

Manipulating resource allocation in plants

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1 **Manipulating resource allocation in plants**

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20 **ABSTRACT**

21 The distribution of nutrients and assimilates in different organs and tissues is in a
22 constant state of flux throughout the growth and development of a plant. At key
23 stages during the life cycle profound changes occur and perhaps one of the most
24 critical of these is during seed filling. By restricting the competition for reserves in
25 Arabidopsis plants the ability to manipulate seed size, seed weight, or seed content
26 has been explored. Removal of secondary inflorescences and lateral branches
27 resulted in a stimulation of elongation of the primary inflorescence and an increase
28 in the distance between siliques. The pruning treatment also led to the
29 development of longer and larger siliques that contained fewer, bigger seeds. This
30 seems to be a consequence of a reduction in the number of ovules that develop
31 and an increase in the fatty acid content of the seeds that mature. The data show
32 that shoot architecture could have a substantial impact on the partitioning of
33 reserves between vegetative and reproductive tissues and could be an important
34 trait for selection in rapid phenotyping screens to optimise crop performance.

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40 **INTRODUCTION**

41 Plants accumulate and redistribute macro and micronutrients throughout their life
42 cycle. Ultimately the plant is seeking to optimise the way it responds to
43 environmental cues and to integrate these with the genetically determined
44 elements of development in order to maximise its reproductive potential and
45 ensure the production and survival of the next generation. Plants, like other living
46 organisms, can be divided into those that have an r- or a K- reproductive strategy
47 (MacArthur and Wilson, 1967; Pianka, 1970). Most weed species adopt an r-
48 strategy and produce many thousands of small seeds with minimum investment of
49 resource per seed; in contrast, many trees invest in relatively few reproductive
50 units per individual but each unit is associated with a substantial quantity of
51 resource to help protect and nurture the subsequent generation (Pianka, 1970). For
52 example, the reproductive propagule of an *Arabis* weed species is a seed weighing
53 less than 1mg and sunflower seeds are about 100mg each, whereas coconuts
54 typically weigh over 1kg.

55 In order to optimise reproductive potential plants need to (re)mobilise nutrients
56 from sources to sinks in a highly orchestrated way. This process is spatially and
57 temporally dependent on the stage of the plant's life cycle and the reproductive
58 strategy of the plant under consideration. For instance, an annual plant will
59 ultimately die after seed filling is complete; in this case the seeds are the means by
60 which the genetic information of an individual over-winters and survives until
61 growing conditions become favourable once again. In some species seed dormancy
62 can last months or even years and provides a highly effective means of spreading

the timing of germination and potentially avoiding adverse environmental challenges (Barton, 1961). Work at the Millennium Seed Bank at the Royal Botanic Gardens, Kew revealed that 200 year old seeds, collected by the Dutch explorer Jan Teerlink during a voyage to the Cape of Good Hope in 1803, were still viable. The species included a *Leucospermum* from the family Proteaceae, and two species from the family Fabaceae including an Acacia and a legume called *Liparia villosa*, indicating a great range of species for which long-term dormancy is a viable option. For annual plants such as Arabidopsis, under optimal growth conditions, the process of resource allocation ensures that ultimately nearly all the nitrogen resources produced during the photosynthetic period will be remobilised from the vegetative tissues into the developing seeds. In contrast, perennial plants commit a more limited proportion of resources to the reproductive phase of their life cycle as it is advantageous to retain some photosynthetic capacity for as long as the environmental conditions allow. For this reason, it has been speculated that the anthocyanins produced in autumnal leaves provide photoprotection to enable maximal re-absorption during times when the leaves are vulnerable to the effects of high light accompanied by low temperatures (Archetti et al., 2009). For a perennial plant it is less essential to ensure reproductive success every year due to their longer life spans, and tolerance to environmental stress is often achieved by slower growth in addition to niche adaptations such as an evergreen habit. Bulbous plants provide an example where temperature is key to regulating source-sink balance; lower temperatures result in delayed leaf senescence and larger bulbs due to an improved equilibrium between carbon fixation capacity and sink strength (Gandin et al., 2011). Having lived for over 4800 years the bistlecone pine,

87 Methuselah, is a prime example of a plant's ability to endure abiotic stresses. Grime
88 (1977) proposed that resource-allocation strategies in plants could be divided into
89 three categories: Competitive, Stress-tolerant and Ruderal Strategies (denoted C-,
90 S- and R-strategies respectively). Grime summarised the consequences of C-, S- and
91 R-strategies on resource allocation for plant growing in three broad habitat
92 categories (Table 1) and it is interesting to review these in the light of considering
93 crop plants and the habitats under which they are grown in a modern agricultural
94 environment.

