15e CONFERENCE INTERNATIONALE TOURNESOL Sunflower ecophysiology: some unresolved issues*

Oléagineux, Corps Gras, Lipides. Volume 8, Numéro 1, 15-21, Janvier - Février 2001, La filière

Auteur(s) : Antonio J. HALL, IFEVA, Facultad de Agronomía (Universidad de Buenos Aires)/CONICET, Av. San Martín 4453, C1417DSE Buenos Aires, Argentina.

Summary : Major unresolved issues in sunflower ecophysiology constrain efforts to improve crop modelling, management, genetic analysis and breeding. Three issues are used here to illustrate this point. Firstly, much of the work on the duration of the emergence to flowering phase has considered the phase as a whole. It is argued that a more detailed analysis based on sub-phases is required, particularly in view of possible intraspecific variability in the durations of the basic vegetative and juvenile phases and evidence that photoperiod responses before, during and after floral initiation may differ between genotypes and even be of opposite sign for the same genotype. Secondly,contrasting responses of grain oil proportion to manipulation of plant population density and incident radiation appear to be linked to variations in kernel oil proportion rather than to kernel: hull ratio, and responses of grain oil proportion to changes in sowing date seem to have a similar origin. More effort should be focused on understanding the controls of oil mass per kernel. It is speculated that there may be a genotype-dependent limit to this variable. A third unresolved issue relates to the nature and strength of the linkage between post-anthesis stay-green and leaf photosynthetic functionality. These variables are poorly related during pre-anthesis senescence of leaves in the lower portion of closed canopies, and for sunflower this linkage appears much weaker than in other crop species. Current interest in post-anthesis stay-green as a possibly useful crop attribute requires clarification of this uncertainty.

Keywords : sunflower, crop development, grain oil content, stay green.

Résumé : D'importants points non résolus chez le tournesol limitent les efforts pour progresser dans la modélisation des cultures, leur conduite, les analyses génétiques et l'amélioration. Trois aspects sont considérés ici pour illustrer ce point. Premièrement, la plupart des travaux concernant la durée de la période comprise entre la germination et la floraison traitent cette phase comme un tout. Le besoin d'un analyse plus détaillée en considérant des sous-phases est évoqué, particulièrement face à la possible variabilité intraspécifique dans la durée de la phase végétative de base et la phase juvénile et à l'évidence d'une réponse photopériodique différente avant, pendant et après l'initiation florale. Cette réponse différente peut aller jusqu'à être de signe contraire pour le même génotype. Deuxièmement, des réponses contrastantes dans la proportion d'huile de la graine comme conséquence de la manipulation de la densité de la population et du rayonnement incident paraissent être plus liées à la variation dans la proportion d'huile de l'amande qu'au rapport coque-amande. La réponse de la proportion d'huile de la graine aux variations de la date de semis semble

avoir la même origine. Un effort particulier devrait être consacré à la compréhension des contrôles du poids de l'huile de la graine. Une limite dépendante du génotype pourrait exister pour cette variable. Le troisième aspect non résolu est lié à la nature et à l'intensité de l'association entre la permanence verte en post-floraison et la fonctionnalité de la photosynthèse. Ces variables sont faiblement reliés pendant la sénescence foliaire en pré-floraison dans la portion basal des canopies fermés. Chez le tournesol cette association semble être plus faible que chez des autres cultures. L'intérêt actuel à la permanence verte en post-floraison en tant que possible attribut utile demande l'éclaircissement de cette incertitude.

Mots-clés : tournesol, développement des cultures, contenu d'huile dans la graine, permanence verte.

ARTICLE

Crop modellers, breeders and crop managers are among those who might benefit from improved understanding of sunflower ecophysiology, particularly in relation to the formation and realization of grain yield and quality and the connections between these characteristics and environment, genotype and management. We know a good deal about sunflower (*cf*. reviews in [1]), and recent advances in genetic analysis, molecular biology and physiology open exciting perspectives of better ways to improve our knowlege about our favourite crop. Nonetheless, the most cursory examination of the present situation suffices to emphasize the number of issues on which our understanding is very limited. Thus, we are forced to use empirical approaches in our descriptions of how the crop explores the soil and takes up water (e.g. [2, 3]) and of how biomass is partitioned among organs [4], and our understanding of the control of seed dormancy and its breakage is fairly rudimentary [5]. Some of the gaps in our knowledge for sunflower have their analogues in other crop species, but there is little doubt that world-wide investment in research on sunflower is considerably less than that for other important crop species such as maize, soybean, wheat or rice.

The unsurprising outcome of this situation is that there is a very broad range of unresolved issues in the ecophysiology of sunflower which merit consideration, far broader than could be dealt with in a single presentation. My choice has been to review uncertainties and recent find-ings that bear on the control of development, grain oil proportion and canopy stay-green in this species. I use these "case histories" to underpin the argument that on-going research into sunflower ecophysiology is a pre-requisite for continued progress in the understanding, modeling, breeding and management of the crop.

Control of crop development

Timing of crop flowering can be critical to optimization of relationships between crop yield potential, environment resource availability and patterns of stress occurrence. Genotype, environment, and their interactions have important effects on crop development. In sunflower there have been a number of attempts to describe these effects, to understand their physiological basis and to develop predictive frameworks for duration of time to flowering. Although there is some common ground, the overall impression is one of fragmentary coverage, results which sometimes appear contradictory, and differing assumptions for the descriptive frameworks. For example, predictive approaches for time to flowering have been based on genotype responses to temperature alone [6],

or to temperature and photoperiod with [7] or without [8] a juvenile phase. Equally, there is still discussion as to whether sunflower development exhibits short-day, long-day or other responses to photoperiod. To compound this impression of disorder, it is ironic that all three predictive frameworks described above have proved reasonably successful within certain limits. It would seem that the time has arrived for a more systematic approach to the issue, not least to provide the best possible framework for attempts to dissect the genetics of the control of flowering (e.g. [9]) and for the improvement of simulation models of the crop. It is quite possible that a complete solution will continue to elude us, as full understanding of environmental and genotypic control of development is still unclear in other species. Nevertheless, it would be useful to take the status of this issue in sunflower up to that of other crop species.

