench is 8 or 9; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Kin treatments are same cultivar or different cultivar. Error d.f. was 300. N=318. Overall model significances was P<0.0001.

Source		$\log_e$ meristem height	
	d.f.	*F*-ratio	*P*-value
Log_e stem mass	1	172.18	**<.0001**
Nutrients	1	8.08	**0.0048**
Bench	1	4.45	**0.0358**
Nutrients x bench	1	6.17	**0.0135**
Cultivar	5	14.46	**<.0001**
Nutrients x cultivar	5	4.97	**0.0002**
Kin	1	0.04	0.8456
Nutrients x kin	1	0.17	0.6775
Number of plants	1	2.66	0.1039

Notes: P-value <0.05 are bolded.

Table 11.1. Effect of cultivar frequency on stem to leaf allocation of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of stem mass was used as the dependent variable, nutrients, bench and cultivar were independent discrete variables and natural logarithm of leaf mass and the frequency of cultivars were covariates. Nutrient level is high or low; Bench is 8 or 9; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi. Error d.f. was 492. N=524. Overall model significances was P<0.0001.

Source		$\log_e$ stem mass	
	d.f.	*F*-ratio	*P*-value
Log_e leaf mass	1	1037.77	**<.0001**
Nutrients	1	38.29	**<.0001**
Bench	1	4.14	**0.0424**
Nutrients x bench	1	1.91	0.1675
Cultivar	5	43.09	**<.0001**
Nutrients x cultivar	5	2.53	**0.0281**
Bench x cultivar	5	0.76	0.5775
Nutrients x bench x cultivar	5	0.85	0.5167
Frequency of broccoli	1	1.49	0.2222
Frequency of cabbage	1	0.08	0.7768
Frequency of cauliflower	1	2.52	0.1130
Frequency of collards	1	6.49	**0.0112**
Frequency of kale	1	8.46	**0.0038**
Frequency of kohlrabi	1	5.18	**0.0233**
Emergence date	1	6.36	**0.0120**

Notes: P-value <0.05 are bolded.

Table 11.2. Effect of social environment and number of plants in the pot on stem to leaf allocation of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of stem mass was used as the dependent variable, nutrients, bench, cultivar and social environment (kin) were independent discrete variables and natural logarithm of leaf mass, emergence date and the number of plants in the pot were covariates. Nutrient level is high or low; Bench is 8 or 9; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Kin treatments are same cultivar or different cultivar. Error d.f. was 472. N=523. Overall model significances was P<0.0001.

Source		$\log_e$ stem mass	
	d.f.	*F*-ratio	*P*-value
Log_e leaf mass	1	964.85	**<.0001**
Nutrients	1	25.75	**<.0001**
Bench	1	3.20	0.0741
Nutrients x bench	1	4.46	**0.0352**
Cultivar	5	60.61	**<.0001**
Nutrients x cultivar	5	2.24	**0.0497**
Bench x cultivar	5	0.88	0.4941
Nutrients x bench x cultivar	5	1.32	0.2524
Kin	1	0.00	0.9633
Nutrients x kin	1	3.88	**0.0495**
Bench x kin	1	0.34	0.5579
Nutrients x bench x kin	1	4.36	**0.0374**
Cultivar x kin	5	0.43	0.8246
Nutrients x cultivar x kin	5	1.66	0.1431
Bench x cultivar x kin	5	0.37	0.8709
Nutrients x bench x cultivar x kin	5	1.43	0.2131
Number of plants	1	7.94	**0.0050**
Emergence date	1	6.97	**0.0085**

Notes: P-value <0.05 are bolded.

Table 12.1. Effect of cultivar frequency on aboveground biomass of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of aboveground biomass was used as the dependent variable, nutrients, bench and cultivar were independent discrete variables and the frequency of cultivars were covariates. Nutrient level is high or low; Bench is 8 or 9; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi. Error d.f. was 492. N=524. Overall model significances was P<0.0001.

Source		$\log_e$ aboveground biomass	
	d.f.	*F*-ratio	*P*-value
Nutrients	1	1066.04	**<.0001**
Bench	1	0.07	0.7860
Nutrients x bench	1	35.55	**<.0001**
Cultivar	5	24.29	**<.0001**
Nutrients x cultivar	5	5.44	**<.0001**
Bench x cultivar	5	3.68	**0.0028**
Nutrients x bench x cultivar	5	3.19	**0.0076**
Frequency of broccoli	1	10.56	**0.0012**
Frequency of cabbage	1	2.07	0.1506
Frequency of cauliflower	1	16.93	**<.0001**
Frequency of collards	1	16.43	**<.0001**
Frequency of kale	1	5.32	**0.0215**
Frequency of kohlrabi	1	8.87	**0.0030**
Emergence date	1	249.53	**<.0001**
Harvest date	1	30.95	**<.0001**

Notes: P-value <0.05 are bolded.

