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REVIEW

Plant photosynthetic production as controlled by leaf growth, phenology, and behavior

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Abstract

In this historical review we summarize discoveries related to the flowering genes in controlling leaf area index (LAI, the leaf area per unit ground area) in sorghum, soybean, or pea crop stands. We also analyze similar work on *Arabidopsis* and dwarf and intermediate stem height genes in wheat and rice.

Additional key words: *Arabidopsis*; cultivar differences; genetics; *Glycine*; leaf area index; *Oryza*; *Pisum*; *Sorghum*; *Triticum*.

Introduction

We analyze below the many processes for controlling leaf and flower bud/fruit growth and phenology as well as effects of environmental stresses on both processes, all of which in turn control stomatal and photochemical photosynthetic processes in a leaf. We explain stages of leaf growth as defined by leaf primordia initiation, appearance, full expansion, and senescence events (after full expansion, leaf photosynthesis peaks, and then steadily declines until death). Pan *et al.* (1998, 2000) have reported or cited a website for plots of such events *vs.* degree days for several crop species (for the latter data, check with M. Huck – m.huck@insightbb.com); with the possible exception of 'Gramene' (software by Xiaokang Pan, see just above) internet sites are not yet a good place to publish. At the whole plant level, one is confronted with a succession of leaves at various stages of their life cycle in the canopy, as well as at different positions on the plant shoot stem, which can be defined by similar phenology models of stem and their extension rates, internode by internode. If the reader understands what Milthorpe (1956) and Šesták (1985) discussed in their books, as well as what the flowering gene scientists Quinby, Buzzell, Bernard, Shoemaker, and Murfet did and reviewed, then read no further. These scientists are all pioneers in photosynthesis research; Borthwick, Hendricks, and their predecessors and colleagues did pioneering work (see Briggs 1976) on photoperiodism while the genetics work was being done. The reader also needs to be aware of what Borlaug, Beachell, and Yuan did with respect to the 'green revolution' as well as past or ongoing GM (genetically modified or engineered) plant research. In an era of concerns about global warming and increasing atmospheric CO_2 (see Long *et al.* 2006), as well as an increasing demand for food, fiber, or wood products, scientists engaged in photosynthesis research should be able to explain on short notice, especially to crop extension workers, crop farmer association lobbyists, and farmers, how their research is critical to solving the above problems. (The best funding example is how crop association lobbyists urged farmers to support funding for the *Arabidopsis* and subsequent crop genome projects, by contacting their congressmen in the USA who controlled the funding legislation.) Their potted plant results need to be calibrated with field results as much as is possible, so they can contribute to an ongoing plant modeling effort directly or indirectly. The reader also needs to be aware of the importance of collaborative interdisciplinary or disciplinary research. We can give numerous examples of all the above.

El-Sharkawy (2005), a prominent African scientist involved in pioneering work on leaf CO_2/H_2O exchange and anatomical aspects of C_4 photosynthesis early in its history, recently reviewed some aspects of the history of crop modeling, emphasizing the role of ongoing research

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supporting a multidisciplinary team modeling effort as well as the complexity of photosynthetic processes in the field. He pointed out the role of plant breeders/geneticists in producing cultivars with optimal LAI (leaf area per unit ground area or the leaf area index); a notable recent example being the development of dwarf or intermediate type wheat and rice cultivars which would not lodge under increased nitrogen (N) applications. He has another equally important paper (El-Sharkawy 2006) reviewing his field research on cassava at the Centro Internacional de Agricultura Tropical (CIAT), with emphasis on C_3-C_4 intermediates found in leaves of some strains growing under dry conditions (also see El-Sharkawy 1993, 2004 for the complexity of such a field system). An important aspect of the LAI work has been the isolation of photoperiod, vernalization, and phytochrome genes, which is an ongoing part of post-genomic research. Here we hope to amplify what breeders and geneticists did with respect to changes in LAI dynamics which, of course, led to increases in yield due to efficient partitioning of photoassimilates into the storage organs of the newly developed high-yielding dwarf cultivars and to the successes of the so-called Green Revolution in transforming agriculture in many countries of Asia, Europe, and the Americas (see Athwal 1971, Nasyrov 1981, Mann 1997). This is an important part of photosynthesis research largely ignored as such in the USA; we hope to rectify this situation. Courses in photosynthesis research offered at the college and graduate level need to greatly improve the coverage of LAI dynamics and leaf function, which El-Sharkawy (2005) pointed out led to Nobel and World Food Prizes, respectively, to Norman Borlaug for his work on wheat, and Henry Beachell and G. Khush on rice. Yuan and Fu (1995) also received the World Food Prize for his work on rice hybrids. Of course there are books on aspects of the subject (Milthorpe 1956, Dale and Milthorpe 1983, Šesták 1995) as well as reviews (Murfet 1977, 1989, Dale 1988).

