

ADVANCES IN THE PHYSIOLOGY OF THE SUNFLOWER CROP: A TEN-YEAR PROGRESS REPORT

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Abstract

The last major review of sunflower physiology was published in 1997, seven years ago as a chapter in *Sunflower Technology and Production*. The present review sets out to examine the principal advances in this field that have taken place during the last decade. During that interval, researchers from many places in the world have made significant contributions to our store of knowledge about how the sunflower crop responds to important environmental cues. We now know more about a series of issues impinging on control of crop development, resource capture, biomass partitioning, yield components and oil quality determination, and stress physiology. The focus of this review is the recent advances in knowledge which improve our understanding of how the crop, environment and management interact and impact on yield, its components and grain quality. Issues relating to physiology at sub-crop levels of organization are considered if they have a clear link with this focus. The present review does not cover important issues related to sunflower seed dormancy and germination or the genetic and biochemical bases of oil quality, recently reviewed elsewhere, nor does it attempt to cover the broad field of crop responses to mineral nutrients.

Introduction

The last major review of sunflower physiology (Connor and Hall, 1997) was published seven years ago as a chapter in *Sunflower Technology and Production*. The nature of the inevitable delays inherent in the preparation of multi-authored books meant that the literature revision on which that review was based had, to all realistic intents and purposes, been completed in 1994. The present review sets out to examine the principal advances in this field that have taken place during the last decade. During that interval, researchers from many places in the world have made significant contributions to our store of knowledge about how the sunflower crop responds to important environmental cues. We now know more about a series of issues impinging on control of crop development, resource capture, biomass partitioning, yield component and oil quality determination, and stress physiology. There have also been some advances in uncovering genetic bases of some of these responses and in strengthening the connection between crop breeding and physiology. Not surprisingly, work leading to some of these advances has also served to emphasize the continuing existence of significant gaps in our knowledge of sunflower crop physiology. The focus of this review is the recent advances in knowledge which improve our understanding of how the crop, environment and management interact and impact on yield, its components and grain quality. Issues relating to physiology at sub-crop levels of organization are considered if they have a clear link with this focus. The present review does not cover important issues related to sunflower seed dormancy and germination or the genetic and biochemical bases of oil quality,

recently reviewed elsewhere (Benech Arnold, 2004; Velasco et al., 2004), nor does it attempt to cover the broad field of crop responses to mineral nutrients.

Discussion

Control of Crop Development. Advances in this field have been patchy, and have served to underline the fact that a lot of work will be needed before we can count on a robust framework which will allow for reliable descriptions of the responses of time to flowering in sunflower to genotype, temperature and photoperiod. Work using artificially extended photoperiods in combination with spring and late summer sowings of a set of inbred lines and hybrids (Hall, 2001; MacDonough et al., 2004) has demonstrated that genotype responses are rather more complex than often envisaged (e.g., Villalobos et al., 1996). Photoperiod extensions, as was already known, can affect the duration of the start of floral initiation to bud visible phase, but can also affect the duration of later phases including the duration of the interval between the start and finish of floret differentiation. In addition, some genotypes actually show reversal of responses to photoperiod between spring and summer sowings. These findings suggest that we need to rethink this whole issue and, if confirmed, indicate that we may need to consider the possibility of temperature/photoperiod interactions of the kind found by Welch et al. (2003) in *Arabidopsis* and suggested by these authors for soybean. Another possible cause to these unexpected findings may lie in some kind of earliness per se gene response to temperature (e.g., Appendino and Slafer, 2003). On a more positive note, the work of León et al. (2000) marks the start of the research needed to uncover the links between genotype responses to photoperiod and the genes underlying those responses. Extrapolating from what is known for *Arabidopsis* (e.g., Mouradov et al., 2002), the gene network controlling time to flowering in sunflower is certain to be complicated and, consequently, difficult to reduce to simple relationships with environmental factors. It may, however, prove possible to achieve useful simplifications by identifying major effects associated with each of the several control pathways (Welch et al., 2003) that make up the network. Further work on the environmental control of time to flowering is needed if we are to progress in our capacity to predict crop development across differing temperature and photoperiod environments associated with cropping or the production of hybrid seed in new areas.

