Manipulating resource allocation in plants

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Received 5 October 2011; Revised 21 November 2011; Accepted 28 November 2011

Abstract

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

Key words: Abscission, Arabidopsis, Brassica, leaf, pod, resource allocation, senescence.

Introduction

Plants accumulate and redistribute macro- and micronutrients throughout their life cycle. Ultimately the plant is seeking to optimize the way it responds to environmental cues and to integrate these with the genetically determined elements of development in order to maximize its reproductive potential and ensure the production and survival of the next generation. Plants, like other living organisms, can be divided into those that have an r- or a K- reproductive strategy (MacArthur and Wilson, 1967; Pianka, 1970). Most weed species adopt an r-strategy and produce many thousands of small seeds with minimum investment of resource per seed; in contrast, many trees invest in relatively few reproductive units per individual but each unit is associated with a substantial quantity of resources to help protect and nurture the subsequent generation (Pianka, 1970). For example, the reproductive propague of an Arabis weed species is a seed weighing <1 mg, and sunflower seeds are ~100 mg each, whereas coconuts typically weigh >1 kg.

In order to optimize reproductive potential, plants need to (re)mobilize nutrients from sources to sinks in a highly orchestrated way. This process is spatially and temporally dependent on the stage of the plant’s life cycle and the reproductive strategy of the plant under consideration. For instance, an annual plant will ultimately die after seed filling is complete; in this case, the seeds are the means by which the genetic information of an individual over-winters and survives until growing conditions become favourable once again. In some species, seed dormancy 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 remobilized 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 >4800 years the bistlecone pine, Methuselah, is a prime example of a plant’s ability to endure abiotic stresses. Grime (1977) proposed that resource allocation strategies in plants could be divided into three categories: competitive, stress-tolerant, and ruderal strategies (denoted C-, S-, and R-strategies respectively). Grime summarized the consequences of C-, S-, and R-strategies on resource allocation for plants growing in three broad habitat categories (Table 1), and it is interesting to review these in the light of considering crop plants and the habitats under which they are grown in a modern agricultural environment.

**Resource allocation strategies of existing crop plants**

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

<table>
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<th>Strategy</th>
<th>Response to stress</th>
<th>Habitat 1&lt;sup&gt;a&lt;/sup&gt;</th>
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<td>Competitive</td>
<td>Large and rapid changes in root:shoot ratio, leaf area, and root surface area</td>
<td>Tendency to sustain high rates of uptake of water and mineral nutrients to maintain dry matter production under stress and to succeed in competition</td>
<td>Tendency to exhaust reserves of water and/or mineral nutrients both in the rhizosphere and within the plant; etiolation in response to shade increases susceptibility to fungal attack</td>
<td>Failure rapidly to produce seeds reduces chance of rehabilitation after disturbance</td>
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<td>Stress tolerant</td>
<td>Changes in morphology slow and often small in magnitude</td>
<td>Overgrown by competitors</td>
<td>Conservative utilization of water, mineral nutrients, and photosynthetic allows survival over long periods in which little dry matter production is possible</td>
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<td>Ruderal plants</td>
<td>Rapid curtailment of vegetative growth and diversion of resources into seed production</td>
<td>Overgrown by competitors</td>
<td>Chronically low seed production fails to compensate for high rate of mortality</td>
<td>Rapid production of seeds ensures rehabilitation after disturbance</td>
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<sup>a</sup> In the early stages of productive, undisturbed habitats (stresses mainly plant induced) and coinciding with competition.

<sup>b</sup> 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.

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

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 gene pool is carried forward 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 localized 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 B. 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 (Fig. 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 abort pods selectively 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) made the same observation and raised the possibility that for a wild plant this was potentially disadvantageous; if seed size is too low, then plants may lose their competitive advantage against those growing nearby.

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

Manipulating source–sink ratios

Using the R-strategy plant Arabidopsis as a model to determine how the manipulation of resource allocation can impact on seed quality and yield, it has been possible to explore how a crop ideotype might be optimized and developed in a breeding programme. Plants were grown under near optimal conditions in order to maximize seed number. The objective was to ascertain how much plasticity in resource allocation was retained by a plant and whether there was potential to increase seed size, yield, and quality to make an R-strategy plant invest additional resources in seeds. If the mechanism of resource allocation can be better understood then it can be manipulated in crop plants that still harbour weedy traits from their ancestors in order to produce improved varieties. Such varieties might be ‘tailored’ to suit differing environmental conditions. Selective ‘pruning’ of parts of the inflorescence was carried out to alter source–sink relationships across the plant. Control plants were compared with those that had either secondary inflorescences removed, or all secondary inflorescences and lateral branches from the main inflorescence removed, thus representing a decrease in sink strength as the pruning treatments became more severe (see Fig. 2A).