The leaf area index (LAI)

Photosynthesis and leaf area are approximated in the British growth analysis equation dW/dt = NAR × LAI, where W = dry mass, NAR = the Net Assimilation Rate of a crop = dW/dt per unit of leaf area per unit ground area, or LAI. The terms dW/dt and NAR do not account for respiration and the transformation/condensation of photosynthetic products to growing tissues and storage organs included in the term W. McCree (1970, 1974) developed an equation (see also Hansen *et al.* 2002 for further refinements) which corrected for some of these, where growth respiration and maintenance respiration can be added to dW/dt and NAR to approximate photosynthesis better. All these include root W and respiration and must be corrected for losses of both LAI and W over time (*e.g.* dead leaves and roots, *etc.*). There are biochemical methods for calculating respiration and photosynthate condensation aspects of the problem; of course the reduction of NO_3 to NH_3 in light by early products from the photosynthetic light reactions must be accounted for (Amthor 1989, 2000). The Starkville (MS, USA) cotton models were based upon actual respiration measurements at different temperatures, as well as canopy photosynthetic rates, *etc.* (see El-Sharkawy 2005).

It would take several books by many competent authors to do justice to what we hope to cover here, particularly on what the breeders/geneticists did. We can do only a brief overview which hopefully can lead to better historical presentations of photosynthesis research in college courses and related textbooks. Recent review papers of El-Sharkawy (2004, 2005, 2006) point out the importance and complexity of the photosynthetic process under field conditions in relation to crop productivity, which is neglected in many college plant physiology or ecology courses. Concepts underlying recent crop models for predicting the effects of germplasm and environment on yield are relevant, but as El-Sharkawy (2004, 2005, 2006) points out, most related papers only review the literature; the related effort may actually be hindering progress as the mathematics involved often is not well presented. In modeling, there seems to be endless theoretical papers with few related research papers; those few are an inspiration!

The Green Revolution (dwarf and semi-dwarf cereal genes)

Hancock (1989) in his book “Lords of Poverty” discussed the shortcomings and failure of the many international organizations where aid money is largely wasted and abused mainly because of poor management. However, some of the international efforts carried out during the past four decades at various research centres on agriculture have been critical in alleviating poverty and preventing famines in many developing countries. First it should be pointed out that the international research centres/labs to their credit: (*1*) advised and pressured countries with food production problems to use updated agricultural technologies and to support vigorous related research programs on agricultural crops. India is one country which reacted quickly to this; (*2*) their staff trained scientists from third world countries who inspired other scientists in these countries and went on to do important research; (*3*) they supported financially the upland and lowland rice genome projects which were successful; and (*4*) results of their effort contributed significantly to the Asian economic boom. We provide further background information below for what it is worth; how the effort was carried out can now be criticized. Internet searches help.

The Japanese scientists developed cv. Norin 10 dwarf wheat in the mid 1900's and did an associated genetic research. The origins of Norin 10 have been discussed elsewhere (Reitz and Salmon 1968, Inazuka 1969/70, Nam and Kim, http://www.woorimie.org). The dwarfing genes apparently came from a Japanese land race Daruma, which may have had ancestors from Korean land races, Japanese breeders having been active there in the early to mid 1900's. USDA scientist Orville Vogel obtained this germplasm and developed the dwarf Gaines wheat from crosses with local cultivars made at Pullman, WA, USA. He had a two-way table in his associated publication (Vogel 1964): dwarf Gaines and normal wheat *vs*. low and high applications of N-fertilization. Gaines wheat yielded 40 % better than the other three treatments. The details of his work can be found on the internet using appropriate key words. Norman Borlaug visited Vogel and saw first hand what he had achieved; he then returned to his international lab in Mexico and crossed the dwarf wheat into Mexican and other lines, coming up with photoperiod-independent cultivars that led to part of the Green Revolution and his Nobel Prize.

Thorne *et al.* (1969) and Thorne and Blacklock (1971) were unable to repeat the Vogel's experiment in the UK; apparently because European tall cvs. did not lodge under high N fertilization. However, other reports showed that higher yields in short wheat cvs., as compared to tall locals, were associated with more grains per spikelet/ears, *i.e.* "sink strength" (Cock 1969, Syme 1969) and with higher rates of photosynthesis in flag leaves and ears, *i.e.* "source strength" (Lupton 1972, Ruckenbauer 1975). It appears therefore that higher yield in short cultivars could be attributed not only to higher harvest indices but also to higher leaf photosynthesis. Among various short and tall cultivars, El-Sharkawy (1975) reported the highest grain yield (>5 t per ha) obtained in a short-stemmed spring wheat cv. Sidi Misri-1 (derived from semi-dwarf Mexican wheat) grown under irrigation with adequate NPK fertilizers in sandy soils of the Libyan Sahara desert. The flag leaves' photosynthetic rates, as estimated from short period growth analysis after ear emergence, ranged from 0.92 to 1.22 mg(CO_2) m^{-2} s^{-1} which were much greater than average rates observed in traditional tall wheat (Stoy 1965) but similar to rates of Norin 10-derived cv. Tl 363/30 as measured by infrared gas analysis techniques and with $^{14}CO_2$ uptake at Cambridge, UK (Ruckenbauer 1975).