On general principles and extrapolating from other crop species, sunflower could be expected to exhibit genotypic variability for time to flowering under the most inductive photoperiod regime for each genotype (a concept similar to the earliness *per se* in cereals, e.g. [10], or the basic vegetative phase (BVP) of Major and Kiniry [11]). Habermann and Wallace [12] reported that a minimum number of leaves had to be formed before sunflower would flower, and intraspecific variability for this characteristic is likely. Some indication of this can be found in apparently irreducible differences between genotypes in time to flowering [13] or in final leaf number in genotypes of similar phyllochron. This BVP might include a juvenile phase, *i.e*. a phase during which development is insensitive to photoperiod. There is some indirect evidence that sunflower exhibits a juvenile phase [14], but a rigorous and quantitative attempt to establish the duration of this phase and its intraspecific variability has yet to be made. This should be achievable using reciprocal transfer experiments between inductive and non-inductive photoperiods, as has been done for maize, soybean and quinoa [15-17].

A second unresolved issue bearing on crop development relates to the apparently contrasting response to photoperiod exhibited by sunflower in the Emergence to Floral Initiation (E-FI) and Floral Initiation-Anthesis (FI-A) phases, with uncertain outcomes on the duration of the Emergence-Anthesis (E-A) phase [18]. Recent greenhouse experiments, using artificially extended (15-h) daylengths in contrast to natural photoperiods of 13 h, have served to confirm the finding [18] that long days hastened FI in some cultivars, and had no effect on others (Balbi, unpubl.). When the duration of the E-A phase has been examined, results are contradictory. In some recent field re-examinations of Rawson and Hindmarsh's [18] results, using artificially extended photoperiods applied early in the E-FI phase, significant lengthening of the FI-A phase ocurred, with little effect on the duration of the E-FI phase (*Figure 1*, see also [19]). In contrast, other experiments show that extended photoperiods consistently shorten the E-A phase (Chapman, unpubl.), and the data of León *et al*. [9] suggests that the thermal time duration of the emergence-anthesis phase may decrease with photoperiod. Finally, there may be an effect of photoperiod on the dynamics of inflorescence development *(Figure 2)*, which may or may not influence time to flowering. In summary, available information is consistent with genotype-dependent long-day or day-neutral responses for floral initiation which may - or may not - be modified later in ontogeny. The contrasting results of experiments suggesting modification of the LD response after FI and those which do not may arise from light quality effects [20] associated with the different sources (incandescent lamps or mixed incandescent/fluorescent) used for photoperiod extension. Resolution of the issue is imperative, particularly given the need for a benchmark technique for photoperiod response studies.

Leaf number and leaf appearance rates are an important issue strongly linked to the control of phasic development. Although a full study of the effect of photoperiod on these variables has yet to eventuate, the data of Balbi (unpubl.) indicate that photoperiod extension, applied as from emergence, although effective in increasing the duration of the emergence-anthesis phase by as much as 16 days, had no significant effect on leaf number. Chapman (unpubl.), on the other hand, found photoperiod effects on leaf number but these did not appear to translate into important changes in the duration of the bud visible-anthesis interval. These experiments do not allow separation of the effects of photoperiod on leaf primordium number and phyllochron, but at the very least suggest that the latter must have varied between photoperiods, as has been found in other species (e.g. wheat [21] and quinoa [22]). Partial reversion of primordium fate after differentiation in response to photoperiod (e.g. [23, 24]) could be involved in determining a stable leaf number at flowering in spite of variations in phase duration.

With the modest objective of satisfying the requirements of the simplest descriptive phenological models (e.g. [11]), what is needed is a systematic study of constrasting genotypes directed at defining intraspecific variability for a) the BVP, b) the existence and the duration of the juvenile phase, and c) the photoperiod response functions (critical and threshold photoperiods, photoperiod sensitivity) for the E-FI phase, the process of floral initiation, and (probably) the FI-A phase. It could be argued that the quantitative descriptions developed by several groups (*i.e*. [6-8]) proved successful in predicting flowering dates over durations of the emergence-flowering phase that varied by up to almost 100 days between extremes [6, 7, 25], in spite of the fact that none of these frameworks incorporated the complexity suggested above. However, the important differences in the basic assumptions of these frameworks should be a sufficient argument for a re-evaluation of the issue.

At a deeper level, we also need to progress beyond description to the identity and understanding of the interactions of the genes involved in controlling phenology. The genetics and physiology of control of flowering in more heavily studied species such as the cereals [10] and *Arabidopsis* [23, 26] are complex and may involve a number of genes, pathways, and their interactions. Studies such as that of León *et al*. [9], represent a useful first step for sunflower. However, we must build on these beginnings to achieve a workable synthesis which quantifies and weights the effects of the various pathways involved in the genetic control of flowering and their responses to the environment (e.g. [27]). Lack of a proper understanding of the genotype and environment controls of development in sunflower can constrain our ability to integrate the descriptive and quantitative relationships that modellers and agronomists need with the genetic patterns that concern breeders and genetecists.