95 ***RESOURCE ALLOCATION STRATEGIES OF EXISTING CROP PLANTS***

96 The major cereal crops have undergone many centuries of domestication and, in
97 the developed world, are typically grown in environments where water and
98 nutrients are plentiful. Selection by 'man' has promoted C-strategy plants that
99 compete well in a monoculture and make large changes in root/shoot biomass as a
100 consequence of stress, meaning that when these crops are grown in environments
101 experiencing prolonged stress they survive less well (see Table 1). This may be one
102 explanation why the major grain crops of the world do not yield well in countries
103 which habitually experience high levels of abiotic (or biotic) stresses, unlike plants
104 native to arid environments which can respond quickly to resource pulses. For
105 instance, high temperatures and low rainfall across southern Australia in 1982,
106 1994 and 2004 restricted the total wheat yield to less than 10 million tonnes,
107 whereas the favourable environment in the 1983/4 season that followed the major
108 drought in 1982 produced in excess of 22 million tonnes (Sutton, 2009). In contrast,
109 more recently domesticated crop plants, such as *Brassica* species, retain the weedy

characteristics of their wild progenitors and continue to adopt an R-strategy. In consequence, these plants produce seed very rapidly, especially when experiencing abiotic stress (Sinniah et al., 1998), and ensure that the genepool is carried forwards to the next generation. In these situations it would appear that some seed can be produced with such speed that very little resource reallocation is required; this is perhaps not surprising since the seed in a Brassicaceous plant is itself photosynthetic in the initial stages of its development, but it is surrounded by a photosynthetic pod that can supply photosynthates at a highly localised site (Hua et al., 2011). However, if *Brassica* crops are grown under conditions of minimal abiotic stress they undergo a normal pattern of leaf and pod senescence that suggests resource reallocation does occur to enhance seed number and quality.

Observations of *Brassica rapa* and *Brassica napus* inflorescences indicates that seed development is frequently terminated following development of the first-formed pods and resumes at the end of flowering, leading to regions of the inflorescence without mature siliques (Figure 1). McGregor (1981) also reported high levels of pod abortion in *B. campestris* and *B. napus* which was attributed to over production of flowers and pod formation sites, so that a plant retains spare pods which can fully develop should any become damaged, indicating that pod abortion and the development of excess pod formation sites is normal and not just a response to injury or biotic/abiotic stress. The ability to selectively abort pods during periods of high abiotic stress, and resume once the stress has diminished, would enable plants to become S-strategists. Bosac et al. (1994) and Stewart et al. (1996) both found that exposing the racemes of *B. napus* or *B. campestris* to ozone caused pod abortion, pod abscission or fewer seeds per pod. Black et al. (2000)

134 made the same observation and raised the possibility that for a wild plant this was
135 potentially disadvantageous; if seed size is too low then plants may lose their
136 competitive advantage against those growing nearby.

137 Crop breeding programmes still largely focus on increasing yield, particularly in the
138 light of the goal to feed an ever-increasing global population. Most crops originate
139 from R-strategy plants, yet breeding programmes are frequently orientated
140 towards C-strategy plants. In those countries where land use for crops is marginal
141 and abiotic stress levels are high it might be more desirable to select for S-strategy
142 plants. Although S-strategy plants can be overgrown by competitors in a wild
143 habitat, in farmed land this is manageable through weed control or less dense seed
144 planting rates. A crop ideotype would be an S-strategy plant with the ability of an R-
145 strategy plant to reproduce rapidly when the environmental conditions become
146 harsh, thus ensuring at least a minimum yield each year.

147 ***MANIPULATING SOURCE:SINK RATIOS***

148 Using the R-strategy plant Arabidopsis as a model to determine how the
149 manipulation of resource allocation can impact on seed quality and yield it has been
150 possible to explore how a crop ideotype might be optimised and developed in a
151 breeding programme. Plants were grown under near optimal conditions in order to
152 maximise seed number. The objective was to ascertain how much plasticity in
153 resource allocation was retained by a plant and whether there was potential to
154 increase seed size, yield and quality to make an R-strategy plant invest additional
155 resources into seeds. If the mechanism of resource allocation can be better
156 understood then it can be manipulated in crop plants that still harbour weedy traits

157 from their ancestors in order to produce improved varieties. Such varieties might
158 be 'tailored' to suit differing environmental conditions. Selective 'pruning' of parts
159 of the inflorescence was carried out to alter source-sink relationships across the
160 plant. Control plants were compared to those that had either secondary
161 inflorescences removed, or all secondary inflorescences and lateral branches from
162 the main inflorescence removed, thus representing a decrease in sink strength as
163 the pruning treatments became more severe (see Fig. 2A).

164 Analyses of the growth morphology of the plants revealed that the main
165 inflorescence became significantly elongated as pruning became more severe, but
166 that the number of pods on the main stem remained the same as a consequence of
167 larger spaces between the pod formation sites (Fig. 2B, C). The rationale for
168 stimulating inflorescence elongation is unclear, as any competition for light would
169 have been reduced not enhanced by the pruning treatment. Whether this change
170 resulted from an alteration in cell number or size has yet to be determined,
171 however Dale (1959) also observed stem elongation in disbudded cotton plants.

172 Apical dominance was mechanically reinforced by the selective removal of lateral
173 branches and secondary stems and this seems to have resulted in the main
174 inflorescence becoming even more dominant, but the advantage of this is not clear.