Table 12.2. Effect of social environment and number of plants in the pot on aboveground biomass of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of aboveground biomass was used as the dependent variable, nutrients, bench, cultivar and social environment (kin) were independent discrete variables and emergence date, harvest date and the number of plants in the pot were covariates. Nutrient level is high or low; Bench is 8 or 9; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Kin treatments are same cultivar or different cultivar. Error d.f. was 473. N=524. Overall model significances was P<0.0001.

Source		$\log_e$ aboveground biomass	
	d.f.	*F*-ratio	*P*-value
Nutrients	1	923.62	**<.0001**
Bench	1	0.00	0.9990
Nutrients x bench	1	33.63	**<.0001**
Cultivar	5	33.16	**<.0001**
Nutrients x cultivar	5	3.76	**0.0024**
Bench x cultivar	5	2.66	**0.0221**
Nutrients x bench x cultivar	5	3.26	**0.0066**
Kin	1	4.14	**0.0423**
Nutrients x kin	1	0.08	0.7765
Bench x kin	1	1.30	0.2552
Nutrients x bench x kin	1	0.44	0.5054
Cultivar x kin	5	1.13	0.3445
Nutrients x cultivar x kin	5	1.99	0.0792
Bench x cultivar x kin	5	1.24	0.2891
Nutrients x bench x cultivar x kin	5	1.30	0.2632
Number of plants	1	10.08	**0.0016**
Emergence date	1	234.41	**<.0001**
Harvest date	1	31.33	**<.0001**

Notes: P-value <0.05 are bolded.

Table 13.1. Effect of cultivar frequency on specific leaf area of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of largest leaf area was used as the dependent variable, nutrients, bench and cultivar were independent discrete variables and natural logarithm of largest leaf mass and the frequency of cultivars were covariates. Nutrient level is high or low; Bench is 8 or 9; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi. Error d.f. was 489. N=520. Overall model significances was P<0.0001.

Source		$\log_e$ largest leaf area	
	d.f.	*F*-ratio	*P*-value
Log_e largest leaf mass	1	4339.89	**<.0001**
Nutrients	1	277.36	**<.0001**
Bench	1	4.20	**0.0409**
Nutrients x bench	1	22.92	**<.0001**
Cultivar	5	6.68	**<.0001**
Nutrients x cultivar	5	2.04	0.0722
Bench x cultivar	5	0.91	0.4733
Nutrients x bench x cultivar	5	3.39	**0.0051**
Frequency of broccoli	1	28.07	**<.0001**
Frequency of cabbage	1	5.54	**0.0190**
Frequency of cauliflower	1	16.93	**<.0001**
Frequency of collards	1	28.18	**<.0001**
Frequency of kale	1	32.22	**<.0001**
Frequency of kohlrabi	1	25.07	**<.0001**

Notes: P-value <0.05 are bolded.

Table 13.2. Effect of social environment and number of plants in the pot on specific leaf area of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of largest leaf area was used as the dependent variable, nutrients, bench, cultivar and social environment (kin) were independent discrete variables and natural logarithm of largest leaf mass and the number of plants in the pot were covariates. Nutrient level is high or low; Bench is 8 or 9; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Kin treatments are same cultivar or different cultivar. Error d.f. was 470. N=520. Overall model significances was P<0.0001.

Source		$\log_e$ largest leaf area	
	d.f.	*F*-ratio	*P*-value
Log_e largest leaf mass	1	4216.23	**<.0001**
Nutrients	1	283.92	**<.0001**
Bench	1	6.42	**0.0116**
Nutrients x bench	1	18.50	**<.0001**
Cultivar	5	12.42	**<.0001**
Nutrients x cultivar	5	2.11	0.0631
Bench x cultivar	5	1.23	0.2934
Nutrients x bench x cultivar	5	3.38	**0.0052**
Kin	1	0.42	0.5152
Nutrients x kin	1	4.55	**0.0335**
Bench x kin	1	0.32	0.5695
Nutrients x bench x kin	1	3.94	**0.0478**
Cultivar x kin	5	0.65	0.6625
Nutrients x cultivar x kin	5	3.12	**0.0088**
Bench x cultivar x kin	5	1.40	0.2225
Nutrients x bench x cultivar x kin	5	0.50	0.7725
Number of plants	1	20.11	**<.0001**

Notes: P-value <0.05 are bolded.

