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, 7-12 August, 2016, Maastricht, The Netherlands

Ülo Niinemets[1,2*], Joseph A. Berry[3], Susanne von Caemmerer[4], Donald R. Ort[5], Martin A. J. Parry[6], Hendrik Poorter[7]

[1] Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 1, Tartu 51014, Estonia

[2] Estonian Academy of Sciences, Kohtu 6, 10130 Tallinn, Estonia

[3] Department of Global Ecology, Carnegie Institution of Washington, 260 Panama St. Stanford, CA 94305

[4] Plant Science Division, Research School of Biology, The Australian National University, Canberra, ACT 0200, Australia

[5] USDA Agricultural Research Service & Department of Plant Biology, University of Illinois. Urbana, IL 61801 USA

[6] Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

[7] Plant Sciences (IBG-2), Forschungszentrum Jülich GmbH, 52425 Jülich, Germany

[*] Corresponding author, e-mail: ylo.niinemets@emu.ee, Fax: +372 731 3738

The 17th Congress on Photosynthesis Research covered an extraordinarily broad range of topics from sub-molecular-scale biophysical details of energy transfer and basic chemistry of artificial photosynthesis to ecophysiology and crop physiology at whole leaf, plant and to global scales by remote sensing and modeling. Recognizing that photosynthesis is the key source of energy for life on Earth and 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 change. In this regard we take note of the decision made this year by the European Space Agency 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 carbon gain has increased somewhat in modern soybean cultivars, it has been due to increased stomatal conductance and lower water use efficiency (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). In the following, we focus on meeting highlights pertaining to rate-limiting processes for which improvement could increase crop yield, and on new advancements in monitoring and predictive modeling of plant photosynthesis.

Limitation of photosynthesis by ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) kinetics and photorespiration

Plant photosynthesis is Rubisco-activity limited much of the time due to its slow catalytic turnover, and oxygenase activity that competes with carbon fixation, especially in conditions

61   of low chloroplastic CO_2 concentration and higher temperatures. That not all Rubiscos are

62   identical has motivated work reported at this meeting on the extensive screening of natural

63   diversity in Rubisco structure and kinetic properties (Galmés *et al.*, 2014b; Whitney *et al.*,

64   2015; Hermida-Carrera *et al.*, 2016; Orr *et al.*, 2016). Such characterisation is essential to

65   underpin attempts to tailor crops to future climates. In particular, model analyses suggest that

66   for many crops replacement of the native Rubisco with the Rubisco of different kinetic

67   properties would increase photosynthesis in future climates/atmospheres (Long *et al.*, 2006;

68   Galmés *et al.*, 2014a). While low expression and poor assembly of transgenic Rubiscos has

69   bedevilled these replacement efforts, Spencer Whitney (Australian National University)

70   showed promising strategies to engineer foreign Rubisco into tobacco. The use of engineered

71   tobacco plants to test the influence of altered Rubisco kinetics under future realistic

72   environmental conditions was further reported by Danielle Way (University of Western

73   Ontario, Canada). Whitney also emphasized the importance of Rubisco assembly within the

74   chloroplasts and indicated that co-evolution of one of the chaperons Raf1 with Rubisco

75   (Whitney *et al.*, 2015) might limit the assembly of foreign Rubisco when Rubisco without

76   Raf1 is engineered into plants. Exciting progress in understanding the complex processes in

77   assembly and activation of Rubisco was discussed in the plenary talk of Manajit Heyer-Hartl

78   (Max Planck Institute of Biochemistry, Germany, Durao *et al.*, 2015; Hauser *et al.*, 2015),

79   revealing promise that the mechanisms of Rubisco assembly may be soon resolved.

80   An alternative to modifying Rubisco is to directly improve photorespiration using

81   novel biochemistries to recover carbon at less energetic cost (Kebeish *et al.*, 2007; Xin *et al.*,

82   2015). This critically depends on the coordination of carbon metabolism and energy supply

83   (Xin *et al.*, 2015). As Hermann Bauwe (University of Rostock, Germany) discussed, some

84   photorespiratory bypasses engineered into plants by now disturb NADH supply to

85   mitochondria and therefore, can be counterproductive due to suppression of mitochondrial

86   ATP synthesis. To further complicate the matters, engineering photorespiration to future

87   conditions also requires consideration of inorganic nitrogen assimilation. Florian Busch

88   (Australian National University) suggested that linking nitrogen assimilation to

89   photosynthesis by removal of a greater fraction of glycine from photorespiratory cycle

90   enhances photosynthesis, which can be particularly relevant under conditions of high CO_2

91   when the use of nitrate assimilation is inhibited (Bloom *et al.*, 2010). The importance of the

92   efforts to improve Rubisco and photorespiration was emphasized by Berkeley Walker

93   (University of Düsseldorf, Germany) who showed that despite photorespiration of crops is

94   predicted to decrease under future realistic climate scenarios due to the effect of increasing

95   CO_2 concentration being stronger than the higher temperature effect on Rubisco kinetics

96   (Walker *et al.*, 2016), photorespiration will remain a very large drag on C_3 photosynthetic

97   efficiency throughout this century.