175 An alternative explanation is that without the drain of lateral branches on
176 photosynthate reserves the pruned plants were able to implement a more extreme
177 shade avoidance response and elongate more than their highly branched
178 competitors in order to capture the available light more effectively. Rosette leaf
179 number and biomass increased significantly with the pruning of lateral and

180 secondary branches (sinks), but the rate of senescence of individual leaves was the
181 same as the control plants. This finding is in agreement with that of Nooden and
182 Penney (2001) who found that stem removal increased the longevity of the plant
183 but not of individual rosette leaves, enabling the rosette to remain a source of
184 photosynthates and other metabolites for much longer (Bennett et al., 2011; Fig
185 2D). In common with findings in soybean (Seddigh and Jolliff, 1986), it would appear
186 that the strength of the sink is the dominant factor in determining resource re-
187 allocation from rosette leaves into the pods. Without the pull from multiple
188 branches containing developing seeds, the rosette continues to develop without
189 overall senescence in the absence of other environmental cues such as day length
190 or temperature change. Other experiments in soybean have shown that in the
191 absence of sufficient sink strength the stomata close, leading to a reduction in
192 photosynthesis, although the consequence of this on the distribution of existing
193 photoassimilates and the timing of senescence was not established (Setter and
194 Brun, 1980). However, some authors contest the theory that reproductive
195 development is intrinsically linked to leaf senescence in Arabidopsis. Hensel et al.
196 (1993) reported that the reproductive organs had no influence on leaf senescence
197 and rosette leaf age was the only driver of senescence; Nooden and Penny (2001)
198 took the idea a step further and argue that loss of meristem activity represents the
199 primary signal for whole plant senescence. Early research on source-sink
200 relationships in plants developed the 'self-destruct hypothesis' (Sinclair and De Wit,
201 1976) which assumed that increased nutrient remobilisation out of the leaves was
202 the driver for early senescence. Later researchers in the field found that the rate of
203 photosynthesis in leaves was reduced when sink strength was reduced

204 (Wittenbach, 1983; Crafts-Brander, 1984) and Seddigh and Jolliff (1986) proposed
205 that increasing sink strength would drive increased production of carbon and
206 nitrogen by the leaves, thus switching the emphasis back in line with our current
207 thinking that sink strength 'pulls' resources from the rosette (Bennett et al., 2011).
208 Wild type Arabidopsis plants have been shown to have sub-maximal levels of
209 nitrogen remobilisation from the leaves into developing seeds, but if over-
210 expression of cytosolic pyruvate, orthophosphate dikinase (PPDK) is engineered
211 then nitrogen is exported more rapidly from senescing leaves and seeds on the
212 transgenic lines were larger than wild type (Taylor et al., 2010). This work
213 demonstrates that rosette nitrogen is present in excess of that demanded by the
214 sink (pods) but it is only metabolised in proportion to the pull from the developing
215 pods. The PPDK over-expressing transgenics provide evidence that it is possible to
216 alter the dynamics of remobilisation and source-sink relationships and the capacity
217 for additional resource accumulation is present in the seeds, even in a species such
218 as Arabidopsis where lipid is the primary form of storage metabolite.

219 ***RESOURCE ALLOCATION TO THE PODS CAN BE ALTERED***

220 Reduction in sink strength from pruning lateral and secondary branches altered pod
221 morphology compared to the control. Resultant pods were longer and with a bigger
222 area (Fig. 2E), however, the total number of seeds within each pod was significantly
223 reduced, yet the total weight of seeds in the most extreme manipulation was
224 significantly heavier (Fig. 2F). These observations indicate that when the number of
225 reproductive sites was reduced the number of seeds that even start to develop
226 within a pod is less than the total that could be theoretically sustained within a pod,

227 as opposed to lots of seeds being formed and then some aborted. These data
228 suggest that the sink strength is determined by the number of pods rather than the
229 number of seeds. For a weedy species such as *Arabidopsis* there is a logic to the
230 argument that the minimum unit that a plant 'measures' is a pod rather than a
231 seed. Since pod shatter will release all the seeds within that pod simultaneously it
232 makes ecological sense that the rate of development of all seeds within a single pod
233 is highly coordinated. If the number of pods is too small to pull sufficient resources
234 from the rosette then the co-ordination sequence could be reprogrammed to
235 enable a few large, viable seeds to develop rather than lots of small seeds with
236 impaired viability. The mechanism by which a pod is able to 'measure' the amount
237 of resource remains unexplained but our observations indicate that if sink strength
238 is low then not all the potential sites of attachment in a pod are used to develop
239 seeds. As a consequence low numbers of seeds develop per pod to guarantee that
240 all the seeds formed will meet a minimum threshold of resources required for
241 viability. One hypothesis is that R-Strategy annual plants operate a 'minimum
242 viability threshold for reproductive success' and ensure that some seeds will be
243 produced with the best chance of survival. If conditions remain favourable and
244 further resources are available then the plant will invest in more units of
245 reproduction (pods), thus increasing sink strength and mobilising resources more
246 fully from the rosette. This is evident when pods from the main inflorescence of un-
247 pruned plants are compared to those from the lateral branches. The pods on the
248 lower section of the main inflorescence are the first formed and contain the
249 heaviest seeds, whereas the later formed pods on lateral branches contain lighter
250 and significantly fewer seeds (Fig. 3). Seeds from pods on lateral branches have high