Table 14.1. Effect of cultivar frequency on leaf shape of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of largest leaf length was used as the dependent variable, nutrients, bench and cultivar were independent discrete variables and natural logarithm of largest leaf width, emergence date and the frequency of cultivars were covariates. Nutrient level is high or low; Bench is 8 or 9; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi. Error d.f. was 492. N=524. Overall model significances was P<0.0001.

Source		$\log_e$ largest leaf length	
	d.f.	*F*-ratio	*P*-value
Log_e largest leaf width	1	1626.81	**<.0001**
Nutrients	1	51.33	**<.0001**
Bench	1	17.79	**<.0001**
Nutrients x bench	1	0.03	0.8718
Cultivar	5	25.90	**<.0001**
Nutrients x cultivar	5	1.11	0.3534
Bench x cultivar	5	3.57	**0.0035**
Nutrients x bench x cultivar	5	1.47	0.1969
Frequency of broccoli	1	7.53	**0.0063**
Frequency of cabbage	1	0.24	0.6278
Frequency of cauliflower	1	5.58	**0.0186**
Frequency of collards	1	0.25	0.6191
Frequency of kale	1	9.65	**0.0020**
Frequency of kohlrabi	1	3.29	0.0701
Emergence date	1	15.24	**0.0001**

Notes: P-value <0.05 are bolded.

Table 14.2. Effect of social environment and number of plants in the pot on leaf shape of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of largest leaf length was used as the dependent variable, nutrients, bench, cultivar and social environment (kin) were independent discrete variables and natural logarithm of largest leaf width, emergence date and the number of plants in the pot were covariates. Nutrient level is high or low; Bench is 8 or 9; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Kin treatments are same cultivar or different cultivar. Error d.f. was 473. N=524. Overall model significances was P<0.0001.

Source		$\log_e$ largest leaf length	
	d.f.	*F*-ratio	*P*-value
Log_e largest leaf width	1	1513.54	**<.0001**
Nutrients	1	81.29	**<.0001**
Bench	1	19.73	**<.0001**
Nutrients x bench	1	1.15	0.2842
Cultivar	5	54.32	**<.0001**
Nutrients x cultivar	5	1.03	0.4005
Bench x cultivar	5	2.74	**0.0186**
Nutrients x bench x cultivar	5	1.07	0.3754
Kin	1	0.07	0.7865
Nutrients x kin	1	0.12	0.7294
Bench x kin	1	1.51	0.2194
Nutrients x bench x kin	1	0.97	0.3244
Cultivar x kin	5	2.19	0.0541
Nutrients x cultivar x kin	5	1.16	0.3284
Bench x cultivar x kin	5	0.64	0.6668
Nutrients x bench x cultivar x kin	5	1.42	0.2166
Number of plants	1	4.81	**0.0289**
Emergence date	1	11.29	**0.0008**

Notes: P-value <0.05 are bolded.

Table 15.1. Effect of cultivar frequency on natural height of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of natural height was used as the dependent variable, nutrients, bench and cultivar were independent discrete variables and natural logarithm of stem mass, harvest date and the frequency of cultivars were covariates. Nutrient level is high or low; Bench is 8 or 9; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi. Error d.f. was 490. N=522. Overall model significances was P<0.0001.

Source		$\log_e$ natural height	
	d.f.	*F*-ratio	*P*-value
Log_e stem mass	1	222.09	**<.0001**
Nutrients	1	16.49	**<.0001**
Cultivar	5	2.40	**0.0360**
Nutrients x cultivar	5	0.61	0.6916
Bench	1	0.63	0.4289
Nutrients x bench	1	4.01	**0.0458**
Bench x cultivar	5	1.52	0.1805
Nutrients x bench x cultivar	5	1.17	0.3227
Frequency of broccoli	1	1.15	0.2850
Frequency of cabbage	1	0.55	0.4584
Frequency of cauliflower	1	1.62	0.2034
Frequency of collards	1	0.91	0.3398
Frequency of kale	1	0.56	0.4537
Frequency of kohlrabi	1	0.16	0.6868
Harvest date	1	4.53	**0.0338**

Notes: P-value <0.05 are bolded.

Table 15.2. Effect of social environment and number of plants in the pot on natural height of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of natural height was used as the dependent variable, nutrients, bench, cultivar and social environment (kin) were independent discrete variables and natural logarithm of stem mass and the number of plants in the pot were covariates. Nutrient level is high or low; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Kin treatments are same cultivar or different cultivar. Error d.f. was 472. N=522. Overall model significances was P<0.0001.