The control of grain oil proportion

Grain oil proportion is affected by kernel: grain ratio (K:G) and kernel oil proportion, and changes in both characteristics have contributed to the increased grain oil proportions achieved by breeders (e.g. [28]). Some understanding of the underlying genetics has also been achiev-ed (e.g. [29]). Because hull growth is completed while kernel mass is still increasing, and the deposition of reserve lipids commences after the start of rapid increase in kernel mass [7], terminal stresses are likely to affect final grain oil proportion simply through changes in the final proportions of hull, kernel and oil (e.g. [30]). Slight increases in K:G have also been found in the inner-most grain on the head in non-stressed crops, and this may explain - in part - the higher oil proportion in these grains. Recent

research [31] has shown that variations in the dynamics of the processes of hull growth, kernel growth and oil deposition during grain filling in genotypes of differing final oil proportion can play a substantial part in determining these differences *(Figure 3)*. These results show, for example, that initial hull size is greater, hull growth continues for longer (+35%) and the duration of oil deposition in the kernel oil shorter (-18%) in the genotype with lower final oil proportion, for similar durations of grain filling. Considerable differences in embryo oil concentration between cultivars were also evident *(Figure 3)*.

Research by Villalobos *et al*. [32] and by Dosio [33] and his associates [34, 35] has pointed up an interesting contrast in grain oil proportion responses to the timing of resource availability *(Figure 4)*. Villalobos *et al*. [32] clearly showed that final grain oil proportion shows a positive response to plant population density (*i.e*. to decreasing seasonal resource availability). In contrast, Dosio *et al*. [34] have shown that reductions in PAR intercepted per plant during the grain-filling phase (*i.e.* decreased resource availability during the last part of the season) can - in one hybrid but not in another - decrease final oil proportion. A feature of these responses of grain oil proportion to both plant population density and to intercepted PAR is that these were due to variations in kernel oil proportion rather than K:G (Villalobos [unpubl.], [35]). Another important result was that in the hybrid responsive to variations in intercepted PAR, grain-filling duration (but not rate) showed a response to resource availability, increasing in the thinned crop with respect to the shaded crop [33].

Interestingly, oil mass per grain (mg oil/grain) in the Villalobos *et al*. [32] experiment tended to remain constant within the 0.5 to 5pl/m^2 range of population densities, contrasting with a continuous fall in individual grain weight over the same range. Above 5pl/m^2, both variables fell together as resource availability decreased, showing a response similar to that found by Dosio *et al*. [34] over the range of intercepted PAR they explored. It may be that the behaviour observed by Villalobos *et al*. reflects an upper limit to oil deposition per grain which is only expressed when individual grain weight can increase a great deal due to the large ovary (hull) size that can develop in spaced plants. Under the more restrictive conditions for potential hull size that exist when resource availability is only varied during grain filling (*i.e*. [34]), this effect may not be expressed. Additional, genotype-dependent, factors presumably apply, as seen by the contrast between hybrids found by Dosio *et al*. [34]. There are obviously many uncertainties that need to be resolved to clarify the apparently contradictory responses to the timing (*i.e*. whole season *vs* grain-filling only) of variations in resource availability. Nevertheless, the results highlight the complex control of grain final oil proportion and underline the importance of kernel oil proportion as a source of these effects. It is further suggested that the notion of a genotype-dependent limit to oil mass per grain, best expressed at low population density, may be worth further exploration. It may be noteworthy that the hybrid that responded to increased resource availability during grain-filling was black-hulled, and the non-responsive hybrid striped [34]. We clearly need to know whether these associations and responses can be linked to phenotype morphophysiological characteristics.

A third important influence on grain oil proportion is the timing of grain filling and the conditions under which this process is completed. Grain filling under lower radiation and somewhat lower temperature conditions, a consequence of late sowing, consistently reduced final grain oil proportion in a set of ten reference hybrids [19]. There were significant G **x** E effects in these experiments, but G effects were non-significant. Late-flowering genotypes derived from a cross between inbred lines grown at a site with a restricted growing season (León *et al*., unpubl.) also showed reduced values of

grain oil proportion. In de la Vega's results [19], the changes in final grain oil proportion were largely due to changes in kernel oil proportion, the effects on K:G, although fairly consistent and in the direction that would reduce oil proportion, contributed little to the observed behaviour *(Figure 5)*. This, in spite of the fact that late sowing also had the effect of reducing the duration of the anthesis-physiological maturity phase in many (but not all) of the hybrids examined. This shortening effect is noteworthy, since low temperatures, within the sub-optimum range, tend to prolong the duration of grain filling [36]. The effects on grain oil proportion described in [19] may therefore be allied to the responses to shading during grain-filling reported in [33]. Other factors may also play a part: extending the photoperiod for late-sown crops did not alter the tendency of grain oil proportion to fall in most of the hybrids, but did induce, in several hybrids, significant increases in this variable with respect to late crops grown under natural photoperiods [19].

Taken as a whole, the results of the above experiments suggest that changes in K:G, either genotype- or environmentally-linked, or arising from interactions between these factors, are a long way from being the whole story behind grain oil proportion responses to management and environment. These results suggest the need for improved understanding of the control of kernel oil proportion. These controls, almost certainly, interact in complex ways. Plant population density, radiation, genotype and, possibly, photoperiod all appear as candidate factors, but we lack critical experiments that dissect out (and, hopefully) quantify the relationships and the interactions between factors. An examination of the origin of an apparent ceiling to oil deposition per grain, as seen in [32], and the notion of a degree of independence in the control of the dynamics of accumulation of carbohydrate, protein and oil in the embryo (such as has been found for wheat grain protein and starch [37]) would be particularly important. We also need to progress beyond the descriptive and explorative stage we are now in towards the biochemistry and molecular biology of the control of grain oil synthesis and grain-filling duration as affected by genotype and environment. Work with model plants such as *Arabidopsis* (e.g. [38]) will probably serve to guide research on similar processes in sunflow-er. Appropriate field studies using sunflower and involving manipulation of management, environmental and genetic factors are needed to identify the nature of responses that require study and to formulate testable hypotheses on the one hand, and to verify the implications of results obtained using model plants, on the other.