Analyses of the growth morphology of the plants revealed that the main inflorescence became significantly elongated as pruning became more severe, but that the number of pods on the main stem remained the same as a consequence of larger spaces between the pod formation sites (Fig. 2B, C). The rationale for stimulating inflorescence

![Fig. 1. Brassica napus floral inflorescence showing regions of pod abortion.](image-url)
elongation is unclear, as any competition for light would have been reduced not enhanced by the pruning treatment. Whether this change resulted from an alteration in cell number or size has yet to be determined; however, Dale (1959) also observed stem elongation in disbudded cotton plants. Apical dominance was mechanically reinforced by the selective removal of lateral branches and secondary stems, and this seems to have resulted in the main inflorescence becoming even more dominant; however, the advantage of this is not clear. An alternative explanation is that without the drain of lateral branches on photosynthate reserves the pruned plants were able to implement a more extreme shade avoidance response and elongate more than their highly branched competitors in order to capture the available light more effectively. Rosette leaf number and biomass increased significantly with the pruning of lateral and secondary branches (sinks), but the rate of senescence of individual leaves was the same as that of the control.
plants. This finding is in agreement with that of Nooden and Penney (2001) who found that stem removal increased the longevity of the plant but not of individual rosette leaves, enabling the rosette to remain a source of photosynthates and other metabolites for much longer (Bennett et al., 2011; Fig 2D). In common with findings in soybean (Seddigh and Jolliff, 1986), it would appear that the strength of the sink is the dominant factor in determining resource re-allocation from rosette leaves into the pods. Without the pull from multiple branches containing developing seeds, the rosette continues to develop without overall senescence in the absence of other environmental cues such as daylength or temperature change. Other experiments in soybean have shown that in the absence of sufficient sink strength, the stoma close, leading to a reduction in photosynthesis, although the consequence of this on the distribution of existing photoassimilates and the timing of senescence was not established (Setter and Brun, 1980). However, some authors contest the theory that reproductive development is intrinsically linked to leaf senescence in Arabidopsis. Hensel et al. (1993) reported that the reproductive organs had no influence on leaf senescence, and rosette leaf age was the only driver of senescence; Nooden and Penney (2001) took the idea a step further and argue that loss of meristem activity represents the primary signal for whole plant senescence. Early research on source–sink relationships in plants developed the ‘self-destruct hypothesis’ (Sinclair and De Wit, 1976) which assumed that increased nutrient remobilization out of the leaves was the driver for early senescence. Later researchers in the field found that the rate of photosynthesis in leaves was reduced when sink strength was reduced (Wittenbach, 1983; Craft-Brander, 1984), and Seddigh and Jolliff (1986) proposed that increasing sink strength would drive increased production of carbon and nitrogen by the leaves, thus switching the emphasis back in line with current thinking that sink strength ‘pulls’ resources from the rosette (Bennett et al., 2011). Wild-type Arabidopsis plants have been shown to have submaximal levels of nitrogen remobilization from the leaves into developing seeds, but if overexpression of cytosolic pyruvate, orthophosphate dikinase (PPDK) is engineered then nitrogen is exported more rapidly from senescing leaves, and seeds on the transgenic lines were larger than wild type (Taylor et al., 2010). This work demonstrates that rosette nitrogen is present in excess of that demanded by the sink (pods) but it is only metabolized in proportion to the pull from the developing pods. The PPDK-overexpressing transgenics provide evidence that it is possible to alter the dynamics of remobilization and source–sink relationships, and the capacity for additional resource accumulation is present in the seeds, even in a species such as Arabidopsis where lipid is the primary form of storage metabolite.