Resource Capture. Understanding what controls the size, functionality and duration of the canopy and root systems of the crop is an important prerequisite for understanding how the crop captures and/or dissipates water, nutrients and radiation. There have been some significant advances in this area during the last ten years. The work of Aguirrezábal and Tardieu (1996) and Aguirrezábal et al. (1993, 1994) has advanced our understanding of how intercepted radiation (a hitherto unresearched factor), internal source-sink relationships, and temperature affect the growth and branching of the root system and has put this area of knowledge on a firmer basis, adding radiation to the list of factors that need to be considered when analysing crop root growth. Dardanelli et al. (1997) made an interesting comparative study of root functionality over rooting depth involving sunflower, soybean, peanut, maize and lucerne. As well as confirming the known capacity of sunflower to explore the soil to greater depths than the other annual crops included in this study, this research also indicated that sunflower has the capacity to extend its root system in depth faster than other crops and more rapidly extract water from a given layer of soil than lucerne and peanut, and possibly the other crops. This and other work by the same group has recently (Dardanelli et al., 2004)

been synthesized in a generic model for root water uptake that allows for the effects of variations in soil properties with depth on the ability of root systems to colonize soil layers and to extract water from them. This model constitutes a significant advance in our ability to describe sunflower root/soil interactions with respect to the previous best approximation to this issue (Meinke et al., 1993). Much of the work on root systems has emphasized the growth and functionality of the system between sowing and flowering or thereabouts, providing a reasonable degree of understanding of the basis for water capture during this phase. What is urgently needed is more research into root functioning after flowering. Direct observation of root systems (Sadras et al., 1989) and measurements of root respiration in the field (Hall et al., 1990) both suggest a gradual loss of root mass and functionality after flowering. We also need to know a great deal more about the dynamics and the controls of crop capacity to capture nutrients and about the patterns of nutrient availability during the life of the crop in different environments.

Leaf appearance, expansion and senescence are the processes underlying the generation and disappearance of the crop canopy. Together with leaf photosynthetic capacity, its variations within the canopy and across crops, and its responses to stress, they are powerful determinants of crop capacity to intercept radiation and fix carbon dioxide. Research prior to 1994 had provided a framework for understanding sunflower leaf photosynthetic responses to photosynthetically active radiation (PAR), temperature, specific leaf nitrogen and water stress, and had explored canopy dynamics in relation to water and nitrogen supply. The intervening decade has seen advances in the understanding of the effects of nitrogen, radiation, leaf position, and water stress on the expansion of individual leaves and their relationships with the underlying processes of cell division and expansion. Granier and Tardieu, in an important series of papers (1998a, 1998b, 1999a and 1999b), explored the relationships between cell division and expansion and leaf growth, suggested a novel framework for describing the effects of leaf position, and added radiation to the list of important factors regulating leaf expansion. The framework for describing leaf expansion was successfully applied by Dosio et al. (2003) to describe the growth of individual leaves at all positions on the stem of two hybrids grown as individual plants and as a crop. Trápani and Hall (1996) and Trápani et al. (1999) worked on the effects of nitrogen and leaf position on leaf expansion and cell division and expansion, and were able to show that the specific leaf nitrogen threshold for leaf expansion in sunflower is clearly higher than the threshold for photosynthesis. This finding provided an empirical basis for the assumed, but hitherto unproven, greater sensitivity of expansion vis-a-vis photosynthesis to specific leaf nitrogen. An important finding of Granier and Tardieu (1999a) was that changes in absorbed PAR affected final leaf size if these changes occurred while cell division was occurring within the leaf, but not afterwards. By contrast, variations in the supply of nitrogen impacted on the rates of leaf expansion during the last two-thirds of leaf expansion, when cell expansion rather than cell division was the dominant process (Trápani and Hall, 1996, Trápani et al., 1999). More work is needed to understand the physiological bases of these apparently contrasting responses.