251 viability, but further detailed experiments are necessary to establish if there is a
252 fitness cost if these smaller seeds are selected over multiple generations. Other
253 researchers have raised the possibility that an R-strategy plant such as *Arabidopsis*
254 makes a late, or even continuous, decision about the volume of seed set based on
255 the available nutrients during the reproductive stage, rather than it being
256 predetermined by growth and development during the vegetative phase (Schulze et
257 al., 1994).

258 The observation that seed size within a pod can be manipulated by source/sink
259 manipulation raises the question whether this is the consequence of altered
260 partitioning of resource allocation into each seed or pod. Seeds accumulate a
261 mixture of lipids, proteins and carbohydrates as they develop. In *Arabidopsis* the
262 protein and carbohydrate are mostly in the embryo, whereas the endosperm
263 contains the majority of the lipid component. The experiments reported here have
264 revealed that enhancing the source strength through selective stem removal causes
265 a trend towards an increase in the fatty acid content of the seeds, although protein
266 content did not alter (Fig. 4A, B). This suggests that the developing embryo is of a
267 fixed size, but the endosperm component can increase beyond a minimum
268 threshold level. Partitioning of individual fatty acids did not change, indicating that
269 the ratio is genetically determined and therefore fixed. In *Arabidopsis* the dominant
270 fatty acids are linoleic acid, eicosenoic acid and linolenic acid which are omega 6,
271 omega 9 and omega 3 unsaturated fatty acids respectively. These were found in
272 similar proportions to that established by other workers (Katavic et al., 1995;
273 Penfield et al., 2004), although less oleic acid (omega 9) was detected than both of

274 these groups who found comparable levels in both the embryo and endosperm of
275 Arabidopsis seeds.

276 ***IMPLICATIONS FOR CROP PRODUCTION***

277 An analysis of all the different parameters we have measured in relation to
278 resource allocation in Arabidopsis has revealed that seed and pod number per plant
279 is more closely related to protein and lipid content than seed mass or pod area (Fig.
280 5). This analysis suggests that if the target is to increase the number of viable seeds
281 per pod the consequence should be further mobilisation of lipid and protein
282 content into each individual pod which will result in a redistribution of these
283 resources amongst a greater number of seeds within those pods. However, the
284 overall mass of seeds per pod is unlikely to be increased so the usefulness of
285 increasing seed number is limited to production scenarios where the aim is to
286 increase the number of seeds that can give rise to viable plants e.g. seed production
287 for the leafy vegetable market. If the target is to increase seed size and nutrient
288 content *per se* then it is necessary to alter the source-sink relationship within the
289 plant and to start to shift the architecture away from that of an obligate R-strategy
290 plant and towards that of an S- or C-strategy plant.

291 There are many reasons why the typical architecture observed in an R-strategy
292 plant that has been adapted for crop production is less than optimal. Most ruderal
293 plants either have a highly branched habit, if they are dicotyledonous, with minimal
294 coordination of pod development and shattering between branches or, in the case
295 of monocotyledonous plants, the natural architecture is to produce numerous
296 tillers with a consequential separation of heading dates and maturation rates on

297 different tillers. In a few examples (e.g. wheat, barley, rice) long-term selection of
298 domesticated crops has enabled much closer development of seed heads present
299 on different tillers, but in years when the environment is less favourable, for
300 example when late season rain affects a wheat crop, new tillers are produced that
301 mature several weeks after the main inflorescence. In crops that have received far
302 less attention from plant breeders, such as the numerous small grain crops grown
303 in Africa and Asia, the coordination between flowering heads is extremely poor,
304 leading to a considerable reduction in the proportion of potential yield from each
305 plant that is actually harvested. For these reasons it would be desirable to replicate
306 the architecture enforced by our selective stem removal experiments, but it is
307 important to appreciate the potential consequences of the change for seed yield
308 and quality.

309 It is well known that adjusting the seed rate (planting density) for numerous crops
310 can have a large influence on plant morphology. Plants grown closely together will
311 reduce the number of branches they produce and adopt a shade avoidance strategy
312 of elongating the main stem to capture the maximum amount of available light
313 (Robson et al., 1996). Whilst excessive stem height can lead to problems with
314 lodging there are ways of preventing this through the introgression of genes that
315 lead to dwarfing, such as *Rht* in wheat, and the resultant plants are then able to
316 concentrate their resource allocation into the seed head or pods on the primary
317 inflorescence. Since non-branched plants are grown in a much more densely
318 planted stand the actual yield per m² may not alter significantly, but the
319 coordination will be greatly improved by achieving a monoculture of primary

320 inflorescences from any crop, meaning more of the seeds formed will actually be at
321 the optimal harvest stage simultaneously.