98

99 CO_2 diffusion limitations of photosynthesis

100   For photosynthesis to occur, CO_2 has to diffuse form the surrounding leaves to the sites of

101   CO_2 fixation, which are in the chloroplast of C_3 species and in the mesophyll cytosol in C_4

102   species. Compared with the control of photosynthesis by CO_2 diffusion from the air to

103   intercellular airspaces due to stomatal conductance, the control by CO_2 diffusion from

104   intercellular airspaces into chloroplasts due to limited mesophyll conductance is much less

105   understood (Flexas *et al.*, 2012). John Evans (Australian National University) discussed the

106   control of mesophyll conductance by leaf anatomical characteristics including the

107   intercellular airspace exposed surface area of mesophyll cells, cell wall thickness and

108   properties of the cell wall and membranes. These are traits that vary among plant functional

109   types and underlay the functional type-specific differences of CO_2 sensitivity of

110   photosynthesis (Niinemets *et al.*, 2011). Jennifer McElwain and Charilaos Yiotis (University

111   College Dublin, Ireland) put such structural controls in an evolution context to explain the

112   shifts in dominance of ferns, gymnosperms and angiosperms as plants encountered varying

113     $CO_2:O_2$ concentration ratio over geological time and are also predicted to alter the

114   distribution of natural vegetation in future atmospheres (Niinemets *et al.*, 2011; Flexas *et al.*,

115   2016).

116   It is currently less clear how we can explain rapid changes in mesophyll conductance,

117   which have sometimes been observed. Several aquaporins have been shown to enhance CO_2

118   permeability of membranes and John Evans suggested that aquaporins may form part of the

119   answer, but pointed out that our quantitative understanding is currently limited by the

120   resolution of techniques that exist for measuring mesophyll conductance (Groszmann *et al.*,

121   2016). Guillaume Théroux-Rancourt (University of California Davis, USA) further suggested

122   that two-dimensional techniques used to quantify mesophyll conductance may lead to

123   misleading inferences on light dependence of mesophyll conductance as different cell layers

124   contribute to photosynthesis at low and high light, suggesting that 3D leaf anatomy needs to

125   be considered in models calculating mesophyll conductance (see also Lloyd *et al.*, 1992).

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

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

145

146   **Improving inefficiencies due to limited response to dynamically changing environmental**
147   **drivers over short and long term**

148   Photosynthetic research in natural field environments and in crop plants has characteristically
149   looked at photosynthesis in steady-state conditions. However, leaves in plant canopies have a
150   light and temperature environment that is under constant fluctuation, and thus, photosynthesis
151   is continually adjusting to such fluctuations. However, reaching full photosynthetic activation
152   upon environmental changes is time-consuming, implying that the environment dynamicity
153   has important consequences for daily carbon gain. Losses in productivity due to limited
154   dynamic responses can result from slow activation of Calvin cycle enzymes, including
155   Rubisco activation by Rubisco activase, time needed to fill up the metabolite pools of the

Calvin cycle, limited rate of relaxation of photoprotective non-photochemical 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 that overexpression of 2-carboxy-D-arabinitol-1-phosphate (CA1P) phosphatase (CA1Pase) to more rapidly dephosphorylate the Rubisco inhibitor CA1P to a non-inhibitory 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 non-photochemical quenching (NPQ) resulted in tobacco plants that had a significantly higher rate of NPQ relaxation, which in turn resulted in significantly higher carbon gain and biomass accumulation in fluctuating light.

Tracy Lawson (University of Essex, UK) showed that due to a mismatch between photosynthetic induction and stomatal response, species differences in stomatal kinetics strongly affect plant water use efficiency (McAusland *et al.*, 2016), and 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, UK) 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

188 community is increasingly starting to appreciate the relevance of fast dynamic responses of
189 photosynthesis and their implications for crop yield.