Current crop leaf area index, during perhaps two-thirds of the crop cycle, is strongly affected by rates of leaf senescence, a process which begins to operate in canopies achieving close to full fractional radiation interception before flowering, and which becomes the dominant determinant of leaf area index after flowering. The last decade has seen advances with respect to the characterization of senescence and its controls in both phases of crop development. Rousseaux et al. (1996, 1997, 1999 and 2000) studied the causes of pre-

anthesis senescence of basal leaves in the canopy and demonstrated that, in addition to the previously known effect of low PAR on leaf duration, there was an additional operative environmental cue: the ratio of red to far-red radiation perceived by the basal leaves. Because leaves preferentially absorb red (R) with respect to far red (FR) radiation, this ratio measured at the base of the canopy changes markedly with leaf area index. It was also found that individual leaf specific leaf nitrogen (SLN, an indicator of photosynthetic capacity) was associated better with R/FR and over a broader range of this variable than with PAR (Rousseaux et al., 1999). This means that it may be possible to better predict the dynamics of SLN for leaves at different depths within the canopy using R/FR rather than PAR. The work of Sadras et al. (2000) has expanded the previous work of Sadras et al. (1993) on the dynamics of nitrogen and chlorophyll losses during grain filling from leaves at different positions in the canopy. Rates of post-anthesis leaf senescence have been shown to vary among genotypes and with time of sowing (de la Vega and Hall, 2002a, 2002b), resulting in varying degrees of "stay green." While interest in this attribute arose initially, in the work of de la Vega, from the realization that it might serve as an indirect selection index for adaptation to subtropical regions, there is also evidence that the stay green genotypes may fix more carbon during post-anthesis and may have better lodging resistance. Although we know there is variability for this attribute and something about its consequences, we still know nothing about the physiology underlying this variability or the genetic basis for it. The time of sowing effect on leaf area duration during grain filling is interesting, because it means that late sown crops not only fill grain under poorer radiation conditions (see below) but also have lower fractional radiation interception. More work in this potentially important topic is required.

Research prior to 1994 and in the last ten years has consolidated an important, although admittedly as yet incomplete, picture of the photosynthetic physiology of sunflower leaves within a canopy. Thus, we are able to predict, with some robustness, leaf and canopy photosynthetic responses to temperature, radiation, and specific leaf nitrogen (e.g., Hall et al., 1995; Bange et al. 1997a, 1997b), we have some tools which would allow us to predict gradients of specific leaf nitrogen within the canopy, we know something about the pattern of nitrogen loss from different layers in the canopy during grain filling (Sadras et al., 1993, 2000), and we know that there is phenotypic variability for stay green. We also know a little more about the relative importance during grain filling in sunflower of respiration, that little-researched process in field crops (Ploschuk and Hall, 1997). This knowledge is enough to start research into the behaviour of hypothetical sunflower canopies as systems for radiation and carbon capture using 3-D modelling (e.g., Maddonni et al., 2001). Models of this type should allow us to examine a range of questions, from the contribution that stay green makes to post-flowering crop carbon economy to more "blue sky" ones such as: Is there a better (from the point of view of biomass accumulation) sunflower canopy than the one we are used to dealing with at the moment?

Biomass Partitioning. The last decade has seen several advances in the topic of biomass partitioning, particularly that occurring after anthesis. In an analysis of the physiological changes which took place in parallel with crop improvement between 1930 and 1995 in Argentina, López Pereira et al. (2000) found that the fraction of crop biomass partitioned to stem at anthesis had decreased, and that changes brought about by breeding were associated with greater harvest index (HI), greater kernel to grain ratio and greater kernel oil concentration. Vega et al. (2000) examined HI responses to crop population density in three crops, including sunflower, and found that HI tended to be lower in high and low crop