Stay green: does one get what one sees?

Increased maintenance of canopy functionality during grain filling, often referred to as stay green, has been identified as a potentially useful trait contributing to higher yields in several species, including sunflower; although emphasis in the latter species has been on stem colour (e.g. [39]). Significant time of sowing (normal vs. late) and G **x** E interactions were exhibited by the dynamics of the intercepted fraction of incident radiation in crops of a set of ten reference sunflower hybrids [40]. Oil yield in these experiments was associated with the integral of fractional interception for the flowering to physiological maturity phase *(Figure 6)*, and with the reduced interception of radiation for the phase arising from the combination of falling incident radiation and reduced interception. Stay green, from the point of view of a breeder or an ecophysiologist short of time and resources, is usually determined by observation of leaf colour and attempts to weight its effects are often derived from these observations. Thus, intercepted PAR is measured for the portion of the canopy which retains green leaves, disregarding the yellow or yellowing ones according to some pre-determined criteria. There is an element of risk in this, in that green leaves do not necessarily equate to

functional leaves [41]. Loss of green colour does not necessarily bear a direct relationship with loss of photosynthetic capacity, possibly because chlorophyll is lost more slowly from the chloroplasts than other components of this organelle [42], and tends to retain its capacity to absorb radiation after becoming functionally disconnected from the photosynthetic process. In soybean, the stay-green behaviour of some mutants is not reflected in maintenance of photosynthetic capacity [43]. Recent results of work with sorghum (see review [44]) emphasize uncertainties in this respect *(Figure 7)*.

Rousseaux *et al*. [45] studied the relationships beween leaf colour and photosynthetic capacity, and between leaf colour and specific leaf nitrogen, in basal leaves of pre-anthesis sunflower canopies. Their observations pose important questions for post-anthesis senescence and stay green in this species. The important result of their experiments, in the present context, is that during pre-anthesis senescence of leaves at the base of the sunflower crop canopy, photosynthetic rates at high irradiance (ca. 1,400 mumoles $PAR.m^{-2}.s^{-1}$) correlated poorly with chlorophyll content, being reduced by 80% from maximum values while chlorophyll content dropped by less than 20% of maximum values *(Figure 8)*. Specific leaf nitrogen, a variable strongly linked to leaf photosynthetic capacity [46], also showed a concave curvilinear relationship with chlorophyll content in the same set of experiments, falling sharply from maximum values with small changes in colour. A comparison of the trajectories of the the relative photosynthetic capacity/ relative chlorophyll content relationship of sunflower with published data for other species (rice, ryegrass, barley, soybean and *Arabidopsis*) showed that sunflower exhibited the most marked drop in photosynthetic capacity for the least change in chlorophyll content [45].

The relationships between the loss of photosynthetic capacity and the loss of colour exhibited by the lower leaves of the canopy during pre-anthesis senescence may differ from that exhibited by the upper leaves of the canopy after anthesis. However, it is important that this issue be studied as soon as possible, so that breeders interested in exploring the uses of stay-green as a useful crop attribute can count on the necessary information.

CONCLUSION

The present status of the three topics considered in this review indicates important gaps in our present knowledge in areas that can impact on how the crop is managed, on how we should formulate simulation models of the crop, and what sort of problems and pitfalls may arise in trying to incorporate physiological attributes into a breeding program or in searching for the genetic basis of crop performance. The nature and breadth of the experimental program required to tackle these issues varies with topic from the more or less straightforward (e.g. the true value of stay-green) to the rather complex and multi-faceted (control of crop development and of grain oil proportion). The case-studies considered in this review are an admittedly reduced and rather personal selection of a wider spectrum, but are sufficient proof of the need for continued work in the field of sunflower crop ecophysiology.

Acknowledgements

It is a pleasure to thank the following colleagues (in alphabetical order of surnames) for their generosity in allowing me access to their results prior to publication and/or for providing useful comments on this review:

Luis Aguirrezábal, Celeste Balbi, Atilio Barneix, Scott Chapman, Guillermo Dosio, Alberto León, Anita Mantese, Mónica López Pereira, Cecilia Rousseaux, Abelardo de la Vega. Assistance by Jorgelina Cárcova in the preparation of the resume is gratefully acknowledged.

* This paper is a modified version of a talk delivered at the 15th International Sunflower Conference, Toulouse, France, 12-15 June 2000.

REFERENCES

1. SCHNEITER AA (1997). *Sunflower Technology and Production*, Agronomy Monograph 35. Madison, USA: American Society of Agronomy; 834 p.

2. MEINKE H, HAMMER GL, WANT P (1993). Potential soil water extraction by sunflower on a range of soils. *Field Crops Res*, 32: 59-81.

3. DARDANELLI JL, BACHMEIER OA, SERENO R, GIL R (1997). Rooting depth and soil water extraction patterns of different crops on a silty loam Haplustoll. *Field Crops Res*, 54: 29-38.

4. TRAPANI N, HALL AJ, VILLALOBOS FJ (1994). Pre-anthesis partitioning of dry matter in sunflower (*Helianthus annuus* L.) crops. *Field Crops Res*, 37: 235-46.

5. FONSECA AE (2000). *Efecto de la temperatura durante el llenado de grano sobre el comportamiento de semillas de girasol*. Trabajo de Intensificación, Facultad de Agronomía, Univ. Buenos Aires.