190   Regarding longer-term dynamics, it has long been thought that rising atmospheric
191 CO_2 would improve crop yields particularly during drought events because it promotes
192 stomatal closure and saves water. ISPR 2016 Calvin Benson Award winner Andrew Leakey
193 (University of Illinois, USA) presented surprising results from 8 seasons of FACE
194 experiments showing that increased sensitivity of stomata to physiological drought signals
195 limited the usual CO_2 stimulation of photosynthesis and that an interaction of CO_2
196 enrichment, drought and the deployment of nitrogen-fixing root nodules in dry soil led to a
197 nitrogen deficit in drought years. Thus, in wet years, elevated CO_2 improved soybean yield
198 by more than 20%, but severe drought eliminated the stimulation altogether (Gray *et al.*,
199 2016).

200

201 **Sink-source activity and implications for whole plant photosynthesis**

202 Sink strength has long been recognized as an important regulator of photosynthetic carbon
203 gain and yield. The ratio between the supply of carbohydrates by the leaves and the
204 consumption by all plant organs has been found to be an important player and this
205 source:sink ratio can up- or downregulate photosynthesis. Congming Lu (Chinese Academy
206 of Sciences, China) reported highly convincing evidence that transgenic rice plants
207 expressing the *Arabidopsis* phloem-specific sucrose transporter AtSUC2, which loads sucrose
208 into the phloem, showed up to 16% increase in grain yield in field trials. Daisuke Sugiura
209 (University of Tokyo, Japan) manipulated the source:sink balance of a range of species by
210 continuously removing the new leaves, providing low levels of nutrients or high levels of
211 light. Soluble sugars and starch accumulated relative to control plants, but a significant
212 negative correlation with photosynthetic capacity was observed in only one of the species
213 studied. He considered the effect of defoliation more closely and found that it strongly
214 increased the total leaf mass and cell wall mass per area, but decreased stomatal and
215 mesophyll conductance. The implication of these findings is that there could be various
216 independent modes by which source and sink interact. Although sink-source effects were
217 seemingly an underrepresented area at the Congress, resolving the controls of sink strength is
218 of paramount significance for efforts targeted to improve crop photosynthesis under future
219 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 due to 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. David Kramer (Michigan State University, USA) described of an approach of 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. 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 with observations of fluorescence emitted from complex canopies. Uwe Rascher (Forschungszentrum Jülich, Germany) presented an overview of the (FLEX) mission recently selected by the European Space Agency (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

253 and aircraft based measurements that have paved the way for this mission. Most important is
254 the visualization of large differences between vegetation types (e.g. crops and forests) in
255 fluorescence that correspond to differences in their photosynthetic rates. Fluorescence was
256 also shown to be a sensitive indicator of the presence of plant stress, supporting the prospect
257 that this satellite will have a major impact on efforts to understand photosynthesis at a
258 planetary scale. Christiaan van der Tol (University of Twente, The Netherlands) described a
259 model developed to simulate and assimilate satellite observations to invert for important
260 vegetation properties (like Rubisco levels) that are known to control productivity (Tol *et al.*,
261 2014). While the recent progress in remote sensing by gauging solar-induced fluorescence
262 has been truly amazing , there are still uncertainties in the mechanistic aspects of
263 fluorescence especially the relative roles of PSI and PSII and non-photochemical quenching
264 in the passive fluorescence observed by aircraft and satellites, and quantification of the
265 relationship between fluorescence and productivity still remains challenging.

266

267 **Outlook and future perspectives**

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

277

278 **Acknowledgements**

281

282 **References**

Adams WW, III, Demmig-Adams B, Rosenstiel TH, Ebbert V. 2001. Dependence of photosynthesis and energy dissipation activity upon growth form and light environment during the winter. *Photosynthesis Research* **67**: 51-62.

Alexandratos N, Bruinsma J. 2012. *World agriculture towards 2030/2050: The 2012 revision No. 12-03*. Rome: Food and Agricultural Organization.

Atkinson N, Feike D, Mackinder LC, Meyer MT, Griffiths H, Jonikas MC, Smith AM, McCormick AJ. 2016. Introducing an algal carbon-concentrating mechanism into higher plants: location and incorporation of key components. *Plant Biotechnology Journal* **14**: 1302-1315.

Barbour MM, Evans JR, Simonin KA, von Caemmerer S. 2016. Online CO_2 and H_2O oxygen isotope fractionation allows estimation of mesophyll conductance in C_4 plants, and reveals that mesophyll conductance decreases as leaves age in both C_4 and C_3 plants. *The New Phytologist* **210** 875-889.

Bloom AJ, Burger M, Rubio Asensio JS, Cousins AB. 2010. Carbon dioxide enrichment inhibits nitrate assimilation in wheat and *Arabidopsis*. *Science* **328**: 899-903.