Source		$\log_e$ natural height	
	d.f.	*F*-ratio	*P*-value
Log_e stem mass	1	220.54	**<.0001**
Nutrients	1	27.26	**<.0001**
Cultivar	5	2.80	**0.0168**
Nutrients x cultivar	5	1.74	0.1233
Kin	1	2.13	0.1447
Nutrients x kin	1	0.98	0.3222
Cultivar x kin	5	1.14	0.3364
Nutrients x cultivar x kin	5	1.21	0.3039
Bench	1	20.06	**<.0001**
Nutrients x bench	1	0.09	0.7622
Bench x cultivar	5	1.78	0.1160
Bench x nutrients x cultivar	5	1.86	0.1001
Bench x kin	1	2.37	0.1246
Nutrients x bench x kin	1	1.43	0.2324
Bench x cultivar x kin	5	1.21	0.3021
Nutrients x bench x cultivar x kin	5	2.78	**0.0175**
Number of plants	1	0.66	0.4166

Notes: P-value <0.05 are bolded.

Table 16.1. Effect of cultivar frequency on root allocation and total biomass of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of average total biomass of a pot was used as the dependent variable, nutrients, root collect method and bench were independent discrete variables and harvest date and the frequency of cultivars were covariates. In the analysis of covariance, the square root of average root mass of a pot was used as the dependent variable, nutrients, root collect method and bench were independent discrete variables and square root of average leaf mass of a pot and the frequency of cultivars were covariates. Nutrient level is high or low; Bench is 8 or 9; Root collection methods are roots or roots and fabric. Error d.f. was 113 for $\log_e$ total biomass and 112 for square root root mass. N=124. Overall model significances was P<0.0001.

Source		$\log_e$ total biomass		square root root mass	
	d.f.	*F*-ratio	*P*-value	*F*-ratio	*P*-value
Square root leaf mass	1			111.38	**<.0001**
Nutrients	1	428.76	**<.0001**	5.29	**0.0232**
Bench	1	0.50	0.4819	11.87	**0.0008**
Nutrients x bench	1	15.47	**0.0001**	5.02	**0.0270**
Frequency of broccoli	1	2.07	0.1527	9.80	**0.0022**
Frequency of cabbage	1	8.64	**0.0040**	0.83	0.3636
Frequency of cauliflower	1	0.10	0.7580	2.08	0.1519
Frequency of collards	1	0.01	0.9420	1.04	0.3104
Frequency of kale	1	3.34	0.0702	1.10	0.2958
Frequency of kohlrabi	1	7.01	**0.0093**	2.98	0.0872
Root collection method	1			41.32	**<.0001**
Harvest date	1	19.50	**<.0001**		

Notes: P-value <0.05 are bolded.

Table 16.2. Effect of social environment and number of plants in the pot on root allocation and total biomass of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of average total biomass of a pot was used as the dependent variable, nutrients, root collect method and bench were independent discrete variables and the number of plants in the pot as the covariate. In the analysis of covariance, the square root of average root mass of a pot was used as the dependent variable, nutrients, root collect method and bench were independent discrete variables and square root of average leaf mass of a pot and the number of plants in the pot were covariates. Nutrient level is high or low; Bench is 8 or 9; Kin treatments are same cultivar or different cultivar; Root collection methods are roots or roots and fabric. Error d.f. was 115 for $\log_e$ total biomass and 113 for square root root mass. N=124. Overall model significances were P<0.0001.

Source		$\log_e$ total biomass		square root root mass	
	d.f.	*F*-ratio	*P*-value	*F*-ratio	*P*-value
Square root leaf mass	1			109.64	**<.0001**
Nutrients	1	657.50	**<.0001**	4.01	**0.0477**
Bench	1	88.73	**<.0001**	8.60	**0.0041**
Nutrients x bench	1	9.92	**0.0021**	5.39	**0.0220**
Kin	1	0.23	0.6303	2.10	0.1502
Nutrients x kin	1	1.69	0.1962	1.52	0.2202
Bench x kin	1	5.28	**0.0234**	1.43	0.2337
Nutrients x bench x kin	1	0.59	0.4423	0.44	0.5066
Number of plants	1	4.30	**0.0403**	0.55	0.4603
Root collection method	1			38.81	**<.0001**

Notes: P-value <0.05 are bolded.

Table 16.3. Root allocation and total biomass analysis of *B. oleracea* cultivars grown in single cultivar groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of average total biomass of a pot was used as the dependent variable, nutrients, bench and cultivar were independent discrete variables and the number of plants in the pot as the covariate. In the analysis of covariance, the square root of average root mass of a pot was used as the dependent variable, nutrients, bench and cultivar were independent discrete variables and square root of average leaf mass of a pot and the number of plants in the pot were covariates. Nutrient level is high or low; Bench is 8 or 9; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi. Error d.f. was 24 for $\log_e$ total biomass and 23 for square root root mass. N=49. Overall model significances were P<0.0001.

