inhibitors. He also described uptake measurements with boron isotopes ($^{10}$B and $^{11}$B), showing that plants possess both high and low-affinity boron transporters that respond differently to changes in boron supply. It is now clear that a major effort is required to identify and fully characterize all the individual nutrient transporters in plants and that this task is greater than anyone guessed five years ago. More work is also needed to understand how the activity of these transporters interacts with other processes to control the distribution of nutrients within plants, and even long-established hypotheses are being challenged. Thus, Widmar Tanner (University of Regenaberg, Germany) described provocative results showing that plants with reduced transpiration rates (a tenth of those in control plants) had shoots with the same weight and ion content as control plants, questioning the idea that transpiration is a major regulator of nutrient flow from the root to the shoot. Tanner suggested that the transpiration of large amounts of water is not needed to provide the shoot with its needs and concluded that transpiration is an unavoidable evil imposed on plants by the need to acquire carbon dioxide.

**Conclusion**

Plant nutrition is entering an exciting phase where a truly molecular understanding of key transport processes is beginning to emerge. The ability of plants to respond to a wide range of nutrient availabilities is probably a reflection of their possession of large gene families of transporters that differ in their affinities for their substrates and are differentially expressed in different tissues. Elucidating the role of each transporter and unravelling its regulatory networks provides a major intellectual challenge as well as new opportunities in the venerable field of plant nutrition.

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**Resource allocation**

Alison Kingston-Smith

**Resource Allocation in Crop Plants, IGER/University of Wales, Aberystwyth, UK 11-13 September 2000.**

Efficient assimilation and use of nutrients by green plants is of prime importance for maximizing productivity of crops. The way in which plants use the available resources, which can occur in limited supply, was addressed at the Resource Allocation in Crop Plants conference organized by the Association of Applied Biologists. A diverse and informative programme of talks and posters embraced cell- to field-scale events. The meeting brought together many aspects of plant biology and a wide selection of the plant kingdom was represented, from temperate to tropical, including crop plants and model species. The talk by Andrew Borrell (Hermitage Research Station, Queensland, Australia) reflected the aims of the meeting by linking events at cell, leaf and whole-plant level in his consideration of nitrogen status in relation to senescence and the stay-green phenotype in sorghum.

**Assimilation and use of carbon**

Green leaves are responsible for primary assimilation of carbon. Atmospheric CO$_2$ is fixed by photosynthesis and used for sucrose synthesis. Olga Koreleva (University of Wales, Bangor, UK) described how the elegant technique of single-cell sampling has been used to show that carbohydrate metabolism is heterogeneous between the different cell types within a green leaf. Carbohydrate accumulation occurs in the photosynthetically active mesophyll cells, but is not present in the epidermis, suggesting a surprising lack of transport between cell types.

Recent advances in our understanding of sugar sensing reveal an increasing role for sucrose as a signal molecule in many aspects of cell biology$^{1-3}$. The poster presented by Joe Gallagher and Chris Pollock (IGER, Aberystwyth, UK) showed that when foliar carbohydrate content was manipulated in different ways, the expression of at least one transcript of the invertase gene family correlated well with foliar contents of soluble carbohydrate. This sugar-sensitive expression can be related to the dual roles of invertase because it catalyses both hydrolysis and polymerization of sucrose.

The enzyme phosphoenol-pyruvate carboxylase (PEPC) exists in different isoforms depending on whether the plant fixes CO$_2$ during the day to the three-carbon compound phosphoglycerate in C$_3$ plants or at night to four-carbon compounds such as malate in CAM plants. PEPC activity in vivo is regulated by reversible phosphorylation. Anne Borland (University of Newcastle upon Tyne, UK) described how this is mediated by a PEPC kinase that is under circadian control of expression. However, Borland’s group has shown that the circadian rhythm of PEPC kinase expression in CAM plants can be overcome by malate. Thus, malate acts as an internal indicator of carbon status in these plants, controlling flux through the assimilatory pathway.

Another example of regulation of carbohydrate metabolism by protein phosphorylation was provided by Nigel Halford (IACR Long Ashton, Bristol, UK). Antisense plants have revealed the role of the SnRK1 family of protein kinases in carbohydrate metabolism. By decreasing the SnRK1 transcript in potato leaves and tubers, plants showed altered sugar sensing, non-typical patterns of gene expression and ultimately an altered sucrose:starch ratio in potato leaves and tubers.

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**References**


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Nitrogen assimilation and remobilization

Nitrogen use by crop plants is not optimal. The carbon cycle enzyme, Rubisco, is the most abundant soluble protein in green leaves, but is produced in excess of the amount required for photosynthetic carbon fixation. Rowan Mitchell (IACR Rothamsted, UK) explained that results to date indicate a strong tendency for wheat plants to over-invest in this enzyme, even under nitrogen limitation. Redirection of nitrogen away from Rubisco and towards root growth or increased leaf area should result in increased yield. The group is currently investigating this with wheat plants produced by antisense technology to contain decreased Rubisco content.