Details of the Chinese or Taiwan origin of dwarfing genes in rice are discussed by Kumar and Singh (1967–2002), Chang *et al.* (1967–2002), and Tasai (1998). Jennings (1964) made crosses involving dwarf rice germplasm at the International Rice Research Institute (IRRI) lab in the Philippines; the then retired USDA rice breeder Henry Beachell selected out from this material growing in the field in the Philippines the famous IR8 dwarf rice, which behaved when fertilized with N much the same as Gaines wheat. In collaboration with Khush from India, an intermediate rice cultivar resistant to diseases was developed (IR 36) which yielded better at certain latitudes. Beachell worked until he was 90, at an Indonesian international lab with Khush; both shared the World Food Prize for what they did (http://www.worldfoodprize.org/laureates/Past/1996.htm). Finding how Norin10 was developed and the genetics involved is a bit more difficult. This rice story must now be qualified somewhat by the claim by Dr. Richharia (www.satavic.org) in India that he also selected a dwarf rice, Taichung Native 1 (TN1) like IR8, which had the same dwarfing genes, before or at the same time as IR8 was bred, which he knew yielded well with fertilizer. It had superior resistance to pests and its grains were more palatable. For further details on how he fared competing with IRRI see Alvares (internet blog; www.satavic.org).

The Asian plant breeders were doing well before the Green Revolution, but it inspired them to greater heights. IRRI distributed its germplasm collection; the natives developed intermediate-height types with superior pest resistance and palatability characteristics (Mann 1997).

The Green Revolution led to a huge increase in the Asian human population indicating how successful it was in increasing food production. There were other kinds of failures along the way such as in Sub-Saharan Africa where Green Revolution had little impact on changing the traditional subsistence-type of farming systems. Due to the predicted increase in world population in the coming decades (before 2030, the United Nations predicts that the world population will likely be over 7 billion, most of them in poor countries), demand for food supply will dramatically increase while there are shortages in arable lands and irrigation water required for intensive agriculture. Furthermore, grain yields of the Green Revolution crops reached their limits with apparently no potential rising in the near future. New innovations *via* scientific research and applicable improved agricultural technology might help the repetition of the Green Revolution, especially in Africa where agricultural productivity is very low. Hopefully, genetic engineering will keep improvements coming, providing better controls of weeds, diseases, and insect pests. Much has been written about these failures (Lappe *et al.* 1998).

Pioneering flowering gene research

Photoperiodism, phytochrome behavior, and vernalization are covered at online sites (Taiz and Zeiger 2002, Gergfield *et al.* 2005) as well as recent physiology textbooks (Hay and Walker 1990, Salisbury and Ross 1992) and reviews (Smith 1995, Levy and Dean 1998, Ballare and Caseel 2000, Kay *et al.* 2002, Struck *et al.*

2003, Sung and Amasino 2005). Borthwick and Hendricks (see Briggs 1976) began their work in the mid-40's, about the same time as Quinby and Karper (1945) wrote their first sorghum flowering gene work. Quinby *et al.* (1973) published a paper on the interactions of photoperiod and temperature on the sorghum flowering genes, as well as an overview of what he did over his scientific career (1973). We liked Welch *et al.* (2003, 2005) for a detailed review of the subject as models for predicting how genes control the flowering processes, with comparisons between long-day (*Arabidopsis*) and short-day (rice) behavior.

Murfet (1977), Slafer (1993), Laurie (1997), Blazuez *et al.* (2001), and Koornneef *et al.* (1998) discussed early and recent work on flowering time genes, which include those associated with phytochrome, vernalization, and photoperiod response. Here we will cover the work of the three pioneers and their colleagues who worked on sorghum (Quinby and Karper 1945, Hesketh *et al.* 1969, Quinby 1973, Quinby *et al.* 1973), soybeans (Bernard 1971, McBlain and Bernard 1987, McBlain *et al.* 1987), and English peas (Murfet 1977, Murfet 1989, Acalde *et al.* 2000). Phytotron research at Duke University, USA, on the effects of photoperiod and temperature on flowering and maturity of the soybean and sorghum collections drew attention to what had been achieved (Quinby *et al.* 1973, McBlain *et al.* 1987) by the geneticists. Morgan *et al.* (2002) reviewed his work on the molecular biology of sorghum flowering genes in recent years, including an early paper with Quinby. Taramoto *et al.* (2005) recently screened for flowering genes in Japanese germplasm.