Source		$\log_e$ total biomass		square root root mass	
	d.f.	*F*-ratio	*P*-value	*F*-ratio	*P*-value
Square root leaf mass				5.32	**0.0304**
Nutrients	1	210.11	**<.0001**	0.60	0.4469
Bench	1	38.57	**<.0001**	11.93	**0.0022**
Nutrients x bench	1	4.35	**0.0479**	2.23	0.1488
Cultivar	5	2.82	**0.0386**	0.77	0.5836
Nutrients x cultivar	5	1.70	0.1725	1.43	0.2522
Bench x cultivar	5	0.49	0.7792	1.16	0.3562
Nutrients x bench x cultivar	5	1.46	0.2399	1.66	0.1854
Number of plants	1	2.81	0.1066	0.01	0.9309

Notes: P-value <0.05 are bolded.

Table 17. Aboveground biomass analysis of *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 2). In the analysis of covariance, the natural logarithm of aboveground biomass as the dependent variable, nutrients as the independent discrete variable and the number of plants in the pot and quadratic number of plants in the pot were covariates. Nutrient level is high or low. Error d.f. was 518. N=524. Overall model significances were P<0.0001.

Source		$\log_e$ aboveground biomass	
	d.f.	*F*-ratio	*P*-value
Nutrients	1	0.00	0.9846
Number of plants	1	2.88	0.0904
Number of plants x nutrients	1	5.02	**0.0254**
Number of plants x number of plants	1	5.36	**0.0210**
Number of plants x number of plants x nutrients	1	3.90	**0.0488**

Notes: P-value <0.05 are bolded.

Table 18.1. Loadings of seedling traits on principle components when grown in groups of 6 plants in a greenhouse at low nutrients. Components are summarized as: component 1-size, component 2-bolting, component 3-rosette.

Trait	**Component 1**	**Component 2**	**Component 3**
Largest leaf length	0.441035	-0.214721	0.355132
Largest leaf area	0.462842	-0.190033	0.271921
Leaf mass	0.464929	-0.168374	0.125195
Stem mass	0.436579	0.124782	-0.150446
Natural height	0.389922	0.099988	-0.829963
Bolting	0.180185	0.929443	0.269804

Table 18.2. Loadings of seedling traits on principle components when grown in groups of 6 plants in a greenhouse at high nutrients. Components are summarized as: component 1-size, component 2-bolting, component 3-height.

Trait	**Component 1**	**Component 2**	**Component 3**
Largest leaf length	0.464084	-0.131011	-0.298529
Largest leaf area	0.474580	-0.147566	-0.207594
Leaf mass	0.484888	-0.102115	-0.070350
Stem mass	0.452775	0.120291	-0.033177
Natural height	0.338473	0.179031	0.895306
Bolting	0.068659	0.950847	-0.245281

Table 19.1. Multilevel selection gradients for a partial regression of component 1 (size), root allocation and emergence date at low and high nutrients performed with individual and group means.

	Low nutrients		**High nutrients**	
Trait	***F*-Value**	***β***	***F*-Value**	***β***
Individual seedling component 1 (size)	0.03	-0.131	**81.5*** **	3.238
Individual seedling root allocation	**36.8*** **	4.402	4.13*	0.674
Individual emergence date	**168*** **	-3.879	**136*** **	-1.354
Group component 1 (size)	1.51	1.286	**5.46***	-1.075
Group root allocation	3.92*	-1.905	4.22*	-0.884
Group emergence date	**43.0*** **	2.961	**43.8*** **	1.070

Notes: Bold numbers indicate significance from bootstrapping 95% confidence intervals.

*P<0.05, **P<0.01, ***P<0.001, //P<0.06

Table 19.2. Multilevel selection gradients for a partial regression of component 2 (bolting), root allocation and emergence date at low and high nutrients performed with individual and group means.

	Low nutrients		**High nutrients**	
Trait	***F*-Value**	***β***	***F*-Value**	***β***
Individual seedling component 2 (bolting)	0.60	-0.443	**11.5*** **	1.227
Individual seedling root allocation	**35.0*** **	4.638	**24.5*** **	1.744
Individual emergence date	**198.5*** **	-3.910	**104*** **	-1.352
Group component 2 (bolting)	2.28	1.170	0.75	-0.425
Group root allocation	4.51*	-2.171	**7.40** **	-1.213
Group emergence date	**49.1*** **	2.855	**37.3*** **	1.177

Notes: Bold numbers indicate significance from bootstrapping 95% confidence intervals.