6. GOYNE PJ, SCHNEITER AA, CLEARY KC (1990). Prediction of time to anthesis of a selection of sunflower genotypes. *Agron J*, 82: 501-5.

7. VILLALOBOS FJ, HALL AJ, RITCHIE JT, ORGAZ, F (1996). Oilcrop-Sun: a development, growth and yield model of the sunflower crop. *AgronJ*, 88: 403-15.

8. HAMMER GL, GOYNE PJ, WOODRUFF DR (1982). Phenology of sunflower cultivars. III. Models for prediction in field environments. *Aust J Agric Res*, 33: 263-72.

9. LEON AJ, LEE M, ANDRADE FH (2001). Quantitative trait loci for growing degree days to flowering and photoperiod response in sunflower (*Helianthus annuus* L.). *Theor Appl Gen* (in press).

10. HAY RKM, ELLIS RP (1998). The control of flowering in wheat and barley: What recent avances in molecular genetics can reveal. *Ann Bot*, 82: 541-54.

11. MAJOR DJ, KINIRY JR (1991). Predicting daylength effects on phenological processes. In: HODGES T, ed. *Predicting crop phenology*. CRC Press: Boca Raton: 15-28.

12. HABERMANN HH, WALLACE RH (1958). Transfer of flowering stimulus from stock to scion in grafted *Helianthus annuus* L. *Am J Bot*, 45: 479-82.

13. GOYNE PJ, SCHNEITER AA (1988). Temperature and photoperiod interactions with the phenological development of sunflower. *Agron J*, 80: 777-84.

14. VINCE-PRUE D (1975). *Photoperiodism in plants.* Maidenhead: McGraw-Hill; 444 p.

15. KINIRY JR, RITCHIE JT, MUSSER, RL, FLINT EP, IWIG WC (1983). The photoperiod sensitive interval in maize. *Agron J*, 75: 687-90.

16. ELLIS RH, COLLINSON ST, HUDSON D, PATEFIELD WM (1992). The analysis of reciprocal transfer experiments to estimate the duration of the photoperiod-sensitive and photoperiod-insensitive phases of plant development: an example in soyabean. *Ann Bot*, 70: 87-92.

17. BERTERO HD, KING RW, HALL AJ (1999). Modelling photoperiod and temperature responses of flowering in quinoa (*Chenopodium quinoa* Willd.). *Field Crops Res*, 63: 19-34.

18. RAWSON HM, HINDMARSH JH (1982). Effects of temperature on leaf expansion in sunflower. *Aust J Plant Physiol*, 9: 209-19.

19. DE LA VEGA AJ (2001). *Interacciones genotipo **x**ambiente y mejoramiento del girasol para las regiones Central y Norte de Argentina*. Ph. D. Thesis, Univ. of Buenos Aires.

20. CONNOR DJ, SADRAS VO (1992). Physiology of yield expression in sunflower. *Field Crops Res*, 30: 333-89.

21. SLAFER GA, RAWSON HM (1997). Phyllochron in wheat as affected by photoperiod under two temperature regimes. *Aust J Plant Physiol*, 24: 151-8.

22. BERTERO HD, KING RW, HALL AJ (2000). Photoperiod and temperature effects on the rate of leaf appearance in quinoa (*Chenopodium quinoa* Willd.). *Aust J Plant Physiol*, 27: 349-56.

23. MARTINEZ-ZAPATER JM, COUPLAND G, DEAN C, KOORNNEEF M (1994). The transition to flowering in *Arabidopsis*. In: MEYEROWITZ EM, SOMERVILLE CR, eds. *Arabidopsis.* Cold Spring Harbor: Cold Spring Harbor Laboratory: 403-33.

24. BERTERO HD, KING RW, HALL AJ (1999). Photoperiod-sensitive development phases in quinoa (*Chenopodium quinoa* Willd.). *Field Crops Res*; 60: 231-43.

25. SADRAS VO, HALL AJ (1989). Patterns of water availability for sunflower crops in semi-arid Central Argentina. A simulation-based evaluation of their interactions with cropping stategies and cultivar traits. *Agric Syst*, 31: 221-8.

26. WEIGEL D (1995). The genetics of flower development: from floral induction to ovule morphogenenesis. *Ann Rev Gen*, 29: 19-39.

27. WELCH SM, ROE J, DONG Z (2000). Modeling the genetic control of flowering in *Arabidopsis thaliana*. 2000 Annual Meeting Abstracts, American Society of Agronomy: 32.

28. LOPEZ PEREIRA M,TRAPANI N, SADRAS VO (2000). Genetic improvement of sunflower in Argentina between 1930 and 1995. III. Dry matter partitioning and grain composition. *Field Crops Res*, 67: 215-21.

29. LEON AJ, LEE M, RUFENER GK, BERRY ST, MOWERS RP (1995). Use of RFLP markers for genetic linkage analysis of oil percentage in sunflower seed. *Crop Sci*, 35: 558-64.

30. HALL,AJ, CHIMENTI CA, VILELLA, F., FREIER G (1985). Timing of water stress effects on yield components in sunflower. *Proc 11th Internat Sunflower Conf Internat Sunflower Assoc: Paris*. Vol. 1: 131-6.

31. MANTESE A (2001). *Base estructural y dinámica de la acumulación de lípidos en cvs. de girasol (*Helianthus annuus *L.) con granos de diferente contenido de aceite*. M. Sc. thesis, Universidad de Buenos Aires.

32. VILLALOBOS FJ, SADRAS VO, SORIANO A, FERERES E (1994). Planting density effects on dry matter partitioning and productivity of sunflower genotypes. *Field Crops Res*, 36: 1-11.