One needs to be aware of the Bernard and Weiss (1973) ASA Soybean Monograph chapter on soybean genes. Tasma *et al.* (2000) and Tasma and Shoemaker (2003) reported some 9 E/e genes controlling flowering in soybean including those reported by Buzzell (1971), Buzzell and Voldeng (1980), and Bonito and Vello (1999). Cober *et al.* (1996, 2001) and Stewart *et al.* (2003) did more controlled environment research similar to that of McBlain *et al.* (1987) using three E/e genes in old cultivar isolines and developed a model for predicting flowering and maturity time based upon the behavior of Bernard's three genes. Also see Boote *et al.* (2003) and Messina *et al.* (2006) for how their SOYGRO model predicts flowering and maturity as well as leaf and stem internode phenology, using information about how the E/e genes behave. Both groups of researchers took field data in Canada, Urbana (Illinois), and Gainesville (Florida) to calibrate the McBlain *et al.* (1987) potted plant phytotron results, an excellent example of how potted plant physiological research has been calibrated for predicting what happens in the field, see below (Messina *et al.* 2006 used Zhang's data of 2001). El-Sharkawy (2005) discussed how potted plant research on plant water relations has similarly been calibrated in rain-protected field plots, *etc*. Soil type is an important factor controlling how field plants behave. Zhang *et al.* (2001) reported on other controlled environment and field studies with Bernard's E/e genes in these isolines. Kumudini (2004) studied the effect of E/e genes on onset and duration of senescence. Ellis *et al.* (1992), Asumadu *et al.* (1998), and Summerfield (1998) did further studies of photoperiod response behavior of the E/e isolines from Bernard's lab. Abe *et al.* (2005) assigned the E4 locus to the classical linkage group 4. Zhang and Du (1999) screened Chinese germplasm for soybean flowering genes. Finally, Tasma *et al.* (2001) at Shoemaker's lab mapped the flowering genes, and with the generous help of Dr. Xiaokang Pan compared the soybean genome map with that of *Arabidopsis*.

Murfet reviewed her work on peas (see above) as well as the early work on the flowering/photoperiod/vernalization genes in *Arabidopsis thaliana*; Koornneef *et al.* (1998), Welch *et al.* (2003, 2005 online), and Acalde *et al.* (2000, in an associated research paper) updated Murfet's (1977) earlier review and more recent research. Other *Arabidopsis* papers on flowering genes can easily be found by an internet search. Welch tried, based upon a literature review, to integrate flowering physiology with classical and post-genomic genetics, comparing gene/physiological behavior between *Arabidopsis* (a long-day plant) and rice (a short-day plant), or a form of comparative post-genomics. He needs to simplify some of his explanations for the generalist, something we all need to do. Both Welch (2003, 2005) and El-Sharkawy (2005) reviewed some of the related crop modeling done.

Holland and Balint-Kurti (2005/6) reported on their progress in identifying the corn flowering genes. The above review is a bit sketchy but is enough for what we wish to discuss here. Of course plant breeders in general have been selecting for the optimum LAI for yields for some time and have been quite successful. The scientists involved were not members of the USA scientific establishment but enjoyed wide recognition for what they did based upon their research in the Duke University Phytotron on interactions between the effects of temperature and photoperiod on how their genes behaved.

Leaf expansion

Byrne (2006) in a new on-line journal (Plos Genetics) points out that ʽa hallmark of land plant evolution has been the development of the leaf'. The normal ultimate top surface of a leaf is immediately adjacent to the shoot apical meristem, paraphrasing what she said. Surgical separation of the initiating leaf primordia from the apical dome resulted in upside-down leaves. *Arabidopsis* mutants showing this trait led to the discovery of the genetics involved. The system is much more complex than we show here; she lists a very large number of citations in her review of the subject. It is must reading for scientists doing photosynthesis research.

Pan *et al*. (2000) included data on a website for leaf appearance (leaf primordial, grass tips, or 1 cm new leaves), full expansion (grass collar appearance rates or the end of leaf extension in dicots) and death rates over a growing season for different crop species including cotton. These rates were expressed as some kind of temperature-time function. Associated genetics controlling leaf primordia appearance at the apical dome (see Byrne 2006), leaf expansion, and leaf senescence will greatly change our understanding of the processes involved; some laboratories have begun work on this. We discuss the potted plant syndrome below and its effect on getting data for a model; controlled environment experiments have to be done with plants growing in some kind of container. Milthorpe (1956), Dale and Milthorpe (1983), and Dale (1988) give historical details in their books and reviews. One, of course, needs a root-LAI transpiration model based upon actual root measurements from excavations in different kinds of soil profiles over a growing season at different soil-water availability contents, with measurements of leaf/internode phenology and expansion/extension rates, along with photosynthetic, plant transpiration, and water stress measurements. This could be done in the field in dry climates at different latitudes and temperatures, but would be a massive undertaking. Begonia *et al.* (1986) did a cotton N × irrigation experiment in rain-protected plots in Starkville, MS, USA; there must be many similar experiments done in irrigated low rainfall areas. A group at Auburn, AL, USA tried to do a root model using rhizotrons or large containers with mixed soils. One would need to quantify crack and holes in field sites as that is where most roots tend to grow (see Wang *et al.* 1986). Associated LAI models should account for leaf photosynthesis *vs*. leaf age for each active leaf on the plant. Also, there needs to be a light interception model *vs*. time of day and each day of the growing season; a theoretical model is a little complicated. It might be best to base such a model on actual photon interception measurements in the crop or on clever use of photographs taken from different angles. Theoretical papers on N and water behavior in the crop really are meaningless without a better root supply model. Also, it would help if theoretical people working on models went to the field and actually took some data, to see the limitations of how such data can be used.