population densities, and that HI stability across population densities for sunflower was intermediate between soybean (high) and maize (low). There has also been some interest in examining the rate of change of HI during grain filling across hybrids and times of sowing, at least partly in the expectation that this attribute would be stable across conditions, thus allowing for its use in crop modelling. Bange et al. (1998) found that the rate of linear increase in HI was stable across genotypes, N supply and radiation, but changed with time of sowing, an effect they suggested might be due to temperature effects. By contrast, when de la Vega and Hall (2002a) examined time of sowing and genotype effects on HI and rate of linear increase in HI, they found strong genotype x sowing date interactions for both HI and linear rate of HI increase. Interestingly, temperature differences between sowing dates were not a factor in these experiments, suggesting there must be some other controls underlying the sowing date effect on rate of linear HI increase. Libenson et al. (2002) examined the responses of several genotypes to the R/FR ratio of light reaching stem internodes, and found that low values of R/FR (the condition expected in dense stands) increased stem growth and reduced grain yield, possibly because of increased competition for assimilates between the stem and reproductive structures. Lastly, Alkio et al. (2002) examined the vascular connections between leaves at different positions on the stem and sectors of the capitulum, and were able to identify the major transport sugar involved in photoassimilate transport.

Clearly, the issue of biomass partitioning, both before and after anthesis, will require more attention as we try to improve our understanding of the controls affecting this process and attempt to exploit possible cultivar differences in responses to environmental cues such as crop population density. The results obtained by López Pereira et al. (2004), suggesting that yield potential of sunflower crops protected from disease and lodging continues to increase up to plant population densities much greater than the usual commercial optimum, call for greater understanding of the causes of the gap between stand densities which set a ceiling to present practice and physiological crop yield potential. Disease and lodging tolerances are important putative causes for this gap. The work of Vega and Sadras (2003) on the issue of the development of plant size and yield asymmetry within crops of maize, soybean and sunflower of differing population densities is a useful starting point for examining the changes in plant HI across individuals in a crop and the effect of stand density on these responses.

Yield Components. The last ten years have seen some important advances in our understanding of the responses of yield components (grain number, unit grain weight and oil content) in sunflower to environmental factors, and some progress in the underlying physiology. A series of papers (Cantagallo et al., 1997, 2004; Cantagallo and Hall, 2002) have explored the relationships between the number of grains per unit crop surface and radiation and temperature or radiation alone. This research has served to map the critical period for grain number determination in the crop, running from floral initiation through to early grain fill, and to distinguish variations in sensitivity to low radiation within that broad window. In passing, it should be noted that the critical window for grain number determination in sunflower is considerably broader than that of other major crops such as maize and wheat. Work on the response of grain number to temperature within the critical window has not progressed as much as for radiation, but Chimenti and Hall (2001) have shown that low temperatures during floral initiation increase the number of florets differentiated, although they also decrease the later viability of these florets. Clearly, grain number responses to temperature and their interaction with radiation is rather more complex than might be expected (and encapsulated in the use [Cantagallo et al., 1997] of a

photothermal quotient to predict grain number). Vega et al. (2001a, 2001b) used a very elegant double-sampling technique to examine the relationships between grain number and plant and inflorescence growth rates in the period bracketing flowering of sunflower, maize and soybean. They were able to show that grain number is linearly associated with plant growth rate at low values of the latter, but this relationship becomes curvilinear (sunflower) or double curvilinear (maize) as plant (and inflorescence or population of flowers) growth rate increases. Although complementarity between the work of Cantagallo (who examined the limits to the critical window using only two levels of radiation) and Vega (who examined responses to a broad range of growth rates in only part of the critical window) is not perfect, together they constitute an important step toward understanding the relationships between radiation and grain number in sunflower. Work at a finer level of resolution by Alkio and Grimm (2003) and Alkio et al. (2003) has thrown more light on the nature of processes affecting seed set in sunflower. Importantly, they were able to demonstrate that vascular connections to the florets in the centre of the capitulum are functional, suggesting that failures in seed set are not linked to insufficient vascularization. These authors also showed how seed set and seed size were associated with leaf area per grain.