33. DOSIO GAA (1998). *Efecto de la radiación solar interceptada durante el llenado de los frutos sobre los componentes del rendimiento de aceite en girasol*. M. Sc. Thesis, Univ. Nacional de Mar del Plata.

34. DOSIO GAA, PEREYRA VR, AGUIRREZABAL LAN (2000). Effect of intercepted solar radiation during the fruit filling period on sunflower oil yield. *Proc 15th Internat Sunflower Conf Internat Sunflower Assoc: Paris*. Vol. 1: D-7-12.

35. NOLASCO SM, DOSIO GAA, RICCOBENE IC, SANTALLA EM, AGUIRREZABAL LAN (2000). Relationships between seed oil percentage and kernel oil percentage and pericarp/kernel ratio as affected by plant density and solar radiation intercepted during seed filling in sunflower. *Proc 15th Internat Sunflower Conf Internat Sunflower Assoc: Paris*. Vol. 1: D-19-24.

36. CHIMENTI CA, HALL AJ, LOPEZ MS (2001). Embryo growth rate and duration in sunflower as affected by temperature. *Field Crops Res*, 69: 81-8.

37. DONOVAN GR, LEE JW (1977). The growth of detached wheat heads in liquid culture. *Plant Sci Lett*, 9: 107-13.

38. SOMERVILLE CR, SOMERVILLE S (1999). Plant functional genomics. *Science*, 285: 380-3.

39. CUKADAR-OLMEDO B, MILLER JF (1997). Inheritance of the stay green trait in sunflower. *Crop Sci*, 37: 150-3.

40. DE LA VEGA AJ, HALL AJ (2000). Physiological bases of genotype by environment interactions for sowing date in sunflower. *Proc 15th Internat Sunflower Conf Internat Sunflower Assoc: Paris*. Vol. 1: D-106-11.

41. THOMAS H, SMART CM (1993). Crops that stay green. *Ann appl Biol*, 123: 193-219.

42. GUIAMET JJ, GIANNIBELLI MC (1996). Nuclear and cytoplasmic "stay-green" mutations of soybean alter the loss of leaf soluble proteins during senescence. *Physiol Plant*, 96: 655-61.

43. GUIAMET JJ, TEERI JA, NOODEN LD (1990). Effects of nuclear and cytoplasmic genes altering chlorophyll loss on gas exchange during monocarpic senescence in soybean. *Plant Cell Physiol*, 31: 1123-30.

44. THOMAS H, HOWARTH CJ (2000). Five ways to stay green. *J Exp Bot*, 51: 329-37.

45. ROUSSEAUX MC, HALL AJ, SANCHEZ RA, PLOSCHUK EL (2000). Leaf photosynthetic capacity, chlorophyll content, and specific leaf nitrogen relationships in sunflower crops prior to anthe-

sis. *Proc 15th Internat Sunflower Conf Internat Sunflower Assoc: Paris*. Vol. 1: D-70-5.

46. CONNOR DJ, HALL AJ, SADRAS VO (1993). Effect of nitrogen content on the photosynthetic characteristics of sunflower leaves. *Aust J Plant Physiol*, 20: 251-63.

47. MARC J, PALMER JH (1981). Photoperiodic sensitivity of inflorescence initiation and development sunflower. *Field Crops Res*, 4: 155-14.

Illustrations

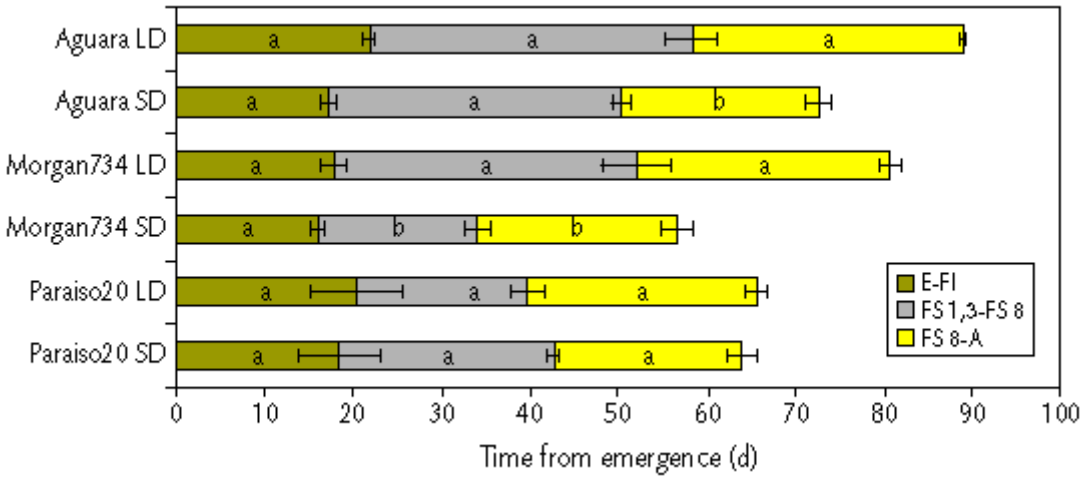

Figure 1. *Durations of the emergence to floral initiation (E-FI); floral stage (FS) 1.3 to FS 8 (FS1.3-FS 8); and FS 8 to anthesis (FS 8-A) subphases for crops of three cultivars grown under natural (SD) and extended (LD, extension of natural photoperiod to 15h with 35mumol PAR $m^2.s^{-1}$) photoperiods in the field. Floral stages from [45]. Mean natural photoperiods for each subphase were 13h25' (E-FI), 12h40' (FS1.3-FS 8), and 11h30' (FS 8-A). Different letters indicate significant (P=0.05) differences in subphase duration within a cultivar, horizontal bars are ± 1SE for subphase duration. Unpublished data of Balbi.*