Leaf function

(*a*) *Field calibrations of laboratory potted plant results*: Musgrave at Cornell University took his students into a corn field at the Robert Musgrave Experimental Farm in Aurora, NY in the late 1950's to early 1960's to measure photosynthesis and transpiration in canopy and leaf chambers, using infra-red CO_2 gas analyzers, water vapor analyzers with chamber cooling, and sometimes corrected for intercepted irradiance by the canopy. The soil was sealed off in the canopy chambers (Hesketh 1963, Baker and Musgrave 1964, Moss and Musgrave 1971). He also used these methods in tropical corn fields in the Philippines (Heichel and Musgrave 1969a,b). El-Sharkawy (1965), El-Sharkawy *et al.* (1965), and Muramoto *et al.* (1965) used the leaf chambers in Univ. Arizona, Tucson irrigated field plots for cotton, and he also did research in the tropics in Colombia at different elevations from sea level to 1 800 m with mean temperatures varying from 29/30 °C to 17/18 °C. Musgrave, El-Sharkawy, and coworkers (El-Sharkawy and Cock 1990, El-Sharkawy *et al.* 1990, 1993, Pellet and El-Sharkawy 1993, de Tafur *et al.* 1997, El-Sharkawy 2004, 2006) also screened corn and cotton germplasms for differences in leaf photosynthetic rates. They were able to correlate for the first time differences in leaf photosynthesis in cassava with final crop yields; this may partly have had something to do with their cassava plants growing under prolonged water stress in the field. Both scientists made incredible contributions to plant water relations which are never acknowledged by the mainstream plant physiologists.

Plant water relations hit bottom in the mid-70's when a prominent book writer and researcher defined 'acclimation' in the lead paper and a large number of scientists followed with papers on their potted plant research. Shortly after in a meeting in New Hampshire, USA everyone was confronted with this syndrome and how it might affect their results, particularly a water relations speaker, who also dwelled on the definition of 'acclimation'. Recently, Long *et al.* (2006) discussed the dangers of using potted plant research done in greenhouses, growth cabinets, field enclosures, *etc.* to predict crop responses to CO_2 in the field, and noted that in respect to the ongoing USA crop research/modeling effort to predict such effects, ‘no agrochemical or plant breeding company would base its business plan for a new chemical or variety solely on greenhouse studies without rigorous field trials’. [It was obvious from his remarks and our experience that increased humidity in enclosures result in a larger response to CO_2; the experimental-modeling effort in a recent US effort to study the problem should have developed a leaf stomatal × humidity × CO_2 × irradiance × temperature, *etc.* model and as Long *et al.* (2006) suggested, the model should have included ozone effects on stomata and internal-leaf photosynthetic behavior.]

El-Sharkawy (2005) discussed how numerous scientists dwelled on the misuse of botanical terminology to cover up their lack of timely research on the C_4 photosynthesis phenomenon; it was also used to enhance the significance of the biochemical C_4 research done. El-Sharkawy (2005) pointed out that *LI-COR* instruments

(*LI-COR*, Lincoln, NE, USA) made it easy to get measurements in the field; pioneers in the development of these instruments, including those at *LI-COR*, *etc*., need to be identified for historical purposes. Potted plants can be used in research, with the essential calibrations made with field-grown plants. Potted plants growing under intense sunlight, sometimes sitting outside, if carefully watered, will give good results (Begonia *et al.* 1996, 1999). For maximum leaf photosynthetic rates, leaf age is a problem. Mauney *et al.* (1979) presented a good and bad (someone forgot to water the plants at least once!) set of potted plant data in their paper (showing incredible levels of leaf starch and sugar under elevated atmospheric CO_2; for possible sink regulation of photosynthetic rates see Paul and Foyer 2001) illustrating this point. Recent potted plant data (Edwards *et al.* 1990) greatly understimated cassava leaf photosynthetic rates found in the field (El-Sharkawy and Cock 1990, El-Sharkawy *et al.* 1992). Murata (1961), his collaborators, and other Japanese scientists did rice research on photosynthesis in the field, obviously before Musgrave *et al.* Someone needs to determine how much he and his collaborators worked in the field from a historical perspective soon; he published in Japanese but English translations are available.

(*b*) There are recent histories of C_4 photosynthesis ignoring what Musgrave and his school of field experimentalists did for various reasons. El-Sharkawy's work over the years is a case in point. His early work is summarized in a Citation Classic (El-Sharkawy and Hesketh 1986, but see Garfield 1992—his paper was one of the most cited 20 in Crop Science), we need to list his accomplishments here for young scientists to see again (the Citation Classic attributes his work to the CSIRO in Canberra, Australia and other institutions, but it was done at the Univ. Arizona in Tucson):

(*b.1*) Comparative effects of irradiance, CO_2, temperature, and water stress on leaf photosynthesis and transpiration for C_4 *vs.* C_3 plants. Such plants then were defined by their CO_2 compensation concentration (Γ) as reported by Meidner (1962) and Moss (1962). The Γ for C_4 plants was close to zero due to the apparent re-assimilation of respiratory CO_2 by efficient photosynthetic dark reactions rather than to the absence of photorespiration (El-Sharkawy 1965, El-Sharkawy and Hesketh 1965, El-Sharkawy *et al.* 1967, 1968, Hatch *et al.* 1967, Jackson and Volk 1969, 1970); for C_3 plants the much higher Γ was associated with photorespiration. C_4 species had lower mesophyll resistance to CO_2 diffusion indicating higher carboxylation efficiency. A method for measuring apparent leaf photorespiration in CO_2-free air with infrared gas analysis in an open system was first developed at Tucson, Arizona, and is used in plant photosynthesis/respiration research until today (El-Sharkawy 1965, El-Sharkawy and Hesketh 1965).