322 What has become clear from the above findings and from existing literature is that
323 increasing the nutrient supply to the plants during the vegetative stage does not
324 guarantee an increase in yield and/or seed quality. Masclaux-Daubresse and
325 Chardon (2011) showed that nitrogen limitation negatively affected plant biomass,
326 yield, and harvest index but did not change the dry weight of individual seeds.

327 There is evidence that the leaves produce photosynthates to an excess of those
328 required by the developing pods and seeds and that there is a positive feedback
329 loop through which the pods (in the case of a Brassicaceous plant) pull the
330 resources they need from the rosette. Whilst supplying adequate nutrition to the
331 leaves and roots will avoid morphological constraints imposed by a starvation
332 stress, more nutrition is not necessarily a guarantee of greater yield (Allen &
333 Morgan, 1972) and a restricted nutrient supply does not necessarily mean that
334 senescence will occur more rapidly; Abdallah et al. (2011) demonstrated that short
335 or long-term sulphur limitation delays senescence and allows the plant to
336 remobilise much more sulphur and nitrogen out of its leaves. Agronomic
337 consideration should be given to treatments that would make plants increase the
338 rate of resource remobilisation from the source to the sink, for example increasing
339 the expression of PPDK (Taylor et al., 2010) or *Arabidopsis thaliana* NITRATE
340 TRANSPORTER2.1 (*ATNRT2.1*; Chopin et al., 2007), or ways to adjust the feedback
341 mechanism between source and sink and how it changes through different stages
342 of development. Since these are rather subtle changes it is likely to fall to plant

343 breeders to target suitable genes that will change developmental patterns of
344 resource allocation and tip the delicate balance of source sink relationships in the
345 appropriate direction at different stages of crop growth.

346 ***PLANT BREEDING TARGETS FOR ALTERED ARCHITECTURE AND RESOURCE***
347 ***ALLOCATION***

348 The control of branch formation in plants has become much better characterised
349 over recent years. Shoot and root branching is in part mediated by the *MAX* family
350 of genes that function through regulating the strigolactone pathway. Recessive
351 mutants of *MAX2* exhibit excessive branching (Stirnberg et al., 2002) and *MAX2*
352 encodes an F-Box leucine rich repeat protein that modulates strigolactone
353 signalling, reportedly by targeting the protein for ubiquitination and degradation by
354 the 26S proteasome. Strigolactones appear to act downstream of auxin, and the
355 two plant growth regulators interact so that auxin is able to mediate apical
356 dominance by inducing the expression of strigolactone biosynthesis genes (Brewer
357 et al., 2009). *MAX2* was originally isolated as *ORE9*, a gene involved in promoting
358 leaf senescence and thereby potentially increasing the source of metabolites
359 available for seed production (Woo et al., 2001). It is interesting to note that
360 *max2/ore9* mutants exhibit increased branching but show delayed plant
361 senescence. In contrast, silencing of the *BRANCHED1b* gene resulted in increased
362 branching in tomato, but no notable change in fruit maturation or seed
363 development (Martin-Trillo et al., 2001). *BRC1b*, along with *FINE CULM1* are
364 believed to be downstream of strigolactone synthesis and presumably downstream
365 of resource allocation during senescence, since fruit development and ripening are

not altered in the plants. Clearly the consequences of this genetic manipulation differs from that brought about by pruning treatments and it would be interesting to determine if the mutations above resulted in the production of more or heavier seeds. Work by Abreu and Munné-Bosch (2009) with the *NahG* transgenics and *sid2* mutations in *Arabidopsis*, both of which reduce salicylic acid synthesis, showed that seed production was increased by 4.4-fold and 3.5-fold respectively, compared to the wild type. Salicylic acid deficiency also resulted in higher seed nitrogen content and increased pro-vitamin A and vitamin E than in wild type plants. *NahG* and *sid2* both exhibited increased branching per plant, along with reduced seed weight per 100 seeds, increased seed number per fruit and per plant. These results support those we found with manipulation of architecture by pruning; in both cases the least branched phenotype has the highest seed weight and the fewest seeds per pod.

Other mutants that have already been characterised have the potential to be utilised in the development of crops with altered resource allocation, many of which are also involved in plant growth regulator signalling (Quirino et al., 2000). Improved resource allocation, and consequentially yield enhancement, was achieved in rice by reducing the expression of the ethylene receptor *ETR2*, which caused a 4% increase in thousand grain weight by adjusting starch acclimation and increasing sugar translocation into the grains (Wuriyanghan et al., 2009). It is well known that several mutants in ethylene signalling pathways result in delayed senescence of the leaves in dicotyledonous plants (Grbic and Bleecker, 1995) and this may have the potential to alter seed filling at a later stage in development. Ma