Resource allocation to the pods can be altered

Reduction in sink strength from pruning lateral and secondary branches altered pod morphology compared with the control. Resultant pods were longer and with a bigger area (Fig. 2E); however, the total number of seeds within each pod was significantly reduced, yet the total weight of seeds in the most extreme manipulation was significantly heavier (Fig. 2F). These observations indicate that when the number of reproductive sites was reduced, the number of seeds that even start to develop within a pod is less than the total that could be theoretically sustained within a pod, as opposed to lots of seeds being formed and then some aborted. These data suggest that the sink strength is determined by the number of pods rather than the number of seeds. For a weedy species such as Arabidopsis, there is a logic to the argument that the minimum unit that a plant ‘measures’ is a pod rather than a seed. Since pod shatter will release all the seeds within that pod simultaneously it makes ecological sense that the rate of development of all seeds within a single pod is highly coordinated. If the number of pods is too small to pull sufficient resources from the rosette, then the coordination sequence could be reprogrammed to enable a few large, viable seeds to develop rather than lots of small seeds with impaired viability. The mechanism by which a pod is able to ‘measure’ the amount of resource remains unexplained, but observations indicate that if sink strength is low then not all the potential sites of attachment in a pod are used to develop seeds. As a consequence, low numbers of seeds develop per pod to guarantee that all the seeds formed will meet a minimum threshold of resources required for viability. One hypothesis is that R-strategy annual plants operate a ‘minimum viability threshold for reproductive success’ and ensure that some seeds will be produced with the best chance of survival. If conditions remain favourable and further resources are available then the plant will invest in more units of reproduction (pods), thus increasing sink strength and mobilizing resources more fully from the rosette. This is evident when pods from the main inflorescence of unpruned plants are compared with those from the lateral branches. The pods on the lower section of the main inflorescence are the first formed and contain the heaviest seeds, whereas the later formed pods on lateral branches contain lighter and significantly fewer seeds (Fig. 3). Seeds from pods on lateral branches have high viability, but further detailed experiments are necessary to establish if there is a fitness cost if these smaller seeds are selected over multiple generations. Other researchers have raised the possibility that an R-strategy plant such as Arabidopsis makes a late, or even continuous, decision about the volume of seed set based on the available nutrients during the reproductive stage, rather than it being pre-determined by growth and development during the vegetative phase (Schulze et al., 1994).

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

Implications for crop production

An analysis of all the different parameters which were measured in relation to resource allocation in Arabidopsis has revealed that seed and pod number per plant is more closely related to protein and lipid content than seed mass or pod area (Fig. 5). This analysis suggests that if the target is to increase the number of viable seeds per pod, the consequence should be further mobilization of lipid and protein content into each individual pod, which will result in a redistribution of these resources amongst a greater number of seeds within those pods. However, the overall mass of seeds per pod is unlikely to be increased so the usefulness of increasing seed number is limited to production scenarios where the aim is to increase the number of seeds that can give rise to viable plants, for example seed production for the leafy vegetable market. If the target is to increase seed size and nutrient content per se, then it is necessary to alter the source–sink relationship within the plant and to start to shift the architecture away from that of

Fig. 3. Comparison of 1000 grain weight and the number of seeds per pod between the main inflorescence and lateral branches in unmanipulated plants. n=10. * indicates significant differences between the control and treatments ($P < 0.05$; determined by ANOVA followed by Tukey’s post-hoc analysis).

Fig. 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 540 nm. (B) Seed fatty acid profile to show the 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 gas chromatograph. Aliquots of 1 μl 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×0.25 mm i.d., 0.25 μm 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$^{-1}$ for 6 min: total analysis time 20 min. FAMEs were identified by comparison with the Supelco FAME mix (Sigma-Aldrich).
an obligate R-strategy plant and towards that of an S- or C-strategy plant.

There are many reasons why the typical architecture observed in an R-strategy plant that has been adapted for crop production is less than optimal. Most ruderal plants either have a highly branched habit, if they are dicotyledonous, with minimal coordination of pod development and shattering between branches, or, in the case of monocotyledonous plants, the natural architecture is to produce numerous tillers with a consequential separation of heading dates and maturation rates on different tillers. In a few examples (e.g. wheat, barley, and rice), long-term selection of domesticated crops has enabled much closer development of seed heads present on different tillers, but in years when the environment is less favourable, for example when late season rain affects a wheat crop, new tillers are produced that mature several weeks after the main inflorescence. In crops that have received far less attention from plant breeders, such as the numerous small grain crops grown in Africa and Asia, the coordination between flowering heads is extremely poor, leading to a considerable reduction in the proportion of potential yield from each plant that is actually harvested. For these reasons it would be desirable to replicate the architecture enforced by selective stem removal experiments, but it is important to appreciate the potential consequences of the change for seed yield and quality.