(*b.2*) C_4 plants of both monocotyledon and dicotyledon families have Kranz anatomy; C_3 plants do not (El-Sharkawy 1965, El-Sharkawy and Hesketh 1965, 1986). This discovery was done without knowing the 19th century classic anatomy work by the German botanist Haberlandt (1914). Comparisons of the effects of internal exposed cell surfaces and diameter of mesophyll cells on leaf photosynthetic rates were made in a wide range of plant species. Laetsch (1974) and Jackson and Volk (1969, 1970) emphasized El-Sharkawy's research, while the biochemists/physiologists of the scientific establishment either ignored his pioneering achievements or used his data without proper acknowledgement of sources (El-Sharkawy, personal communication).

(*b.3*) Several C_4 dicots were identified within the genus *Amaranthus* (*A. palmeri, A. retroflexus*, weedy types; *A. edulis*, cultivated grain amaranth by the native Amerindians, the Aztecs, and Incas before the time of Cortez – El-Sharkawy 1965, El-Sharkawy and Hesketh 1965, 1986, El-Sharkawy *et al.* 1967, 1968). These species had very high leaf photosynthetic rates associated with leaf Kranz anatomy and apparent lack of CO_2 releases in CO_2-free air and light. The grain amaranth, *A. edulis*, is currently widely used in photosynthesis research as a model plant system, particularly in manipulating the genetics of the C_4 pathway by using mutants with altered photosynthetic capacities and the C_4 phosphoe*nol*pyruvate carboxylase (PEPC) content (Dever *et al.* 1997, Lacuesta *et al.* 1997, Sheen 1999).

(*b.4*) Leaf transpiration rates tended to be lower in C_4 plants, associated with differences in leaf resistances to gas exchanges and with higher photosynthetic rates, resulting in much higher leaf water use efficiency in C_4 species (El-Sharkawy 1965, El-Sharkawy and Hesketh 1965, 1986). This was an incredible advance in plant water relations indicating the comparative advantage of the terrestrial C_4 species over C_3.

(*b.5*) Leaf photosynthetic rates were screened among cotton species, races, and cultivars, with the incredible geneticist Muramoto at the Univ. Arizona (Muramoto *et al.* 1965), where a wide range of genetic variations were found for the first time with some of the highest rates found in wild cotton species (El-Sharkawy *et al.* 1965). This work was continued with cassava germplasm at CIAT, Cali, Colombia; for perhaps the first time leaf photosynthetic rates, as measured in the field over a wide range of germplasm grown in diverse environments, correlated well with final yields, as they often do those for plants growing in an atmosphere enriched in CO_2 (El-Sharkawy *et al.* 1990, 1993, El-Sharkawy and Cock 1990, Pellet and El-Sharkawy 1993, de Tafur *et al.* 1997). The association was attributed mainly to non-stomatal factors (*i.e.* biochemical/anatomical). This high correlation with yield occurred in well watered and droughty conditions; after a prolonged drought photosynthesis was significantly correlated with the activity of the C_4 enzyme PEPC in leaves (El-Sharkawy 2004). Nasyrov (1978, 1981) working in Tajikistan found the same response with PEPC under salt stress. After screening among cotton genotypes, Nasyrov e*t al*. produced higher yielding cvs. and hybrids.

(*b.6*) Intermediate C_3-C_4 behavior was found in the C_3 cassava for some genotypes growing under both well-watered and drought conditions (Cock *et al.* 1987, El-Sharkawy and Cock 1987, El-Sharkawy 2004, 2006). Once again, this is an incredible achievement in plant water relations, compared to what was going on at the time. A biochemical assay for stress tolerance was developed based upon a C_4 and C_3 photosynthetic enzyme behavior in cassava leaves under prolonged stress. Activity of the C_4 PEPC enzyme remained stable or increased while that of the ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) C_3 enzyme declined. The assay was successful in revealing cassava lines that were drought tolerant, leading ultimately to better cultivars. CMC 40 and CM 489-1 cassava lines selected for drought tolerance had high dry root yields, high leaf photosynthetic rates, high PEPC activity, and high ratios of PEPC/RuBPCO activities (El-Sharkawy 2004, 2006). Moreover, very high PEPC activities (>25 % of the values observed in typical C_4 species such as maize and sorghum) were found in wild *Manihot* species such as *M. rubricaulis* and *M. grahami* (El-Sharkawy 2006). These wild species are important genetic sources for further improvement of photosynthesis in cultivated cassava.

(*b.7*) Other innovative research by El-Sharkawy is reviewed in three recent papers (El-Sharkawy 2004, 2005, 2006).

(*b.8*) Between 1966 to 1980, El-Sharkawy took a leading role in helping with the establishment of higher education institutes and applied field research in the rain-fed and irrigated agricultural systems of the Great Sahara Desert of North Africa. Some of his research achievements are reported in local journals and books (El-Sharkawy 1975).

