

## PREFACE

### Plant Responses to Water Stress

H. GRIFFITHS<sup>1,\*</sup> and M. A. J. PARRY<sup>2</sup>

<sup>1</sup>*Department of Plant Sciences, Downing Street, University of Cambridge, Cambridge CB2 3EA, UK and*

<sup>2</sup>*Crop Performance and Improvement Division, IACR Rothamsted, Harpenden, Herts AL5 2JQ, UK*

Received: 27 March 2002 Returned for revision: 16 April 2002 Accepted: 18 April 2002

This Special Issue comprises a series of papers that develops the theme of plant responses to water stress, encompassing recent developments at the molecular level, through responses of photosynthesis and metabolism, to their application in crop selection and yield. The consideration of water deficits is particularly timely, given the huge developments in this area in the past decade. This issue specifically sets out to place molecular and physiological processes and their agronomic applications in an environmental context.

© 2002 Annals of Botany Company

**Key words:** Stomatal inhibition, midday depression, photosynthesis.

Since the publication of texts such as Smith and Griffiths (1992) major advances in genomics have allowed a progression from characterizing individual genes and their specific responses to stress, towards determining the cascade of processes likely to be associated with both inter- and intracellular signalling of water deficits, as effected, for instance, by abscisic acid. The use of microarrays, as reviewed in the contribution from Bray (2002), will identify the suite of genes for which expression is moderated in response to stress (whether up- or down-regulated). This will improve understanding of cell- and tissue-specific responses to water deficits, as well as characterizing the interplay between signalling processes and subsequent metabolic responses. These, of course, include the up-regulation of amino acid metabolism, as considered in two subsequent papers, since synthesis and transport allow compatible solutes to protect from both direct (hydration) and indirect (radical scavenging) effects of water deficits.

The effects of water deficits on Rubisco, photosynthesis and photorespiration are then examined in some detail: the mechanism by which Rubisco may be down-regulated in the light due to tight-binding inhibitors (Parry *et al.*, 2002) could be pivotal for tolerance and recovery from stress, and, as discussed below, may be central to integrating the midday depression of photosynthesis. Additionally, enhanced rates of oxygenase activity and photorespiration maintain the electron transport rate in response to drought and are quantitatively much more important than the Mehler reaction (Haupt-Herting and Fock, 2002; Noctor *et al.*, 2002). Indeed, the high absolute concentrations of hydrogen peroxide likely to be generated in association with photorespiratory activity re-emphasize the importance of antioxidant systems for maintaining the integrity of cellular

processes and also for signalling responses to drought (Noctor *et al.*, 2002).

One area of major interest, highlighted by the Special Issue, is the contrasting interpretation of ‘stomatal’ and ‘non-stomatal’ inhibition of photosynthetic metabolism. Controversy surrounds the extent to which photosynthesis recovers under elevated CO<sub>2</sub> during the onset of a water deficit (Tezara *et al.*, 1999; Cornic, 2000; Lawlor and Cornic, 2002). The differences may relate, in part, to diverse means for assessing such responses, whether measuring oxygen evolution using a leaf disc electrode, CO<sub>2</sub> exchange or fluorescence. For instance, in succulent plants such as those with CAM, there is a huge discrepancy between rates of net CO<sub>2</sub> exchange measured with an IRGA system, and net O<sub>2</sub> exchange measured with a leaf disc electrode (Griffiths *et al.*, 2002). To develop this debate, the paper by Boyer and colleagues (Tang *et al.*, 2002) initially suggests that there is a combination of stomatal and non-stomatal effects, dependent on the extent of water deficit. This suggestion is an outcome of experiments in which diffusion limitations were manipulated by stripping away the lower epidermis. David Lawlor gives a major overview of his work, and specifically identifies two generalized responses distinguished by the relative water content at which non-stomatal (metabolic) effects develop (Lawlor, 2002). However, during the gradual imposition of moderate water deficits (usually down to –1.8 MPa over 15 d or longer), Cornic and Fresneau (2002) find that the responses are almost exclusively based on stomatal limitation.

How might these differing stances be resolved? First, by studying several species differing in drought tolerance, or by using knockout mutants to determine the contribution from individual metabolic constituents. Secondly, it would be useful to vary the duration and intensity of the imposed drought in the short- (5 d) and long-term (2–3 weeks). In addition, results should be evaluated using a combination of available technologies, combining fluorescence and gas exchange, preferably in association with gross O<sub>2</sub> measure-

\* For correspondence. E-mail hg230@cam.ac.uk

ments made using a mass spectrometer (c.f. Haupt-Herting and Fock, 2002), as well as detailed time courses of metabolic profiles and ATPase activity and expression. The likely resolution is that both groups will be partly correct, in that metabolic limitation will depend both on the extent of drought and the susceptibility of an individual species. However, neither stomatal nor non-stomatal effects alone explain the responses that are reversible on a daily basis for plants in the field. One of the first papers to measure photosynthetic limitation and water deficit on a diurnal basis, under field conditions in the Mediterranean, characterized the midday depression of photosynthesis in *Quercus suber* (Tenhunen *et al.*, 1984). Here, abbreviated CO<sub>2</sub> response curves (*A/C<sub>i</sub>* analyses) followed the progressive reduction in carboxylation efficiency as stomata closed at midday, and a concomitant increase in CO<sub>2</sub> compensation point reflected increased photorespiratory activity.