389 and Wang (2003) identified the *ETR1* homologue in wheat and initial experiments
390 suggest that it is involved in integrating signals from other hormones, such as
391 jasmonic acid, to regulate leaf senescence. Experiments that modulated cytokinin
392 signalling via a SAG12 feedback loop have shown that leaf senescence can be
393 significantly delayed if cytokinin content in the leaves is kept high (Gan and
394 Amasino, 1995) and that this can enhance yield, although the impact of this
395 manipulation has been shown to be dependent on nutrient availability and under
396 limited N supply the transgenics had significantly lower fruit dry weight (Wingler et
397 al., 2005). Using this strategy to specifically increase cytokinin content in the roots
398 of tomato plants has been reported to increase fruit yield by 30% (Ghanem et al.,
399 2011). Cytokinins also appear important in modulating stress responses; when IPT
400 was placed under the regulation of a stress-responsive SARK promoter in rice
401 source/sink modifications led to improved drought tolerance and increased grain
402 yield under water-stress (Peleg et al., 2011). As a staple food crop, rice architecture
403 has been extensively researched and a recently identified point mutation in
404 *OsSPL14* was reported to result in the “ideal” plant architecture by producing a
405 taller plant with fewer tillers, denser panicles and enhanced grain yield per panicle
406 (Jiao et al., 2010). The identification of such alleles, which not only affect rice
407 architecture but also yield, may provide targets for future breeding programs.

408 ***IMPLICATIONS FOR CROP DEVELOPMENT***

409 The example given in the section above is a prime illustration of how below-ground
410 events influence the development of above-ground development and architecture.
411 Soil compaction can have serious consequences for the development of above-

412 ground biomass. Dry mass in barley was reduced by over 50% when soil bulk
413 density was increased from 1.1 to 1.7 g.cm⁻³ (Mulholland et al., 1996) with a
414 concomitant increase in xylem abscisic acid content in the compacted samples.
415 Some attempts have been made to relate soil compaction in different soils types to
416 yield in cereals (Hamza and Anderson, 2005), but without the ability to directly
417 observe below ground root architecture it will be difficult to assess how resource
418 allocation is related to soil structure across the whole plant.

419 The need for rapid phenotyping methods for plants growing *in vivo* has led to the
420 advent of techniques such as microscale X-ray Computed Tomography (microCT)
421 which enables root systems to be investigated in sufficient detail to provide
422 information about architecture as well as biomass (Lucas et al., 2011). Other
423 phenomics centres are being established to investigate above-ground architecture
424 (Berger et al., 2010). Together these techniques will provide a better understanding
425 of how overall plant architecture is regulated, the relationship of architecture to
426 crop yield, an understanding of the variability that exists even between plants
427 grown in a monoculture, and therefore how best precision agriculture can be
428 exploited to optimise plant growth and seed/fruit development.

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TABLE

Table 1. Morphogenetic responses to desiccation, shading, or mineral nutrient stress of competitive, stress tolerant, and ruderal plants and their ecological consequences of three types of habitat (Reproduced from Grime, 1977).

Strategy	Response to stress	Habitat 1 ^a	Habitat 2 ^b	Habitat 3 ^c
Competitive	Large and rapid changes in root:shoot ratio, leaf area and root surface area	Tendency to sustain high rates of uptake of water and mineral nutrients to maintain dry matter production under stress and to succeed in competition	Tendency to exhaust reserves of water and/or mineral nutrients both in rhizosphere and within the plant; etiolation in response to shade increases susceptibility to fungal attack	Failure rapidly to produce seeds reduces chance of rehabilitation after disturbance
Stress tolerant	Changes in morphology slow and often small in magnitude	Overgrown by competitors	Conservative utilisation of water, mineral nutrients and photosynthate allows survival over long periods in which little dry matter production is possible	
Ruderal plants	Rapid curtailment of vegetative growth and diversion of resources into seed production		Chronically low seed production fails to compensate for high rate of mortality	Rapid production of seeds ensures rehabilitation after disturbance

^a In the early stages of productive, undisturbed habitats (stresses mainly plant induced) and coinciding with competition.

^b In other continuously unproductive habitats (stresses more or less constant and due to unfavourable climate and/or soil) or in the late stages of succession to productive habitats.

^c In severely disturbed, potentially productive habitats (stresses either a prelude to disturbance e.g. moisture stress preceding plant fatalities or plant induced), between period of disturbance.

FIGURE LEGENDS

Figure 1. *Brassica napus* floral inflorescence showing regions of pod abortion.

Figure 2. Morphological influences on resource allocation in *Arabidopsis*. (A) The three selective stem removal treatments; from left to right: control, secondary branches removed, secondary and lateral branches removed (B) Height of the main inflorescence from each treatment (C) Distance between the pods on the primary inflorescence (D) Images of the rosettes at the end of flowering (E) Pod area and length for each treatment (F) Seed number and weight per pod. N=10 unless otherwise stated on graph. * indicates significant differences between the control and treatments ($P < 0.05$; determined by ANOVA followed by Tukey's post-hoc analysis). Plants were grown under controlled conditions with a 16h light, 8h dark cycle. Temperature was maintained throughout at 20°C and 55% RH.