The C_4 pathway research in Hawaii and Australia broke at about the same time; publication of the Hawaiian work being held up seven years by the journal it was published in. (The Karpilov 1960 Russian paper on the biochemistry of early products of photosynthesis in maize was not discovered until much later and is cited often.) The subsequent C_4 pathway work and simple hindsight made his findings obvious, so obvious apparently his work quickly did not need to be cited (the association of Kranz anatomy and C_4 behavior is one example). El-Sharkawy's accomplishments (*b.1–b.5*) are now listed in reviews and books, credited with an earlier reviewer. One history of C_4 photosynthesis ignores this research completely, except for Kranz anatomy, with no citation. Of course, popular plant physiology textbooks (Devlin 1975, Salisbury and Ross 1992) published some of his data from his Citation Classic.

(*c*) Pest effects on leaf photosynthesis have been covered by Coviella and Trumble (1999) and Aldea *et al.* (2005). DeLucia (Aldea *et al.* 2005) is a botanist with many papers on pest effects. Leaves with insect holes have low photosynthetic rates when leaf area is corrected for the holes; pest effects obviously contribute to leaf aging and associated effects on photosynthesis. Recent insect eradication efforts and bioengineered insect-resistant plants mitigate such effects.

(*d*) C_4 photosynthesis has been found in single cells (see Edwards *et al.* 2004), suggesting that Kranz anatomy somehow is not needed, but key C_3 and C_4 are apparently separated and compartmentalized within the same cell.

(*e*) Nasyrov (1978, 1981, see above), after finding high correlations of photosynthesis with PEPC under salt stress and selecting superior cultivars discussed the inevitable importance of genetically modifying the CO_2 carboxylation reactions of photosynthesis. Ku *et al.* (1999, but see Ku 2000) working in Matsuoka's laboratory in Japan reported enhanced activities of the C_4 PEPC enzyme for transgenic rice with enhanced leaf photosynthesis and 35 % increases in yield in the field (see Sheehy 1999, Curtis 2004, Matsuoka *et al.* 2001, Hausler *et al.* 2002 for this and additional information regarding photosynthesis and leaf anatomy in transgenic plants). This now is at the cutting edge of photosynthesis research. The USA seed companies, of course, pioneered this research for other plant attributes, see (*c*) above.

(*f*) Peng *et al.* (2002) increased rice yields by inoculating the seed before planting with N-fixing bacteria; they found that increased yields were highly correlated with increased leaf photosynthetic rates.

(*g*) We have not discussed the work of the Canadians, Krotkov, Nelson, Tregunna, and Forrester (Tregunna *et al.* 1964, Forrester *et al.* 1966a,b), as well as that of the Somerville couple working with Ogren (Somerville and Ogren 1982) in Illinois on the C_2 pathway, and the extensive work on the progeny of crosses between C_4 and C_3 plants. We did not have the time or space here, with our emphasis on what Musgrave and El-Sharkawy did. Of course, like the flowering gene work, there is a little unsung army of researchers making significant contributions from the bench.

General discussion

What follows is a general overview of the many topics discussed, the details of which a photosynthesis specialist should be very familiar. We had available El-Sharkawy's (2005) recent paper and wish to comment. Apparently the point-release CO_2 experiments have led to progress in science (see Coviella and Trumble 1999, Long *et al.* 2006, and the Brookhaven Face Website cited in our list of references). They will soon elaborate on their discoveries. Point release experiments should be heavily fortified with experimentalists taking measurements in the field and laboratory and working on models for various subsystems of their system (see below).

Crafts-Brandner and Salvucci (2000) have an interesting biochemical paper which shows how one models the effects of leaf temperature and CO_2 on photosynthesis. Hopefully others will comment further on historical paper of El-Sharkawy (2005) on the complexity of photosynthetic systems. Here we emphasized effects of flowering genes on LAI. Using a new yield data set and a model, Boaken and Zhang (2005) have redrawn the maturity group (MG) (E/e) lines for cultivars that yield best with latitude in the USA. Zhang *et al.* (2001) also have found the best MG to plant as the season progresses at Stoneville, MS because of planting date delays due to weather or multiple cropping season used. Zhang *et al.* (2001) cited some of the soybean research on the flowering genes in their papers. They are also pioneering methods for tabulating soybean cv. yield trials, for study by farmers, and use as a modeling tool (Zhang *et al.* 2004).