That temperature affects unit grain weight in sunflower, mediated through changes in duration or rate of grain growth, has been known for some time (e.g., Ploschuk and Hall, 1995) and was predictable from what was known for other crops (e.g., Chowdhury and Wardlaw, 1978). However, the details of these responses, over a broad range of temperatures, had not been defined in sunflower. Chimenti et al. (2001) were able to define the cardinal (base, optimum and maximum) temperatures needed to quantify the duration of growth of the kernel, and were also able to define a response curve for kernel growth rate. This important advance needs to be complemented with an analysis of temperature effects on hull growth, as the latter constitutes an important proportion of grain weight. Because daytime sunflower head temperatures can greatly exceed air temperatures on sunny days (Ploschuk and Hall, 1995), even in temperate climates, and because of the trend toward expanding the sunflower cropping area to more subtropical conditions, interest has grown in exploring the nature of grain responses (size, oil content, oil composition) to brief periods of exposure to very high temperatures (Rondanini et al., 2003). The last ten years have also seen important advances in defining response functions for unit grain weight to radiation intercepted by each plant in the crop and to crop population density (Andrade and Ferreiro, 1996; Aguirrezábal et al., 2003). A very useful synthesis of these effects is provided by a limiting factor response where population density defines the plateau for grain size and intercepted radiation the slope of the below-plateau response line (Aguirrezábal et al., 2003). The work of Karyagina et al. (1999) has provided descriptions of the dynamics of kernel cell division and kernel length, and of dry matter and lipid deposition during grain growth which fill out the picture of these processes that had emerged from pre-1994 research. Bolyakina and Raikhman (1999) provide some information on parenchyma cell size evolution during grain growth.

Grain oil content, the third yield component in this crop, has also received significant attention in the last ten years. Important advances with respect to the previously-known determinants of this component (especially hull proportion and kernel oil content) have emerged from studies on the effects of radiation, a hitherto little-studied factor (Dosio et al., 2000; Aguirrezábal et al., 2003); grain position on the head (Santalla et al., 2002), time of sowing (de la Vega and Hall, 2002b), and exposure to stressful high temperatures (Rondanini et al., 2003). León et al. (1996, 2003) have established the genetic basis between hypodermis color and grain oil content. It is unfortunate that work on the anatomical bases of grain oil

content dynamics (Mantese, 1999) has yet to be published in a journal, but complementary work on the anatomical bases of the accumulation of grain protein, another important reserve compound in the kernel, is now available (Bolyakina and Raikhman, 1999).

The genetic and biochemical bases of triacylglycerol composition of sunflower oil and their control by environmental factors has recently been reviewed by Velasco et al. (2004). However, there have been a few advances in recent years that merit separate comment. One is the elegant demonstration by Izquierdo et al. (2002) that it is night, rather than mean or day, temperature that affects the oleic:linoleic ratio in the oil of standard sunflower hybrids. This work also established the window of development, within grain filling, in which oil composition was most strongly affected by temperature. These findings open up the possibility of more precise prediction, on a robust physiological basis, of the expected oil composition of sunflower oils from crops across locations and seasons. This approach should, in principle, be more fruitful than attempts based on regression analysis and broad developmental windows (Sobrinho et al., 2003). The work of Rondanini et al. (2003, 2004) complements the findings of Izquierdo et al. insofar as it shows how short exposures to stressful high temperatures can interact with cultivar and sub-phase of grain filling to determine final grain oil composition.

Stress Physiology. Tardieu et al. (1996) revisited the question of whether hydraulic (i.e., leaf water potential) or non-hydraulic (i.e., abscisic acid) signals were the dominant effect controlling leaf stomatal conductance in plants subjected to water stress under both field and glasshouse conditions. Their results show that the conductance/xylem ABA relationship, over a broad range of both variables, was unaffected by variations in leaf water potential. Chimenti et al. (2002, 2004), building on earlier (pre-1994) work on osmotic adjustment, were able to show that osmotic adjustment can make a substantial contribution to yield maintenance under conditions of protracted drought in each of both the pre-anthesis and post-anthesis phases of crop growth. This work also established the linkages between capacity for osmotic adjustment, extraction of water deep in the soil profile, and maintenance of crop leaf area duration during and after drought. The demonstration that osmotic adjustment in sunflower can have a substantial effect on yield under drought is particularly interesting given the argument (Serraj and Sinclair, 2002) that osmotic adjustment is only important for survival (in contrast to yield), and therefore irrelevant for commercial crop production. Yields of the low osmotic adjustment (i.e., drought susceptible) families tested by Chimenti et al. would have justified harvesting, so those obtained with high osmotic adjusting families would certainly be of commercial interest. What still remains to be done in order to take advantage of this attribute for breeding purposes is to find a marker that will allow it to be tracked during the selection process.