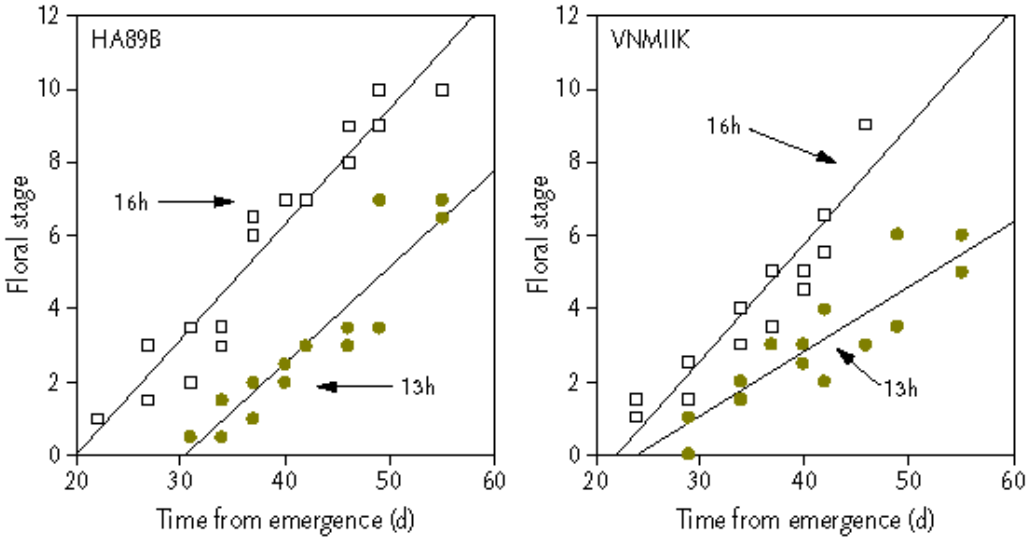

Figure 2. *Progress of floral initiation under natural (13h) and extended (16h) photoperiods in HA89B (left) and VNMIIK (right). Floral stages from Marc and Palmer [47]. Unpublished data of Balbi.*

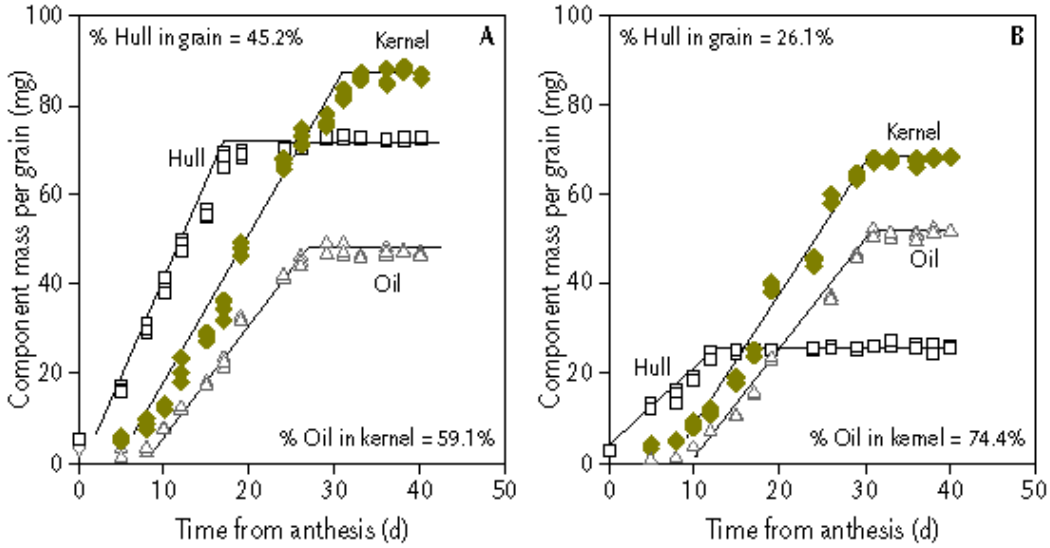

Figure 3. *Dynamics of mass increase for grain components in hybrids of low (ca. 30%, left) and high (ca. 58%, right) final oil proportion in grain. Values for hull as % of grain and oil as % of kernel also shown. Data from Mantese [31].*

