Meetings

Photosynthesis: ancient, essential, complex, diverse . . . and in need of improvement in a changing world

The 17th International Congress on Photosynthesis Research – Photosynthesis in a Changing World, Maastricht, the Netherlands, August, 2016

The 17th International Congress on Photosynthesis Research covered an extraordinarily broad range of topics from submolecular-scale biophysical details of energy transfer and basic chemistry of artificial photosynthesis to ecophysiology and crop physiology at whole leaf, whole plant and global scales. Recognizing that photosynthesis is the key source of energy for life on Earth and given the rapid pace of global environmental change, and the pressure of an increasing human population (e.g. Tilman *et al.*, 2011; Alexandratos & Bruinsma, 2012), the photosynthesis research community faces two important challenges: (1) understanding the mechanisms, vulnerabilities and potentials for improvement of the photosynthetic process; and (2) developing better techniques for monitoring, modeling and rapid screening of photosynthesis at scales ranging from the individual genotype (Fiorani & Schurr, 2013) to fields, bread-baskets (Guan *et al.*, 2016; Pinto *et al.*, 2016) and global vegetation units (Rogers *et al.*, 2016). Addressing these challenges is essential to identify and incorporate new genetic improvements in the basic mechanism, and to understand and anticipate the role of photosynthesis in the responses of the global biosphere to climate and anthropogenic changes. In this regard we take note of the decision made this year by the European Space Agency (ESA) to build a satellite, Fluorescence Explorer (FLEX) mission, intended specifically for studies of photosynthesis by monitoring a product of photosynthesis, chlorophyll fluorescence. While this will provide an unprecedented new measurement capability, there remain many questions about how to relate this measurement to photosynthesis (Schlau-Cohen & Berry, 2015) and this challenge will, no doubt, be a major issue in future congresses.

Another challenge to crop improvement is the fact that the photosynthetic process has been fine-tuned by billions of years of natural selection, and is subject to deeply rooted genetic controls shaped in the native environments of the crop ancestors. These may be difficult to change and may not be optimal for current agro-ecosystems. This was nicely demonstrated at the meeting by Lisa Ainsworth (USDA ARS, USA) who reported on mechanisms underlying the historical 80-year improvement in soybean yield showing that soybean yield has been driven largely by a near doubling of harvest index. While the rate of carbon gain per unit leaf area has increased somewhat in modern soybean cultivars, it has been due to increased stomatal conductance and lower water-use efficiency, rather than via increases in photosynthetic capacity (Koester *et al.*, 2016). Yet, photosynthesis is the only yield determinant that is not close to its biological limits (Zhu *et al.*, 2008; Ort *et al.*, 2015), suggesting that increases in photosynthesis might indeed lead to increases in yield. In the following, we focus on meeting highlights pertaining to rate-limiting processes for which improvements could increase crop yield, and on new advancements in monitoring and predictive modeling of plant photosynthesis.

Limitation of photosynthesis by Rubisco kinetics and photorespiration

Plant photosynthesis is limited by Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) activity much of the time due to its slow catalytic turnover, and concurrent oxygenase activity that competes with carbon fixation, especially in conditions of low chloroplastic CO_2 concentration and higher temperatures. That not all Rubiscos are identical has motivated work, reported at this meeting, on the extensive screening of natural diversity in Rubisco structure and kinetic properties (Galmés *et al.*, 2014b; Whitney *et al.*, 2015; Hermida-Carrera *et al.*, 2016; Orr *et al.*, 2016). Such characterization is essential to underpin attempts to tailor crops to future climates. In particular, model analyses suggest that for many crops replacement of the native Rubisco with the Rubisco of different kinetic properties would increase photosynthesis in future climates/atmospheres (Long *et al.*, 2006; Galmés *et al.*, 2014a). While low expression and poor assembly of transgenic Rubiscos has bedevilled these replacement efforts, Spencer Whitney (Australian National University, Australia) showed promising strategies to engineer foreign Rubisco into tobacco. The use of engineered tobacco plants to test the influence of altered Rubisco kinetics under future realistic environmental conditions was further reported by Danielle Way (University of Western Ontario, Canada). Whitney also emphasized the importance of Rubisco assembly within the chloroplasts and indicated that co-evolution of one of the chaperons, Raf1, with Rubisco (Whitney *et al.*, 2015) might limit the assembly of foreign Rubisco when Rubisco without Raf1 is engineered into plants. Exciting progress in understanding the complex processes in assembly and activation of Rubisco was discussed in the plenary talk of Manajit Heyer-Hartl (Max Planck Institute of Biochemistry, Germany; Durão *et al.*, 2015; Hauser *et al.*, 2015), revealing promise that the mechanisms of Rubisco assembly may be soon resolved.