Durao P, Aigner H, Nagy P, Mueller-Cajar O, Hartl FU, Hayer-Hartl M. 2015. Opposing effects of folding and assembly chaperones on evolvability of Rubisco. *Nature Chemical Biology* **1**: 148-194.

Farquhar GD, von Caemmerer S, Berry JA. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta* **149**: 78-90.

Fiorani F, Schurr U. 2013. Future scenarios for plant phenotyping. *Annual Review of Plant Biology* **64**: 267-291.

Flexas J, Barbour MM, Brendel O, Cabrera HM, Carriquí M, Diaz-Espejo A, Douthe C, Dreyer E, Ferrio JP, Gago J, Gallé A, Galmés J, Kodama N, Medrano H, Niinemets Ü, Peguero-Pina JJ, Pou A, Ribas-Carbó M, Tomás M, Tosens T, Warren CR. 2012. Mesophyll diffusion conductance to CO_2: an unappreciated central player in photosynthesis. *Plant Science* **193-194**: 70-84.

Flexas J, Díaz-Espejo A, Conesa MA, Coopman R, Douthe C, Gago J, Gallé A, Galmés J, Medrano H, Ribas-Carbo M, Tomàs M, Niinemets Ü. 2016. Mesophyll conductance to CO_2 and Rubisco as targets for improving intrinsic water use efficiency in C_3 plants. *Plant, Cell & Environment* **39**: 965-982.

Galmés J, Conesa MÀ, Díaz-Espejo A, Mir A, Perdomo JA, Niinemets Ü, Flexas J. 2014a. Rubisco catalytic properties optimized for present and future climatic conditions. *Plant Science* **226**: 61-70.

Galmés J, Kapralov MV, Andralojc PJ, Conesa MA, Keys AJ, Parry MA, Flexas J. 2014b. Expanding knowledge of the Rubisco kinetics variability in plant species: environmental and evolutionary trends. *Plant, Cell & Environment* **37**: 1989-2001.

Gillon JS, Yakir D. 2000. Internal conductance to CO_2 diffusion and $(COO)-O^{18}$ discrimination in C_3 leaves. *Plant Physiology* **123**: 201-213.

Gray SB, Dermody O, Klein SP, Locke AM, McGrath JM, Paul RE, Rosenthal DM, Ruiz-Vera UM, Siebers MH, Strellner R, Ainsworth EA, Bernacchi CJ, Long SP, Ort DR, Leakey ADB. 2016. Intensifying drought eliminates the expected benefits of elevated carbon dioxide for soybean. *Nature Plants* **2**: 16132.

Groszmann M, Osborn HL, Evans JR. 2016. Carbon dioxide and water transport through plant aquaporins. *Plant Cell and Environment* **xx**: in press.

Guan K, Berry JA, Zhang Y, Joiner J, Guanter L, Badgley G, Lobell DB. 2016. Improving the monitoring of crop productivity using spaceborne solar-induced fluorescence. *Global Change Biology* **22**: 716-726.

Hauser T, Popilka L, Hartl FU, Hayer-Hartl M. 2015. Role of auxiliary proteins in Rubisco biogenesis and function. *Nature Plants* **1**: 5065.

Hermida-Carrera C, Kapralov MV, Galmés J. 2016. Rubisco catalytic properties and temperature response in crops. *Plant Physiology* **171**: 2549-2561.

Kebeish R, Niessen M, Thiruveedhi K, Bari R, Hirsch H-J, Rosenkranz R, Stbler N, Schönfeld B, Kreuzaler F, Peterhänsel C. 2007. Chloroplastic photorespiratory bypass increases photosynthesis and biomass production in *Arabidopsis thaliana*. *Nature Biotechnology* 25: 593-599.

Koester RP, Nohl BM, Diers BW, Ainsworth EA. 2016. Has photosynthetic capacity increased with 80 years of soybean breeding? An examination of historical soybean cultivars. *Plant, Cell and Environment* 39: 1058-1067.

Kuriata AM, Chakraborty M, Henderson JN, Hazra S, Serban AJ, Pham TVT, Levitus M, Wachter RM. 2014. ATP and magnesium promote cotton short-form ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activase hexamer formation at low micromolar concentrations. *Biochemistry* 53: 7232-7246.

Lloyd J, Syvertsen JP, Kriedemann PE, Farquhar GD. 1992. Low conductances for CO_2 diffusion from stomata to the sites of carboxylation in leaves of woody species. *Plant, Cell and Environment* 15: 873-899.