*P<0.05, **P<0.01, ***P<0.001, //P<0.06

Table 19.3. Multilevel selection gradients for a partial regression of component 3 (rosette/height), root allocation and emergence date at low and high nutrients performed with individual and group means.

	Low nutrients		**High nutrients**	
Trait	***F*-Value**	***β***	***F*-Value**	***β***
Individual seedling component 3 (rosette/height)	**44.5*** **	-7.322	**115*** **	6.964
Individual seedling root allocation	**45.9*** **	4.605	0.68	-0.293
Individual emergence date	**241*** **	-4.036	**263*** **	-1.936
Group component 3 (rosette/ height)	2.30	2.155	**12.7*** **	-3.067
Group root allocation	3.82//	-1.704	0.05	-0.106
Group emergence date	**49.2*** **	2.579	**36.7*** **	1.080

Notes: Bold numbers indicate significance from bootstrapping 95% confidence intervals.

*P<0.05, **P<0.01, ***P<0.001, //P<0.06

Table 20.1. Aboveground biomass analysis of broccoli and cauliflower *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 3). In the analysis of variance, the natural logarithm of aboveground biomass was used as the dependent variable and bench, cultivar and the frequency of broccoli were independent discrete variables. Bench is 1, 2, 3, 4, 5 or 6; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Frequency of broccoli is high or low. Error d.f. was 72. N=80. Overall model significances was P<0.0052.

Source		$\log_e$ aboveground biomass	
	d.f.	*F*-ratio	*P*-value
Bench	4	1.77	0.1438
Cultivar	1	10.46	**0.0018**
Frequency of broccoli	1	0.00	0.9928
Cultivar x frequency of broccoli	1	0.00	0.9490

Notes: P-value <0.05 are bolded.

Table 20.2. Aboveground biomass analysis of kohlrabi and collards *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 3). In the analysis of variance, the natural logarithm of aboveground biomass was used as the dependent variable and bench, cultivar and the frequency of broccoli were independent discrete variables. Bench is 1, 2, 3, 4, 5 or 6; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Frequency of kohlrabi is high or low. Error d.f. was 69. N=77. Overall model significances was P<0.0002.

Source		$\log_e$ aboveground biomass	
	d.f.	*F*-ratio	*P*-value
Bench	4	1.32	0.2729
Cultivar	1	25.56	**<.0001**
Frequency of kohlrabi	1	2.02	0.1600
Cultivar x frequency of kohlrabi	1	0.16	0.6863

Notes: P-value <0.05 are bolded.

Table 20.3. Aboveground biomass analysis of broccoli and kohlrabi *B. oleracea* cultivars grown in groups of 6 plants in a greenhouse (Experiment 3). In the analysis of variance, the natural logarithm of aboveground biomass was used as the dependent variable and bench, cultivar and the frequency of broccoli were independent discrete variables. Bench is 1, 2, 3, 4, 5 or 6; Cultivars are broccoli, cabbage, cauliflower, collards, kale or kohlrabi; Frequency of kohlrabi is high or low. Error d.f. was 87. N=96. Overall model significances was P<0.0001.

Source		$\log_e$ aboveground biomass	
	d.f.	*F*-ratio	*P*-value
Bench	5	5.48	**0.0002**
Cultivar	1	14.67	**0.0002**
Frequency of kohlrabi	1	4.71	**0.0326**
Cultivar x frequency of kohlrabi	1	0.40	0.5310

Notes: P-value <0.05 are bolded.

DISCUSSION

We tested a method for determining the fitness consequences of plant allocation and morphological traits through the use of family-level selection. In particular, we were interested in predicting the fitness consequences of plant kin recognition responses. Kin recognition responses of plants grown with relatives are hypothesized to be altruistic traits. Various traits of seedling plants were measured in the phenotyping experiment and the cultivar average of several functional traits were estimated, some of these traits have previously shown kin responses. Subsequently, the fitness of juvenile plants was measured in the fitness and competition experiment. The traits and fitness data were analysed using multilevel selection. We found that *B. oleracea* cultivars had varying phenotypes and showed that the putative competitive traits measured in this study were under selection. A competitive trait is a selfish trait, thus should be favoured at the individual level but selected against at the group level. Most of the putative competitive traits did have the predicted pattern of opposing selection at the individual and group level. Our results support the hypothesis that root allocation is in fact a competitive trait. Although plants were experiencing competitive interactions within the pots, there was no evidence of cultivar recognition or resource partitioning. Overall, using family level selection and measuring traits before selection proved effective at establishing how natural selection acts on kin recognition traits.