Senescence is an important process for the plant because it allows remobilization and repartitioning of many of the nutrients contained in the dying leaf. Dimah Habash (IACR Rothamsted, UK) explored the changing isomoroph profile of glutamine synthetase (which catalyses ammonium assimilation) as leaves turn from green to yellow. One isomoroph, GS1, which was dominant in senescing, but not mature, wheat leaves has been increased in transgenic plants. These plants show improved nitrogen assimilation characteristics, suggesting routes for future improvements in nitrogen use by wheat plants.

The 14.3.3 proteins are a conserved family that regulate proteolysis by binding, and hence protecting, target proteins. Valerie Cotelle (University of Dundee, UK) explained that this system appears to be important during periods of carbohydrate limitation, such as senescence induced by nutrient deficiency. In this instance, valuable nutrients contained within the older leaves need to be remobilized for transport to younger plant parts. Hence the lack of 14.3.3 protein-binding in senescing leaves permits remobilization of nutrients within the plant and survival of what could be transient nutrient stress.

Sulfur requirements

Both micro- and macro-nutrients are extremely important for continued plant growth and survival. Because of recent improvements in the environment, especially reduction of atmospheric pollution, many modern crop plants suffer through lack of sulfur. Steve Thomas (University of Wolverhampton, UK) explained how the effects of sulfur limitation might not be visible but can have consequences for processing, such as the losses in extractable sulfur from sulfur-deficient sugar beet (Beta vulgaris). Mechteld Blake-Kalfe (IACR Rothamsted, UK) explained why it was extremely difficult to diagnose sulfur-deficient plants in the field. Environmental and growth-stage dependent variations in composition make it nearly impossible to use quantitation of sulfur-containing compounds as indicators of health or deficiency. She described an exciting new technique involving the ratio of the malate:sulfate peaks as revealed by ion-chromatography of leaf extracts. This has the potential to become a reliable and rapid technique for the diagnosis of on-farm sulfur status, such that sulfur can be added only when really needed. This would benefit both the environment and the finances of the farmer.

Oil seed rape (Brassica napus) is a sulfur-demanding crop and in many varieties this sulfur is present as a glucosinolate pool in the seeds. Glucosinolates are formed from the sulfur-containing amino acid, methionine, and are believed to function in plant defence. One example of this is the specialized, glucosinolate-rich, ‘S-cells’ that exist along the length of the phloem. Legal limits are set for the concentration of these potentially toxic compounds in seed that is used for oil production. Roger Wallsgrove (IACR Rothamsted, UK) described radiolabelling experiments that showed that the commercially desirable low glucosinolate cultivars of oilseed rape have not arisen as a result of impaired sulfur-transport capacity between pod and seed. It now seems that a metabolic lesion in the glucosinolate biosynthetic pathway might explain the occurrence of low glucosinolate varieties.

Breeding for the future

It was clear from many presentations at the meeting that transgenic plants are being effectively used in conjunction with physiological and biochemical tools for the elucidation of key steps in the regulation of resource partitioning. Much of the work described in the meeting goes beyond science for the sake of academic interest. Transgenic plants, even if not an end in themselves, can be used to indicate the path for breeders to tread. Because breeding a new plant variety can take up to 20 years, early identification of selection criteria is extremely important. The continued use of genetic mapping techniques to improve crop plants should contribute to the attainment of improved yields, such as harvesting wheat at the 20 t per ha goal indicated by Roger Sylvester-Bradley (ADAS, Cambridge, UK).

Quantitative trait loci (QTL) analysis is one genetic mapping technique currently being used to elucidate complex traits such as the interactions involved in regulation of carbohydrate metabolism (Lesley Turner and Andy Cairns; IGER Aberystwyth, UK). It is believed that by increasing the sugar content of pasture forage, plant material can be more efficiently used during digestion by the animal. Accurate genetic maps are being constructed for traits such as sucrose and starch accumulation and metabolism. These should aid considerabily in the selection and breeding of improved crops.

Conclusions

There can be no doubt that centuries of plant breeding have significantly improved the varieties of crop plants we have at our disposal today. We are also aware of the requirement for additional supplies of certain nutrients to improve poor soils or to increase yield. However, western agriculture is also moving towards considerations of quality rather than quantity. This meeting has shown that we can still make improvements to crop plants by both addition of desirable traits and removal of the undesirable ones. Multidisciplinary approaches promise much for increased knowledge and future improvements of what are complex, often interdependent systems. A combination of biochemical and genetic approaches will surely be exploited in the next generation of improved crop plants.

References


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