Figure 3. Comparison of thousand grain weight and the number of seeds per pod between the main inflorescence and lateral branches in un-manipulated plants. N=10. * indicates significant differences between the control and treatments ($P < 0.05$; determined by ANOVA followed by Tukey's post-hoc analysis)

Figure 4. Resources allocated to the seeds. (A) Seed protein concentration from each treatment. Total protein quantification was performed using the Thermo Scientific Pierce BCA protein assay kit according to the manufacturer's protocol. The microtitre plate was read at an absorbance of 540nm. (B) Seed fatty acid profile to show amounts and proportional quantification of seeds from each treatment. N= 10 replicates per treatment. No significant differences were detected but the trend was for an increase in fatty acid content as the manipulations become more severe.

Seeds were freeze dried and the fatty acids measured via direct transmethylation (Smooker et al., 2011). Pentadecanoic acid and methyl heptadecanoate were used as internal standards, the former being present during the transmethylation process whilst the later was added just before the samples were run on the GC. 1 μ l aliquots of the heptane phase containing the fatty acid methyl esters (FAMES) were analysed by gas chromatography with flame ionization detection (Agilent G1530a) using a CP-Sil 88 column (50 m length x 0.25 mm id., 0.25 μ m film thickness; Chrompack). The GC conditions were: split mode injector (50:1), flame ionizer detector temperature 260°C, oven temperature 130°C for 3 min and increasing at 10°C/min for 6 min: total analysis time 20 min. FAMES were identified by comparison to the Supelco FAME mix (Sigma-Aldrich).

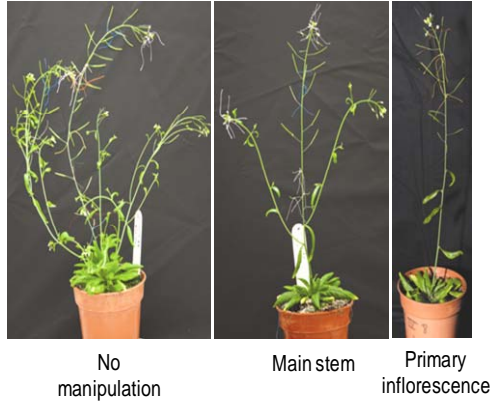
Figure 5. Dendrogram of resource allocation variables generated by cluster analysis illustrating the relationship between plant architecture and the partitioning of resources.

Figure 1.

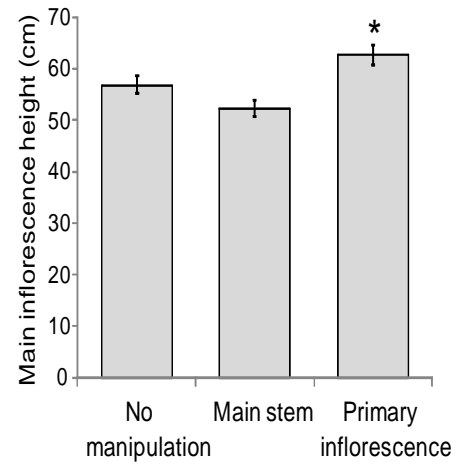


Figure 2.

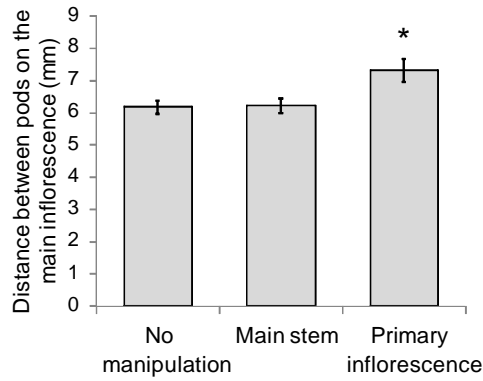
A



B



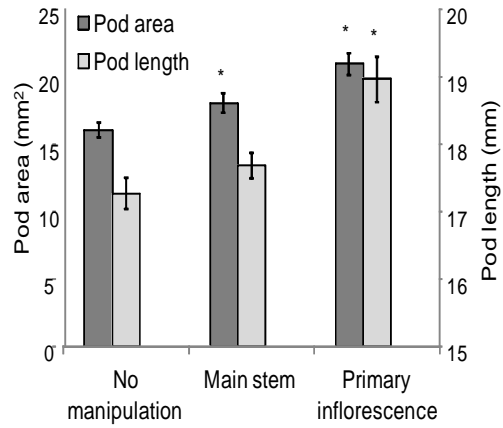
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E



F

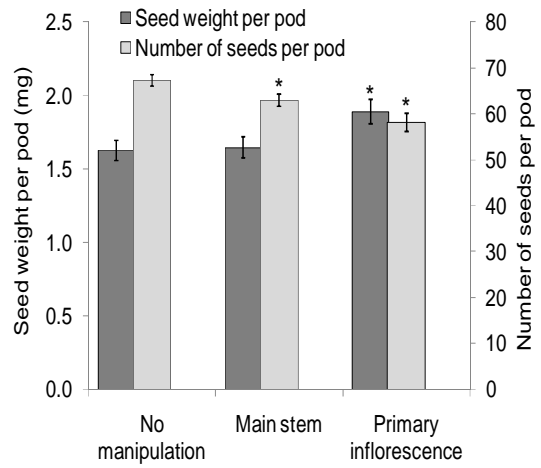


Figure 3.