The two alternatives to modifying Rubisco are suppression of photorespiration by introducing CO_2-concentrating mechanisms such as those present in C_4 plants, and direct improvement of photorespiration using novel biochemistries to recover carbon at less energetic cost (Kebeish *et al.*, 2007; Xin *et al.*, 2015). So far, the progress on both fronts has been disappointingly moderate. In a plenary talk, Andreas Weber (University of Düsseldorf, Germany) discussed the recent developments in identification of the intermediate states in the evolution from C_3 to C_4 photosynthesis by quantitative genetic approaches (Schlueter & Weber, 2016). Identification of such intermediaries is the key to engineering C_4 photosynthesis into C_3 plants (Schuler *et al.*, 2016).

Direct improvement of photorespiration depends on resolving the mismatch between carbon metabolism and energy supply (Xin *et al.*, 2015). As Hermann Bauwe (University of Rostock, Germany) discussed, some photorespiratory bypasses that have been engineered into plants disturb NADH supply to mitochondria and, therefore, can be counterproductive due to suppression of mitochondrial ATP synthesis. To further complicate matters, engineering photorespiration to future conditions also requires consideration of inorganic nitrogen assimilation. Florian Busch (Australian National University, Australia) suggested that linking nitrogen assimilation to photosynthesis by removal of a greater fraction of glycine from the photorespiratory cycle enhances photosynthesis; this can be particularly relevant under conditions of high CO_2 when the use of nitrate assimilation is inhibited (Bloom *et al.*, 2010). The importance of the efforts to improve Rubisco and photorespiration was emphasized by Berkeley Walker (University of Düsseldorf, Germany) who showed that despite photorespiration of crops being predicted to decrease under future realistic climate scenarios due to the effect of increasing CO_2 concentration being stronger than the higher temperature effect on Rubisco kinetics (Walker *et al.*, 2016), photorespiration will remain a very large drag on C_3 photosynthetic efficiency throughout this century.

CO_2 diffusion limitations of photosynthesis

For photosynthesis to occur, CO_2 has to diffuse from the surrounding leaves to the sites of CO_2 fixation, which are in the chloroplasts in C_3 species and in the mesophyll cytosol in C_4 species. Compared with the control of photosynthesis by CO_2 diffusion from the air to intercellular airspaces due to stomatal conductance, the control by CO_2 diffusion from intercellular airspaces into chloroplasts as a result of limited mesophyll conductance is much less understood (Flexas *et al.*, 2012). John Evans (Australian National University, Australia) discussed the control of mesophyll conductance by leaf anatomical characteristics including the intercellular airspace exposed surface area of mesophyll cells, cell wall thickness, and properties of the cell wall and membranes. These are traits that vary among plant functional types and underlay the plant functional type-specific differences in the CO_2 sensitivity of photosynthesis (Niinemets *et al.*, 2011). Jennifer McElwain and Charilaos Yiotis (University College Dublin, Ireland) put such structural controls in an evolutionary context to explain the shifts in dominance of ferns, gymnosperms and angiosperms as plants encountered varying $CO_2 : O_2$ concentration ratios over geological time. Furthermore, the structural controls are also predicted to alter the distribution of natural vegetation in future atmospheres (Niinemets *et al.*, 2011; Flexas *et al.*, 2016).