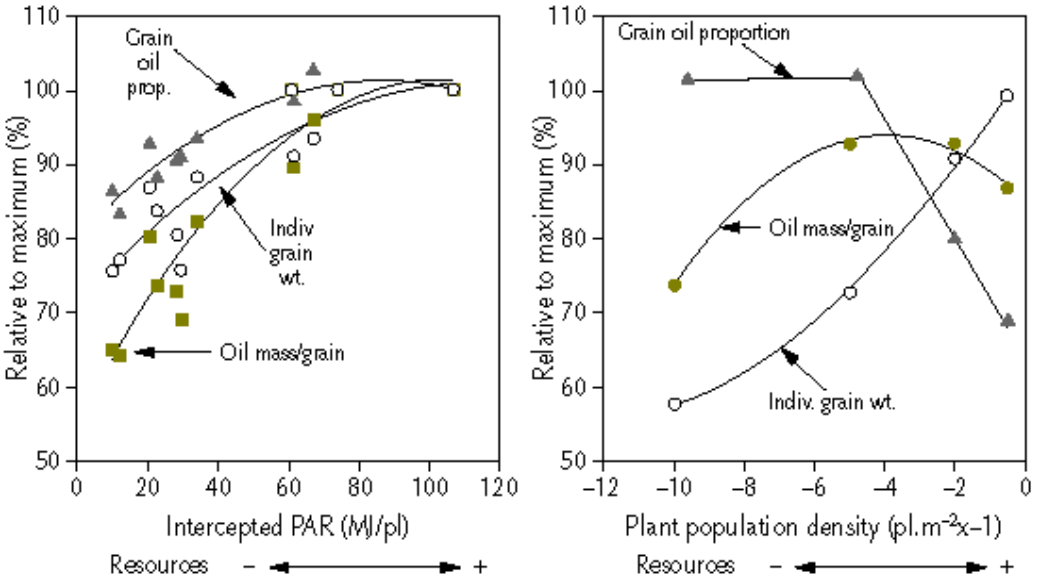

Figure 4. *Responses (relative to maxima) of grain oil proportion, individual grain mass and oil mass/grain to variations in resource availability determined by thinning and shading treatments (responsive hybrid only [34], left) or by variations in plant population density (mean of four hybrids [32], right). Note reversed x-axis in right-hand panel.*

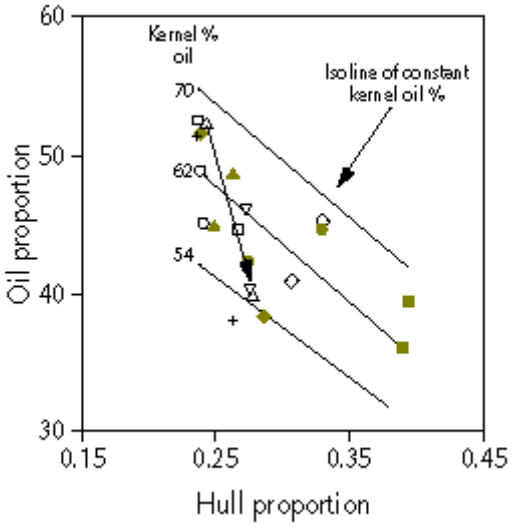

Figure 5. *Final oil proportion as a function of proportion of hull for a set of 10 hybrids sown early (S1) and late (S2) and late in the season. For each hybrid (different symbol), the higher y-value is the S1 result, the lower S2 (exemplified by arrow for hybrid 6). Diagonal isolines represent response to hull proportion expected with the indicated constant kernel oil proportions. Data from De la Vega [19].*

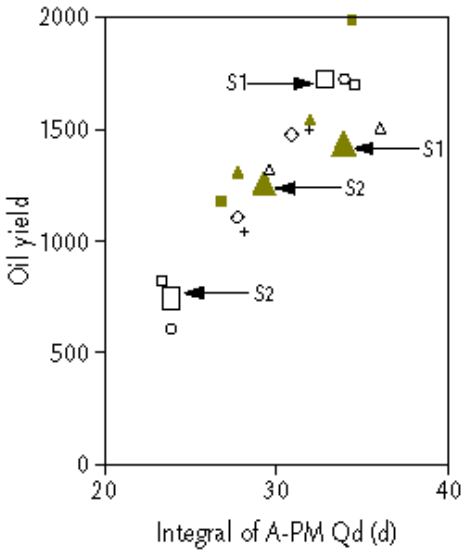

Figure 6. *Oil yield as a function of the integral of daily fractional radiation interception for a set of 10 hybrids sown early (S1) and late (S2) and late in the season. Highest values for each hybrid (different symbol) on both axes are S1 data, lower ones S2 data. Oversize symbols exemplify the nature of G* **x** *E interactions observed in these experiments. Data from De la Vega [19].*

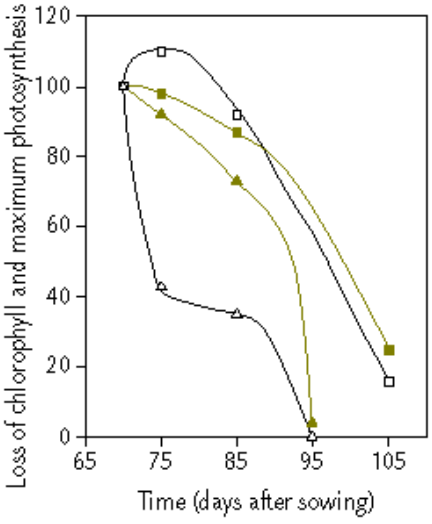

Figure 7. *Dynamics of loss of chlorophyll (filled symbols) and maximum photosynthesis (empty symbols) in sorghum lines QL 41 (squares) and R16 (triangles) during grain filling. Data from Thomas and Howarth [44].*

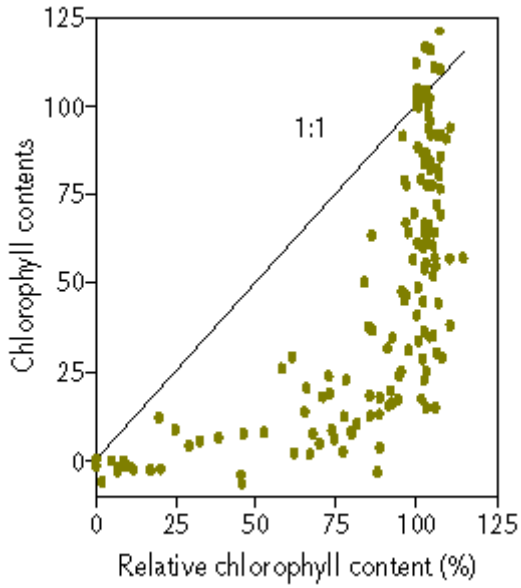

Figure 8. *Relative (to maxima) photosynthetic rates at ca. 1,400mumoles.m^{-2}.s^{-1} PAR as a function of relative chlorophyll content for sunflower leaves at the base of the canopy during senescence. Data from Rousseaux* et al. *[45].*