Long SP, Zhu X-G, Naidu SL, Ort DR. 2006. Can improvement in photosynthesis increase crop yields? *Plant, Cell and Environment* 29: 315-330.

McAusland L, Vialet-Chabrand S, Davey P, Baker NR, Brendel O, Lawson T. 2016. Effects of kinetics of light-induced stomatal responses on photosynthesis and water-use efficiency. *The New Phytologist* xx: in press.

Niinemets Ü, Flexas J, Peñuelas J. 2011. Evergreens favored by higher responsiveness to increased CO_2. *Trends in Ecology & Evolution* 26: 136-142.

Orr DJ, Alcântara A, Kapralov MV, Andralojc PJ, Carmo-Silva E, Parry MAJ. 2016. Surveying Rubisco diversity and temperature response to improve crop photosynthetic efficiency. *Plant Physiology* xx: doi://10.1104/pp.1116.00750.

Ort DR, Merchant SS, Alric J, Barkan A, Blankenship RE, Bock R, Croce R, Hanson MR, Hibberd JM, Long SP, Moore TA, V. MJ, Niyogi KK, Parry MAJ, Peralta-Yahya PP, Prince RC, Redding KE, Spalding MH, van Wijk KJ, Vermaas WFJ, von Caemmerer S, Weber APM, Yeates TO, Yuan JS, Zhu X. 2015. Can photosynthesis be redesigned to sustainably meet global food and bioenergy demand. *Proceedings of the National Academy of Sciences of the United States of America* 112: 8529-8536.

Pearcy RW, Gross LJ, He D. 1997. An improved dynamic model of photosynthesis for estimation of carbon gain in sunfleck light regimes. *Plant, Cell and Environment* 20: 411-424.

Pinto F, Damm A, Schickling A, Panigada C, Cogliati S, Müller-Linow M, Balvora A, Rascher U. 2016. Sun-induced chlorophyll fluorescence from high-resolution imaging spectroscopy data to quantify spatio-temporal patterns of photosynthetic function in crop canopies. *Plant Cell and Environment* 39: 1500-1512.

Rogers A, Medlyn BE, Dukes JS, Bonan G, von Caemmerer S, Dietze MC, Kattge J, Leakey ADB, Mercado LM, Niinemets Ü, Prentice IC, Serbin SP, Sitch S, Way DA, Zaehle S. 2016. A roadmap for improving the representation of photosynthesis in Earth system models. *The New Phytologist* xx: submitted.

Schlau-Cohen GS, Berry J. 2015. Photosynthetic fluorescence, from molecule to planet. *Physics Today* 68: 66.

Sharkey TD. 1985. Photosynthesis in intact leaves of C_3 plants: physics, physiology and rate limitations. *The Botanical Review* 51: 53-105.

Terashima I, Hanba YT, Tholen D, Niinemets Ü. 2011. Leaf functional anatomy in relation to photosynthesis. *Plant Physiology* 155: 108-116.

Tilman D, Balzer C, Hill J, Befort BL. 2011. Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences of the United States of America* 108: 20260-20264.

383   **Tol C, Berry JA, Campbell PKE, Campbell P, Rascher U. 2014. Models of fluorescence and**
384   **photosynthesis for interpreting measurements of solar-induced chlorophyll fluorescence.**
385   *Journal of Geophysical Research - Biogeosciences* **119: 2312–2327.**

386   **von Caemmerer S, Evans JR. 2015. Temperature responses of mesophyll conductance differ greatly**
387   **between species.** *Plant Cell and Environment* **38: 629-637.**

388   **Wachter RM, Henderson JN. 2015. Photosynthesis: Rubisco rescue.** *Nature Plants* **1: 1.**

389   **Walker BJ, VanLoocke A, Bernacchi CJ, Ort DR. 2016. The costs of photorespiration to food**
390   **production now and in the future.** *Annual Review of Plant Biology* **67: 107-129.**

391   **Whitney SM, Birch R, Kelso C, Beck JL, Kapralov MV. 2015. Improving recombinant Rubisco**
392   **biogenesis, plant photosynthesis and growth by coexpressing its ancillary RAF1 chaperone.**
393   *Proceedings of the National Academy of Sciences of the United States of America* **112:**
394   **3564-3569.**

395   **Xin C-P, Tholen D, Devloo V, Zhu X-G. 2015. The benefits of photorespiratory bypasses: how can**
396   **they work?** *Plant Physiology* **167: 574-585.**

397   **Zhu X-G, Long SP, Ort DR. 2008. What is the maximum efficiency with which photosynthesis can**
398   **convert solar energy into biomass?** *Current Opinion in Biotechnology* **19: 153-159.**

399

400