It is currently less clear how we can explain rapid changes in mesophyll conductance, which have sometimes been observed. Several aquaporins have been shown to enhance CO_2 permeability of membranes and John Evans suggested that aquaporins may form part of the answer; however, he pointed out that our quantitative understanding is currently limited by the resolution of techniques that exist for measuring mesophyll conductance (Groszmann *et al.*, 2016). Guillaume Théroux-Rancourt (University of California Davis, USA) further suggested that two-dimensional techniques used to quantify mesophyll conductance may lead to misleading inferences on light dependence of mesophyll conductance, as different cell layers contribute to photosynthesis at low and high light. This suggests that three-dimensional (3D) leaf anatomy needs to be considered in models calculating mesophyll conductance (see also Lloyd *et al.*, 1992).

Most of our information on mesophyll conductance has been obtained in C_3 species where several measuring techniques exist, including measurements of ^{13}C isotope discrimination or chlorophyll fluorescence combined with gas exchange. These techniques cannot be used to measure mesophyll conductance in C_4 species. An exciting advancement has been the use of stable isotopes of oxygen (^{18}O) in CO_2 to estimate mesophyll conductance (Gillon & Yakir, 2000; Barbour *et al.*, 2016). Asaph Cousins and his team (Washington State University, USA) have used this technique to quantify mesophyll conductance in several C_4 species, demonstrating that mesophyll conductance in C_4 species is quantitatively similar to that of C_3 species at comparable photosynthetic rates (Ubierna *et al.*, 2016). Furthermore, Cousins demonstrated that mesophyll conductance in C_4 species *Zea mays*, *Setaria viridis* and *Miscanthus* × *giganteus* strongly increased with temperature, as had previously been observed for C_3 species (von Caemmerer & Evans, 2015).

Improving C_3 plant photosynthesis by introducing carbon-concentrating mechanisms (Atkinson *et al.*, 2016) or facilitating diffusion by increasing carbonic anhydrase activity (Terashima *et al.*, 2011) have also been suggested as possible targets for improving photosynthesis. However, the progress has been moderate (Atkinson *et al.*, 2016), and as Bernard Genty (Centre Energie Atomique et Energies Alternatives, France) demonstrated, CO_2 backdiffusion and lack of intrachloroplastic compartmentalization implies that faster inorganic carbon conversion to CO_2 has only limited effects on photosynthesis.

Improving inefficiencies due to limited response to dynamically changing environmental drivers over the short and long term

Photosynthetic research in natural field environments and in crop plants has characteristically looked at photosynthesis in steady-state conditions. However, leaves in plant canopies have a light and temperature environment that is under constant fluctuation, and thus, photosynthesis is continually adjusting to such fluctuations.

However, reaching full photosynthetic activation upon environmental changes is time-consuming, implying that the environment dynamicity has important consequences for daily carbon gain. Losses in productivity due to limited dynamic responses can result from slow activation of Calvin cycle enzymes, including Rubisco activation by Rubisco activase, time needed to fill up the metabolite pools of the Calvin cycle, limited rate of relaxation of photoprotective nonphotochemical quenching (NPQ), as well as sluggish stomatal movements.