The use of multilevel selection to investigate natural selection of competitive traits has been common practice in plant studies (Stevens et al. 1995; Aspi et al. 2003; Donohue 2004; Weinig et al. 2007; Boege 2010; Weis et al. 2015). However, there was a

problem with doing a longitudinal multilevel selection study in plants to look at the fitness consequences of kin recognition responses. Plant traits are measured early in life, while the fitness measurement is measured later in life. However, this is difficult when looking at traits that are measured destructively. A variation of multilevel selection, known as family-level selection (Rausher 1992) helped overcome this problem. Through the use of cultivars, we measured the trait on one individual and the fitness of another individual of that cultivar. A study that uses regression to look at natural selection can get a more accurate measure of selection by increasing the phenotypic variation. In our experiment, six cultivars were used to extend the range of phenotypes within the species. Our results confirmed that the traits expressed in seedling plant varied between cultivars.

In plants, it is the hypothesized that groups of relatives cooperate by expressing altruistic traits, while groups of strangers express competitive traits (Murphy and Dudley 2009). Under multilevel selection, a competitive trait will increase individual fitness, but individuals within a group that are competing will have decreased fitness. In experiment three, we looked at proposed competitive traits and found that these traits were subject to selection. It was predicted that traits might be selected differently at high and low nutrients because some traits may only be competitive in certain environments. However, no traits at the same level (individual or group) had opposing selection at the two different nutrient levels, which would have indicated that the trait was competitive in one environment, but altruistic in another. Simply, some traits were only under selection at one nutrient level, but not the other.

When plants were given a high level of nutrients, size, bolting and height were under selection. Individual selection acted in favour of increased bolting, height and size. Group selection favoured a reduction in size and height only. Size, bolting and height were competitive traits when there was high nutrients, as competition is mostly aboveground (Goldberg 1990) and a plant that is larger in size, is bolted and is taller can facilitate shade avoidance, as it helps prevent the plant from being shaded by its neighbours and the plant has more access to light (Weiner and Thomas 1992; Pigliucci and Schmitt 1999). The size and height results support previous findings that these are competitive traits (Donohue 2003; Donohue 2004; Weinig et al. 2007; Boege 2010). An individual in a group with a smaller average size and height would reduce aboveground competition for light with neighbours and increasing neighbour survival and reproduction. Thus, neighbours perform better because the group share light access.

Earlier emergence time was a competitive trait regardless of nutrient availability. Parallel to a study looking at emergence in *Brassica rapa* (Weis et al. 2015), our results corroborated that individual selection favours early emergence. However, there was also group selection favouring a group with late emergence. Plants that emerge earlier have fewer competitors and have a head start on growth (Weis et al. 2015). An individual in a group with later emergence time has higher fitness because the group avoids forming size hierarchies (Weiner and Thomas 1986). Late emergence is an altruistic behaviour because the focal individual will suffer the cost as the focal plant loses a head start on growth, but will reduce the shading of neighbours (Weis et al. 2015). Therefore late emergence imparts a fitness benefit to the group.

To the best of our knowledge, this study is the first to look at selection on root allocation. There were two different patterns of selection on root allocation depending on nutrient availability. At low nutrients, root allocation was selected to increase at the individual level only, but there was no group selection. When the nutrient content of the soil was low, competition between individuals occurred belowground. Plants with increased root allocation are able to acquire more water and nutrients (Casper and Jackson 1997), effectively reducing the resources their neighbours can acquire. At high nutrients, individual selection increased root allocation to enhance resource capture, while group selection favoured the reduction in root allocation. This result was only found in the high nutrient model including root allocation, emergence and bolting. A reduction in root growth allows for energy to be redirected to another structure. Moreover, a decrease in root allocation reduces direct competition with the group and decreases the overall impact on neighbour fitness. Thus, decreasing root allocation as a group is an altruistic behaviour.

Although there is a substantial amount of research documenting kin recognition responses (reviewed in Dudley et al. 2013), in this study no cultivar recognition in *B. oleracea* in any traits, including root allocation was found. This is not surprising as the cultivars used were artificially selected, thus the cultivars did not evolve together in the same population and therefore there has been no opportunity for kin selection to arise. However, same cultivar pots had higher aboveground biomass than pots with mixed cultivars indicating that same cultivar had higher fitness overall. This shows that plants have higher fitness when grown with same cultivar plants than with different cultivar

plants. Furthermore, the benefit of growing with related plants has been seen in other studies where it was hypothesized that siblings did not suppress each other as much as mixed groups (Tonsor 1989; Donohue 2003).