In the plant genome effort, there is the sequencing phase, the gene location/function phase and finally the genetic engineering phase. The seed companies and others have bypassed the first two phases bioengineering plants that have had a huge impact on agricultural practices (weed and pest control) and yields in the US. [For background information and history, see http://cls.casa.colostate.edu/TransgenicCrops/history.html, Thomashow (1999), Lurquin (2001), Pray and Naseem (2005), or look up history of transgenic plants.] The work by Beyer *et al.* (2002) in Potrykus' lab, reviewed in 2002 (http://www.goldenrice.org), on bioengineered rice with high vitamin A is a public example of what can be done to increase the impact of science on societies. The work by plant breeders/geneticists and crop physiologists in the past to optimize LAI and harvest indices for maximum yields fits in the same category, the result of which was the Green Revolution of the 1960's. The Cotton Boll Weevil Lab in Starkville, MS (renamed something else now) did research which led to the eradication of the boll weevil; this needs a better history, especially on the development of the sex pheromone trap to detect weevils in a field. Oxford University developed a method involving bioengineering for the production of large numbers of male sterile insects, which the Boll Weevil Lab was unable to do. The University of California-Riverside used this method to produce male sterile pink bollworms which can be used for eradication in the Western USA. A CSIRO group has bioengineered a male insect that only produces males. And of course we discussed the maturity group (MG) or E/e work, based upon others, which can be used by farmers to decide what MG to plant during the growing season at different latitudes. These accomplishments at the moment are much more significant than the cell/plant genomes completed or in progress; however, future crop plant bioengineering will be speeded up using this new information. The seed companies are at the forefront of getting these genomes done, with genes identified and their function determined. Of course there are interactions among genes and between genes and the material connecting them. We need, of course, a history of what bench scientists did in the seed companies.

Bioinformatics includes (*a*) the design of experiments and statistical analysis of data, (*b*) crop modeling and the synthesis of associated plant and environmental processes in a whole, and (*c*) software associated with genomic research. Software or instructions on how to make associated calculations are research tools. It is not clear how far the theoretical modelers will get without testing their hypotheses in the field; such modelers and water-relations–soils scientists should be supported (financially) to develop a sound root behavior × soil profile characteristics × available soil water model. Any discussion of a plant's water and N budget is a bit irrelevant until this is done (see above). We mentioned above the need for a stomatal resistance model based upon atmospheric humidity and CO_2, irradiance, water stress, and ozone levels as well as a need for a model for starch and sugar dynamics and possible feedback control. We also suggested research and modeling of the effect of humidity/temperature on canopy photosynthetic or yield responses to CO_2. Long *et al.* (2006) suggested that the modeling effort associated with the US global change/increased atmospheric CO_2 study was somewhat deficient because of the use of potted plant or field enclosure research results. Hopefully we now can put the problems associated with using potted plants in experiments behind us after it had been covered up for so many years. Potted plants led to discoveries about photoperiodism and its interaction with temperature, and after calibration with field data valid models were developed for predicting field behavior. Potted plants have also led to many discoveries in photosynthesis research.

Some conclusions from this and earlier El-Sharkawy papers (2004, 2005, 2006): (*1*) Field photosynthesis is a complex process, but higher leaf photosynthetic rates, genetic, or by enriching the air with CO_2 in small open-top chambers or in large free air CO_2 enrichment experiments, often lead to higher yields. But other complex plant processes such as source-sink relations in the whole plant, feedback inhibition because of accumulation of starch and soluble saccharides in leaves as well as the nutrient content of plant tissues, particularly N, may interfere with this correlation. (*2*) The potted plant/indoors syndrome is an important part of the history of ecological aspects of photosynthesis and transpiration, though with little impact on what may take place in crop communities. (*3*) Botanists (*e.g.* De Lucia and coworkers, see Aldea 2005) have contributed to agricultural photosynthetic research. (*4*) Research-based calibrated crop modeling has led to the integration of information from plant physiology, soil, and genetic research as reported by El-Sharkawy (2005) and here. (*5*) As team efforts become more international, junior members of a team should be first author of relevant papers, possibly including review papers. Often it becomes in the best interest of scientific progress if one concedes first authorship to a collaborator from another discipline and act, in effect, like a technician to get the expertise needed to get the job done. This can be abused, of course, when evaluated for promotion purposes. (*6*) Physiological and ecological discoveries by agriculturalists need to be part of the history of the development of related sciences, and some of us must take the initiative to see that this is done. For example, the discoveries of R. Musgrave, his students, and their students in the field of plant photosynthesis as related to crop productivity and to soil-plant-water relations, will quickly be forgotten if this is not done, but this paper takes care of the problem. Water relations experts have ignored what they did from the beginning; Nasyrov's work (1978) with salt tolerance has gotten exposure.

We pointed out how most of the successful researchers discussed were not members of the biological/ scientific establishment. The reader should also be aware of what Craig Venter and colleagues (Adams *et al.* 1991, 1993a,b) did, or how much money he saved the taxpayers by buying expensive equipment he felt he needed to speed up the human genome effort. Also the reader needs to understand thoroughly what Chris and Shuana Somerville did as *Arabidopsis* geneticists when they worked with Ogren, a photosynthesis biochemist on the biochemistry and genetics of photorespiration (Somerville and Ogren 1982) or how much money the Somervilles saved the taxpayer when they borrowed Craig Venter's techniques to do the *Arabidopsis* genome with the help of a large international group of *Arabidopsis* geneticists. These scientists need as much study as the ones we and El-Sharkawy discussed here and in another Photosynthetica papers.

Now let us hear from the Japanese on their photosynthesis work in the field, as well as from the British leaf development, growth, and function experts with an agricultural base. Let us also hear further about what the Asian plant breeders did to actually bring about the Green Revolution. And everyone should brace themelves for an onslaught of physiological genes explaining plant/leaf behavior in ways we could not have foreseen.

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