Rebekka Wachter (Arizona State University, USA) described new mechanisms for the assembly and regulation of Rubisco activase from higher plants and explained the possible mechanisms underlying the Rubisco activation kinetics (Kuriata *et al.*, 2014; Wachter & Henderson, 2015), while Elizabete Carmo-Silva (Lancaster University, UK) reported on natural variation in the response of Rubisco and Rubisco activase that holds promise for improving daily carbon gain by maintaining a higher average Rubisco activation state in fluctuating light. Ana Lobo (Universidade Federal do Ceará, Brazil) tested the hypothesis that overexpression of 2-carboxy-D-arabinitol-1-phosphate (CA1P) phosphatase (CA1Pase) to more rapidly dephosphorylate the Rubisco inhibitor CA1P to a noninhibitory compound would stimulate Rubisco activity and photosynthesis by decreasing the amount of CA1P in wheat leaves. The surprising outcome was that CA1Pase overexpression resulted in a large drop in Rubisco abundance and photosynthesis, proving that not every good idea goes as planned.

Although there is considerable biological variability in the rate of NPQ relaxation (e.g. Adams *et al.*, 2001), there have been surprisingly few efforts to enhance it. Johannes Kromdijk (University of Illinois, USA) reported exciting results showing that the transgenic manipulation of three genes involved in regulating the formation and relaxation of NPQ resulted in tobacco plants that had a significantly higher rate of NPQ relaxation. This, in turn, resulted in significantly higher carbon gain and biomass accumulation in fluctuating light.

Tracy Lawson (University of Essex, UK) showed that owing to a mismatch between photosynthetic induction and stomatal response, species differences in stomatal kinetics strongly affect plant water-use efficiency (McAusland *et al.*, 2016. The implications of dynamic environmental conditions on simulated carbon gain at leaf and canopy scales were further considered by Silvere Vialet-Chabrand (University of Essex) and Alejandro Morales Sierre (University of Wageningen, the Netherlands). Compared with past dynamic photosynthesis models (e.g. Pearcy *et al.*, 1997), these new models include mesophyll conductance, chloroplast movements and relaxation of fast and slow components of NPQ, providing tools for rigorous quantification of the dynamic adjustment of photosynthetic traits on plant productivity. Our general feeling from this meeting was that the photosynthesis community is increasingly starting to appreciate the relevance of fast dynamic responses of photosynthesis and their implications for crop yield.

Regarding longer-term dynamics, it has long been thought that rising atmospheric CO_2 would improve crop yields, particularly during drought events, because it promotes stomatal closure and saves water. ISPR 2016 Calvin Benson Award winner Andrew Leakey (University of Illinois, USA) presented surprising results from eight seasons of FACE experiments showing that increased sensitivity of stomata to physiological drought signals limited the usual CO_2 stimulation of photosynthesis, and that an interaction of CO_2 enrichment, drought and the deployment of nitrogen-fixing root nodules in dry soil led to a nitrogen deficit in drought years. Thus, in wet years, elevated CO_2 improved soybean yield by more than 20%, but severe drought eliminated the stimulation altogether (Gray *et al.*, 2016).

Sink–source activity and implications for whole plant photosynthesis

Sink strength has long been recognized as an important regulator of photosynthetic carbon gain and yield. The ratio between the supply of carbohydrates by the leaves and the consumption by all plant organs, the source : sink ratio, has been found to be an important player that can upregulate or downregulate photosynthesis. Congming Lu (Chinese Academy of Sciences, China) reported evidence that transgenic rice plants expressing the *Arabidopsis* phloem-specific sucrose transporter AtSUC2, which loads sucrose into the phloem, showed up to 16% increase in grain yield in field trials. Daisuke Sugiura (University of Tokyo, Japan) manipulated the source : sink balance of a range of species by continuously removing the new leaves, providing low levels of nutrients or high levels of light. Soluble sugars and starch accumulated relative to control plants, but a significant negative correlation with photosynthetic capacity was observed in only one of the species studied. He considered the effect of defoliation more closely and found that it strongly increased the total leaf mass and cell wall mass per leaf area, but decreased stomatal and mesophyll conductance. The implication of these findings is that there could be various independent modes by which source and sink interact. Although sink–source effects were seemingly an underrepresented area at the Congress, resolving the controls of sink strength is of paramount significance for efforts targeted to improve crop photosynthesis under future climates.