Two key points emerge from the study by Tenhunen *et al.* (1984). First, the carboxylation efficiency recovered during the afternoon, and secondly, the internal CO<sub>2</sub> concentration remained constant throughout the day, with no additional drawdown by Rubisco at midday. This suggests that, under natural conditions, there is no simple division between stomatal and non-stomatal effects. The leaves would probably not respond to elevated CO<sub>2</sub> at midday because of the down-regulation of Rubisco activity, perhaps associated with inhibitors (Parry *et al.*, 2002) and reduced Rubisco activase activity (Crafts-Brandner and Salvucci, 2000). Photosynthetic metabolism, however, recovered in the afternoon, showing that the effect was not a long-term, non-stomatal effect. Were ATP levels to have been measured, they would no doubt have shown a reduction at midday, since the increased non-photochemical quenching inferred from a subsequent study (Demmig Adams *et al.*, 1989) showed how efficiency of light harvesting is tightly coupled to photosynthetic carbon and photorespiratory metabolism.

The final part of this Special Issue considers how these integrated mesophyll responses translate under Mediterranean field conditions for a range of natural vegetation and crops, with implications for phenology of growth and development of yield components, and their evaluation using stable isotopes. The genotypic variations in stress response have implications for crop selection, with consideration given to variations in both wheat and sugar beet as typical crops. Ultimately, however, we must translate these physiological and developmental markers into a more rigorous genetic framework, and, as illustrated by Tuberosa *et al.* (2002), the insights generated by quantitative trait loci analysis can now be linked to the expression of genes and their associated products.

This Special Issue of *Annals of Botany* represents selected papers from the symposium 'Plant Responses to Water Stress' which was part of the Society of Experimental Biology AGM held at the University of Kent at Canterbury, UK, in April 2001. Since the Symposium was organised to mark the work of David Lawlor, it seems particularly appropriate that the Special Issue has such an integrated

context, setting recent developments in the selection for crop yield against underlying photosynthetic, metabolic and molecular responses to water deficits. Whilst this latest set of Canterbury Tales may not quite achieve a citation half-life to match Chaucer's originals, we hope that the papers reflect the spirited discussions at the meeting and we are convinced that the Special Issue will make a major contribution to future studies of plant responses to water deficits.

## LITERATURE CITED

- Bray EA.** 2002. Classification of genes differentially expressed during water-deficit stress in *Arabidopsis thaliana*: an analysis using microarray and differential expression data. *Annals of Botany* **89**: 803–811.
- Cornic G.** 2000. Drought stress inhibits photosynthesis by decreasing stomatal aperture- not by affecting ATP synthesis. *Trends in Plant Science* **5**: 187–188.
- Cornic G, Fresneau C.** 2002. Photosynthetic carbon reduction and carbon oxidation cycles are the main electron sinks for photosystem II activity during a mild drought. *Annals of Botany* **89**: 887–894.
- Crafts-Brandner SJ, Salvucci ME.** 2000. Rubisco activase constrains the photosynthetic potential at high temperature and CO<sub>2</sub>. *Proceedings of the National Academy of Sciences of the USA* **97**: 13430–13435.
- Demmig-Adams B, Adams III WW, Winter K, Meyer A, Schreiber U, Pereira JS, Kruger A, Cygan FC, Lange OL.** 1989. Photochemical efficiency of photosystem II, photon yield of CO<sub>2</sub> evolution, photosynthetic capacity and carotenoid composition during the midday depression of net CO<sub>2</sub> uptake in *Arbutus unedo* growing in Portugal. *Planta* **177**: 377–387.
- Griffiths H, Helliker B, Roberts A, Haslam RP, Girnus J, Robe WE, Borland AM, Maxwell K.** 2002. Regulation of Rubisco activity in CAM plants: better late than never. *Functional Plant Biology* **29**: (in press).
- Haupt-Herting S, Fock HP.** 2002. Oxygen exchange in relation to carbon assimilation in water-stressed leaves during photosynthesis. *Annals of Botany* **89**: 851–859.
- Lawlor DW.** 2002. Limitation to photosynthesis in water-stressed leaves: stomata vs. metabolism and the role of ATP. *Annals of Botany* **89**: 871–885.
- Lawlor DW, Cornic G.** 2002. Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant, Cell and Environment* **25**: 275–294.
- Noctor G, Veljovic-Jovanovic S, Driscoll S, Novitskaya L, Foyer CH.** 2002. Drought and oxidative load in leaves of C<sub>3</sub> plants: a predominant role for photorespiration? *Annals of Botany* **89**: 841–850.
- Parry MAJ, Androlojc PJ, Khan S, Lea PJ, Keys AJ.** 2002. Rubisco activity: effects of drought stress. *Annals of Botany* **89**: 833–839.
- Smith JAC, Griffiths H.** 1992. *Water deficits: plant responses from cell to community*. Oxford: Bios.
- Tang A-C, Kawamitsu Y, Kanechi M, Boyer JS.** 2002. Photosynthetic oxygen evolution at low water potential in leaf discs lacking an epidermis. *Annals of Botany* **89**: 861–870.
- Tenhunen JD, Lange OL, Gebel J, Beyschlag W, Weber JA.** 1984. Changes in photosynthetic capacity, carboxylation efficiency and CO<sub>2</sub> compensation point associated with midday depression of net CO<sub>2</sub> exchange in leaves of *Quercus suber*. *Planta* **193**: 193–203.
- Tezara W, Mitchell VJ, Driscoll SP, Lawlor DW.** 1999. Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. *Nature* **401**: 914–917.
- Tuberosa R, Salvi S, Sanguineti MC, Landi P, Maccafferri M, Conti S.** 2002. Mapping QTLs regulating morpho-physiological traits and yield: case studies, shortcomings and perspectives in drought-stressed maize. *Annals of Botany* **89**: 941–963.