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

What has become clear from the above findings and from existing literature is that increasing the nutrient supply to the plants during the vegetative stage does not guarantee an increase in yield and/or seed quality. Masclaux-Daubresse and Chardon (2011) showed that nitrogen limitation negatively affected plant biomass, yield, and harvest index, but did not change the dry weight of individual seeds. There is evidence that the leaves produce photosynthates in excess of those required by the developing pods and seeds and that there is a positive feedback loop through which the pods (in the case of a Brassicaceous plant) pull the resources they need from the rosette. Whilst supplying adequate nutrition to the leaves and roots will avoid morphological constraints imposed by a starvation stress, more nutrition is not necessarily a guarantee of greater yield (Allen and Morgan, 1972), and a restricted nutrient supply does not necessarily mean that senescence will occur more rapidly; Abdallah et al. (2011) demonstrated that short- or long-term sulphur limitation delays senescence and allows the plant to remobilize much more sulphur and nitrogen out of its leaves. Agronomic consideration should be given to treatments that would make plants increase the rate of resource remobilization from the source to the sink, for example increasing the expression of PPDK (Taylor et al., 2010) or Arabidopsis thaliana NITRATE TRANSPORTER2.1 (ATNRT2.1; Chopin et al., 2007), or ways to adjust the feedback mechanism between source and sink and how it changes through different stages of development. Since these are rather subtle changes, it is likely to fall to plant breeders to target suitable genes that will change developmental patterns of resource allocation and tip the delicate balance of source-sink relationships in the appropriate direction at different stages of crop growth.

Plant breeding targets for altered architecture and resource allocation

The control of branch formation in plants has become much better characterized over recent years. Shoot and root branching is in part mediated by the MAX family of genes that function through regulating the strigolactone pathway. Recessive mutants of MAX2 exhibit excessive branching (Stirnberg et al., 2002), and MAX2 encodes an F-box leucine-rich repeat protein that modulates strigolactone signalling, reportedly by targeting the protein for ubiquitination and degradation by the 26S proteasome. Strigolactones appear to act downstream of auxin, and the two plant growth regulators interact so that auxin is able to mediate apical dominance by inducing the expression of strigolactone biosynthesis genes (Brewer et al., 2009). MAX2 was originally isolated as ORE9, a gene involved in promoting leaf senescence and thereby potentially increasing the source...
of metabolites available for seed production (Woo et al., 2001). It is interesting to note that max2lore9 mutants exhibit increased branching but show delayed plant senescence. In contrast, silencing of the BRANCHED1b gene resulted in increased branching in tomato, but no notable change in fruit maturation or seed development (Martin-Trillo et al., 2001). BRC1b, along with FINE CULMI, is believed to be downstream of strigolactone synthesis and presumably downstream of resource allocation during senescence, since fruit development and ripening are not altered in the plants. Clearly the consequences of this genetic manipulation differ from those 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, with 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, and increased seed number per fruit and per plant. These results support those that were 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 characterized have the potential to be utilized 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 1000 grain weight by adjusting starch acclimation and increasing sugar translocation into the grains (Wu, 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 and Wang (2003) identified the ETR1 homologue in wheat, and initial experiments suggest that it is involved in integrating signals from other hormones, such as jasmonic acid, to regulate leaf senescence. Experiments that modulated cytokinin signalling via a SAG12 feedback loop have shown that leaf senescence can be significantly delayed if cytokinin content in the leaves is kept high (Gan and Amasino, 1995), and that this can enhance yield, although the impact of this manipulation has been shown to be dependent on nutrient availability, and under limited N supply the transgenics had significantly lower fruit dry weight (Wingler et al., 2005). Using this strategy specifically to increase cytokinin content in the roots of tomato plants has been reported to increase fruit yield by 30% (Ghanem et al., 2011). Cytokinins also appear important in modulating stress responses; when isopentenyltransferase (IPT) was placed under the regulation of a stress-responsive SARK promoter in rice, source/sink modifications led to improved drought tolerance and increased grain yield under water stress (Peleg et al., 2011). As a staple food crop, rice architecture has been extensively researched, and a recently identified point mutation in OsSPL14 was reported to result in the ‘ideal’ plant architecture by producing a taller plant with fewer tillers, denser panicles, and enhanced grain yield per panicle (Jiao et al., 2010). The identification of such alleles, which affect not only rice architecture but also yield, may provide targets for future breeding programmes.

Implications for crop development

The example given in the section above is a prime illustration of how below-ground events influence the above-ground development and architecture. Soil compaction can have serious consequences for the development of above-ground biomass. Dry mass in barley was reduced by >50% when soil bulk density was increased from 1.1 g cm⁻³ to 1.7 g cm⁻³ (Mulholland et al., 1996) with a concomitant increase in xylem abscisic acid content in the compacted samples. Some attempts have been made to relate soil compaction in different soils types to yield in cereals (Hamza and Anderson, 2005) but, without the ability to observe below-ground root architecture directly, it will be difficult to assess how resource allocation is related to soil structure across the whole plant.

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

Acknowledgements

EB would like to thank Tozer Seeds, the University of Nottingham, and the University of Reading Endowment Trust Fund for funding her PhD.

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