High temperature stress is likely to be an increasingly significant factor limiting the expansion of sunflower cropping into warmer climates. Rondanini et al. (2003, 2004) have made some progress towards defining the nature of grain responses to brief exposures to high temperature stress and establishing the threshold temperature for these effects. This work has also shown the importance of the match between active grain growth processes (i.e., growth of the hull, kernel or oil) and the timing of the stress event in determining the final effects on yield and oil quality.

Direct observations of crop responses to waterlogging and associations between yield reductions and high rainfall during grain filling have led to an interest in examining the nature of this response, particularly given the frequent suggestion that these yield losses are

attributable to disease. Trápani et al. (2004) have shown that waterlogging evokes alterations in the grain-filling process, and that these alterations are affected by the timing of the stress and the nature of the soil. This finding calls for an examination of possible intraspecific variability for tolerance to waterlogging as a route towards reducing the negative effects of this factor in commercial crops.

Physiology, Breeding, and Genetics Interface. Over the last decade, several different approaches have been used to try and shed more light on the important, but still poorly understood, interface between physiology, breeding, and genetics, and/or to suggest ways in which breeding might advance more rapidly towards achieving its goals. These approaches have included the use of simulation models for goal-setting; the analysis of the physiological changes associated with the generation of commercial genotypes over time (i.e., lessons from history); the attempts to identify and—where possible—take advantage of the association between traits and genes or markers supported by molecular genetic linkage maps (e.g., Yu et al., 2003); and the application of a combination of classification and ordination techniques with documentation of crop physiological responses to changes in environmental cues (e.g., site conditions, time of sowing). Sadras and Villalobos (1994) used a simulation model to examine the interactions between crop cycle duration and management condition (rainfed vs. irrigation, soil depth) in an attempt to define breeding objectives for the Mediterranean sunflower growing areas. Aguera et al. (1997) used a model (informed by the values of specific attributes determined in disruptively selected populations) to examine the possible impact of the early-vigor trait on the water economy of the crop. Models are sometimes regarded as playthings or non-science (e.g., Passioura, 1996), but the fact remains that good models are a very cost-effective way of making initial tests of our ideas prior to designing and executing experiments. As suggested elsewhere in this review, several of the advances in our knowledge of sunflower physiology during these last ten years, together with the advances in modeling techniques (e.g., 3-D models) could be usefully combined to make some initial tests of the advantages (or otherwise) of various possible avenues for crop improvement. The historical approach to a better understanding of why breeding has been successful in raising crop yields (thus, hopefully, providing useful insights for future developments) is exemplified, for sunflower, in the work of López Pereira et al. (1999a, 1999b, 2000). These researchers used a set of genotypes, released for commercial use at different times between 1930 and 1995 in Argentina, to explore the changes in crop attributes related to crop cycle duration, source-sink relationships, biomass partitioning, etc., that took place over this period. Important messages arising from this study included the step-change in many physiological attributes which accompanied the switch from the open-pollinated varieties to the hybrids, the shortening of the duration of the pre-(but not post-) anthesis phases of the crop cycle, the strong changes in partitioning as reflected in leaf/shoot biomass, grain/total biomass, kernel/grain and oil/kernel ratios. In addition, a tendency toward smaller grain was shown to have occurred. Although this review does not seek to explore the connections between physiology and genetics in any depth, it is appropriate to note that attempts have been made, over the last ten years, to seek genes and/or markers for yield-related attributes. For example, León et al. (1996, 2003) examined the relationships between the color of the grain hypodermis, and one of its underlying genes (*hyp*), and grain oil content. Analyses of this type can help us to understand the nature of past improvement, and map the gene (or marker) networks that operate on the trait of interest. We can expect a great deal of work on this front in the future. Another important development at this interface over the last ten years has been the use of classification and ordination techniques, combined with observations of