Improvements in predicting and monitoring photosynthesis

The steady-state photosynthesis model of Farquhar *et al.* (1980) is now widely used in simulating photosynthesis at scales ranging from leaf to globe because of its simplicity, ease of parameterization and extensive validation. Since the model development, there have been uncertainties in description of the light reactions of photosynthesis, in particular, about how the balance of ATP and NADPH is achieved, and what limits photosynthesis in feedback-inhibited conditions (Sharkey, 1985). Xinyou Yin (University of Wageningen, the Netherlands) extended the Farquhar *et al.* (1980) steady-state model by including cyclic and pseudocyclic electron flows and distribution of light between photosystems I and II (PSI and PSII). David Kramer (Michigan State University, USA) described an approach using cost-effective distributed, cloud-linked instrumentation based on measurements of chlorophyll fluorescence for studies of photosynthesis in agriculture, ecology and climate research. Point measurements taken by a large number of operators all over the world are automatically reported to a central cloud-based server where machine learning algorithms can be used to analyze simultaneous data from many locations, revealing hidden relationships and allowing for efficient gap-filling strategies and integrated estimates to be made. This is highly promising, as measuring light reactions of photosynthesis is principally the only option for simple and fast screening of photosynthetic activity in multiple locations and for large-scale assessment of photosynthetic activity of plants (Guan *et al.*, 2016; Pinto *et al.*, 2016).

Several talks focused on remote sensing of fluorescence emitted from chlorophyll of photosynthetic organisms in response to passive solar illumination. Unlike other forms of remote sensing, this measurement is tied specifically, and mechanistically, to the photosynthetic process (Schlau-Cohen & Berry, 2015). The fact that this signal can now be measured from space opens up new possibilities for investigating photosynthetic mechanisms at a planetary scale, and new challenges to interpret this measurement. Presentations dealt with retrieval of fluorescence from the global oceans and from the land; with measurements at smaller scales designed to provide 'ground-truth' for the global measurements, and with model development designed to bridge the gap between mechanistic studies of photosynthesis at the leaf or chloroplast scale and experimental observations of fluorescence emitted from complex canopies. Uwe Rascher (Forschungszentrum Jülich, Germany) presented an overview of the FLEX mission recently selected by the ESA. FLEX will be the first satellite designed specifically for retrieval of fluorescence from terrestrial plants, and is expected to launch in 2022. Rascher also described extensive ground- and aircraft-based measurements that have paved the way for this mission. Most important is the visualization of large differences between vegetation types (e.g. crops and forests) in fluorescence that correspond to differences in their photosynthetic rates. Fluorescence was also shown to be a sensitive indicator of the presence of plant stress, supporting the prospect that this satellite will have a major impact on efforts to understand photosynthesis at a planetary scale. Christiaan van der Tol (University of Twente, the Netherlands) described a model developed to simulate and assimilate satellite observations to invert for important vegetation properties (like Rubisco levels) that are known to control productivity (Tol *et al.*, 2014). While the recent progress in remote sensing by gauging solar-induced fluorescence has been truly amazing, there are still uncertainties in the mechanistic aspects of fluorescence, especially the relative roles of PSI and PSII and NPQ in the passive fluorescence observed by aircraft and satellites, and therefore, quantification of the relationship between fluorescence and productivity still remains challenging.

Outlook and future perspectives

The conference showed exciting examples where steps forward were made in understanding and manipulating components of the photosynthetic process, in part by clever experimentation, in part by changing genes or gene expression. What we hope to see for the next meeting in 2020 in Rotorua, New Zealand, is that people are able to combine these insights to stack various changes onto each other, thereby reaching improvements in productivity that would go beyond the values that have been reported for those changes individually. Another great step forward would be the maturation of techniques for satellite-based remote sensing of traits of the photosynthetic process such that they will indeed reveal new possibilities for investigating photosynthesis and photosynthetic mechanisms at a planetary scale.

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