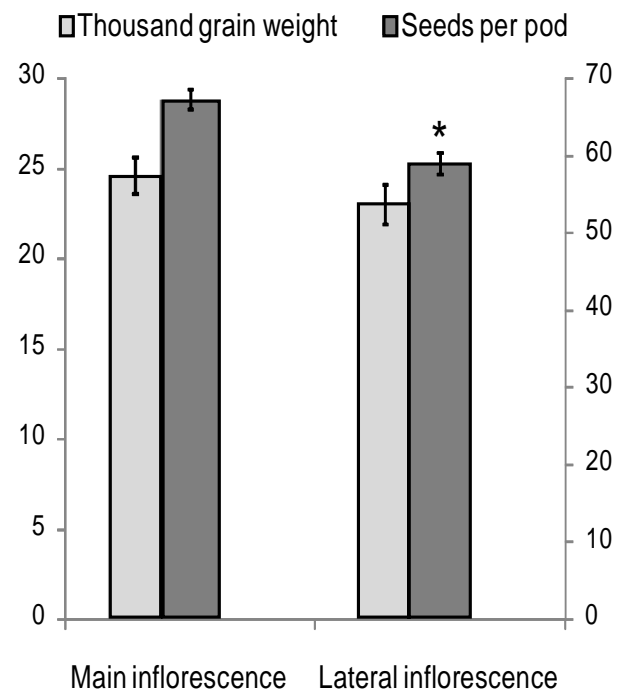


Figure 4.

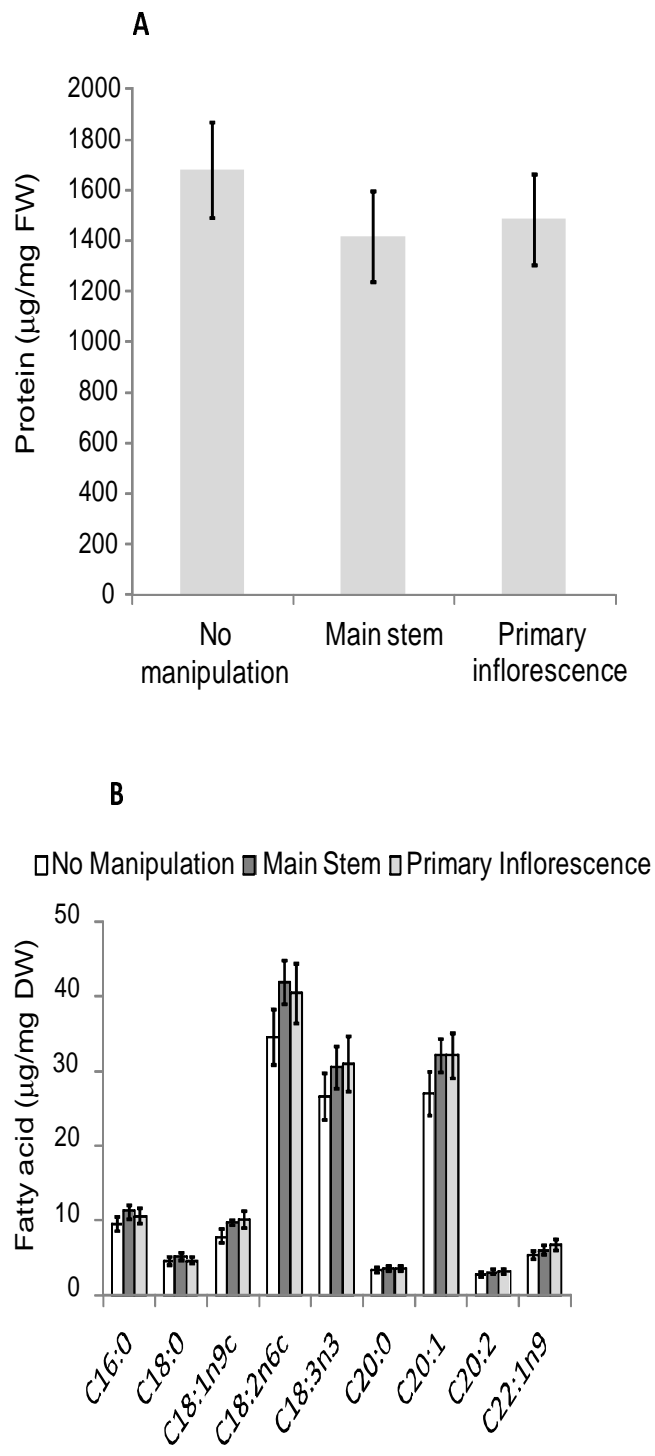


Figure 5.