physiologically significant attributes, for the study of the underlying causes of genotype x environment (G x E) interactions (de la Vega and Chapman, 2001; de la Vega and Hall, 2002a, 2002b; de la Vega et al. 2001, 2002; Chapman and de la Vega, 2002). This work, based on the study of the behaviour of a reference set of genotypes across a multisite network spanning environments and years, is important in the context of this review for several reasons. It moved the "observed attribute" frontier back from the final end-products of crop-environment interactions (i.e., grain yield and oil yield) towards the underlying components and determinants of yield, thus improving the understanding of the causes of GxE interactions and expanding the possibility of exploiting this understanding. It also led to an improvement in the degree of attention paid to environmental cues and their variations between sites and years (an issue often relegated to the "art" component of a breeder's routine business) in determining crop and genotype responses. Finally, it also resulted in the identification of two indirect selection attributes (seed set in the central portion of the head and stay green) useful in selection for improved adaptation to the conditions of Northern Argentina, and refocused attention on the role of stay green in sunflower canopies as a source of yield improvement and better stem strength (Cukadar-Olmedo and Miller, 1997).

Conclusions

As set out above, the last decade has seen the application of significant research efforts to a range of aspects of sunflower physiology, resulting in many useful advances. Equally apparent is the fact that there are still many issues which will require much further work before a reasonable degree of understanding is achieved. The way forward in dealing with some of these emerging requirements is fairly straightforward, such as the need to identify a marker for osmotic adjustment, to complete the examination of the nature and consequences of stay green for crop yield and stem resistance, to complete the description of grain responses to stressful high temperatures, and to evaluate intraspecific variability for tolerance to waterlogging. Other issues are going to require newer and more sophisticated approaches, and the approach that may produce advances is less evident. These include the study of post-anthesis root system functionality and control of time to flowering. A study of the causes of the apparent gap between optimum plant population density shown to be appropriate for commercial cropping and that which allows full expression of crop yield potential is needed. Here, if lodging resistance is important, perhaps it will prove possible to build on the recent advances in the understanding of the mechanical underpinnings of lodging resistance in other crops such as wheat (Baker et al., 1998; Berry et al., 2000, 2003). Pre- and post-1994 research into the photosynthetic characteristics of sunflower leaves, and the growth and senescence of these structures, together with recent advances in 3-D canopy modelling, should provide a basis for testing hypothetical sunflower canopies in order to determine whether a "better" canopy exists and, if so, whether it can be usefully pursued in the search for a higher yielding crop. We can also draw some lessons from work in the last decade on what is needed to progress on the physiology/breeding/genetics front. Each of these three disciplines can contribute to progress in the remaining ones, but will only do so if teamwork (as against research in isolation) is the operative paradigm. It is also important that sufficient time (sometimes, a number of years) be allowed for research to become fruitful. Chimenti's work is an example of this; examples for other crops and attributes can be found in Sinclair et al. (2004). Finally, much of the work on sunflower physiology has focussed on the responses of the crop to particular environmental cues (radiation, temperature, water supply,

photoperiod, and so on). The usefulness of this kind of information for those interested in breeding and/or managing sunflower crops is greatly restricted because information on those cues for particular breeding trials or crops is very rarely collected and even more rarely used. Managers trying to understand crop yield variations across fields and years, and breeders seeking to make sense of the results of multi-environment trials through the fog of quantitative genetics, gene actions pathways and G x E interactions are likely to gain more insight if they also had available better records of the environment to which their crops or plots were exposed and invested some efforts into trying to associate variations in crop responses to patterns of environmental factor variation (Chapman and de la Vega, 2002).

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