Some recognition studies have found that plants grown with strangers had more root allocation than plants grown with siblings (Dudley and File 2007; Biedrzycki et al. 2010; Bhatt et al. 2011; Biernaskie 2011; Mercer and Eppley 2014), while others studies found that plants grown with strangers had lower root allocation than plants grown with siblings (S. A. Dudley et al. unpublished data; Murphy and Dudley 2009). At high nutrients, our results confirmed that strangers are increasing their competitive ability by increasing root allocation, while relatives are reducing root allocation indicating altruism. In order for root allocation to meet the criteria of a trait under kin selection, root allocation must be heritable, its expression must depend on neighbour relatedness and the fitness of a focal individual must depend on the root allocation of its neighbours (Kelly 1996). Providing that root allocation is heritable, root allocation is under kin selection as it does depend on relatedness of neighbour and multilevel selection results show that the fitness of an individual depends on the root allocation of its neighbours (i.e. there is group selection).

Resource partitioning predicts stronger competition between same cultivar compared to different cultivars because individuals within a cultivar have uniform phenotypes. Our results did not support this prediction. Negative frequency dependence can lead to the coexistence of two species that have niche overlap and that are therefore competing (Antonovics and Kareiva 1988). We found no evidence for negative frequency

dependence by means of competition between two different cultivars. Only one of the cultivar pairs was affected by frequency dependence, where both broccoli and kohlrabi had higher fitness with an increase in kohlrabi in the pot. This result shows positive frequency dependence when the two cultivars are grown together (Antonovics and Kareiva 1988). The possible explanation for this outcome is that kohlrabi had a weaker competitive ability compared to broccoli. This is supported by other results showing that broccoli did have a stronger competitive effect as it negatively affected other cultivars aboveground biomass more so than the other cultivars. The lack of observed resource partitioning within *B. oleracea* does not mean that it is not occurring. Rather, cultivars could be competing for a resource that was not captured by the study (Silvertown 2004).

Although no kin selection or resource partitioning was detected with this highly domesticated species, both processes may be operating in natural plant communities where relatives frequently co-occur (File et al. 2012). Depending on which force is stronger, there are different outcomes in fitness when plants are grown with siblings compared to when grown with strangers. If resource partitioning is stronger than kin selection, plants grown with strangers will have higher fitness. When kin selection is stronger, plant grown with siblings will have higher fitness. If kin selection and resource partitioning are equal and opposite, there may be no difference in stranger and sibling fitness. A study using *A. thaliana* found kin selection and resource partitioning acting in equal magnitudes. In this study, when *A. thaliana* plants were grown with relatives, they horizontally oriented leaves (Crepy and Casal 2015). Horizontally reoriented leaves increase self-shading but reduce light competition with neighbouring plants. This

altruistic response was not observed when plants were grown with strangers. The researchers believed that resource partitioning was masking the positive fitness benefits expected from kin selection.

Plants were experiencing competition in both seedling experiments. Density decreased plant size indicating that plants were experiencing competitive interactions in the pots. Following the predictions of game theory (Laird and Aarssen 2005), the pot biomass decreased with density, but only in the first experiment. In response to competition cues, plants increased root allocation compared to alone plants. This result was found in previous studies (Gersani et al. 2001; Maina et al. 2002; O'Brien et al. 2005; Murphy and Dudley 2007; Murphy and Dudley 2009). Root proliferation increases a plants ability to forage for belowground resources (Casper and Jackson 1997). Also, with an increase in density, plants were allocating more to stem over leaf and bolting more. Both stem allocation and bolting allow for better light access and help shade neighbouring plants (Smith 1995) and show support that not only are plants competing belowground, but also aboveground.

Multilevel selection analysis has been a common approach to studying competitive traits (Stevens et al. 1995; Aspi et al. 2003; Donohue 2003; Donohue 2004; Weinig et al. 2007; Boege 2010).The aim of this study was to identify whether specific morphological and allocation traits expressed in a group of strangers are competitive, while the traits expressed in a group of relatives are altruistic. The addition of family-level selection (Rausher 1992) to a kin recognition study provides a powerful tool for studying the costs of phenotypic plasticity to neighbour relatedness, as one can determine

if kin recognition leads to kin selection. Although this study found no evidence of cultivar recognition in any traits, the relatedness of plants in these experiments was unknown. Hence, future studies should use *B. oleracea* with known parentage or another species that has high phenotypic variation between genotypes such as recombinant inbred lines (RILs) or double haploid lines. In addition to finding no resource partitioning, no cultivar recognition was detected. This is perhaps owing to the fact these cultivars were artificially selected and therefore there has been no opportunity for kin selection to evolve. Though my experiments were conducted in an artificial environment, future studies should apply this methodology to a natural environment. Kin recognition has been found across many plant genera, but the consequences of kin recognition responses in plants are still largely unknown. Using multilevel selection analyses and by measuring plant traits early in life, we were able to shed some light on the evolutionary basis for root allocation and other morphological traits.

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