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SUNFLOWER ECOPHYSIOLOGY: SOME UNRESOLVED ISSUES

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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. 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. 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.

Introduction

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 Schneiter, 1997), 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 (Meinke et al., 1993; Dardanelli et al., 1997) and of how biomass is partitioned among organs (Trapani et al., 1994), and our understanding of topics such as the control of grain numbers or the control of seed dormancy and its breakage is fairly rudimentary . 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 findings that bear on the control of development, grain oil proportion and canopy stay-green in this species.

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 (Goyne et al., 1990), or to temperature and photoperiod with (Villalobos et al., 1996) or without (Hammer et al., 1982) 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. León et al., 2000) 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. Hay and Ellis, 1998) or the basic vegetative phase (BVP) of Major and Kiniry, 1991). Habermann and Wallace (1958) 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

(Goyne and Schneiter, 1988) 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 (Vince-Prue, 1975), 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 (Kiniry et al.,1983, Ellis et al., 1992, Bertero et al., 1999b).

A second unresolved issue 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 (e.g. Rawson and Hindmarsh,1982). In some field experiments with artificially extended photoperiods applied early in the E-FI phase, significant lengthening of the E-A phase (de la Vega [unpubl.], Balbi [unpubl.]) ocurred, even in cultivars which show a long-day (LD) response for the E-FI phase (Fig. 1). In contrast, other experiments show that extended

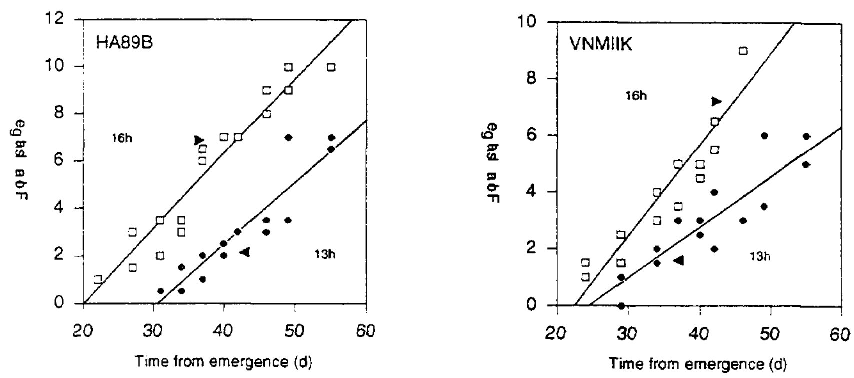

Fig. 1. Progress of floral initiation under natural (13 h) and extended (16 h) photoperiods in HA89B (left) and VNMIIK (right). Floral stages from Marc and Palmer (1981), data of Balbi (unpubl).

photoperiods consistently shorten the E-A phase (Chapman, unpubl.). In addition, there may be an effect of photoperiod on the dynamics of inflorescence development (Fig. 1), 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 (Connor and Sadras, 1992) 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.

With the modest objective of satisfying the requirements of the simplest descriptive phenological models (e.g. Major and Kiniry, 1991), 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 Hammer et al. (1982), Goyne et al. (1990) and Villalobos et al. (1996) proved successful in predicting flowering dates over durations of the emergence-flowering phase that varied by up to almost 100 days between extremes (Sadras and Hall, 1989; Goyne et al., 1990, Villalobos et al., 1996), in spite of the fact that none of these frameworks incorporated the complexity suggested above. The differences in the assumptions between these frameworks should be a sufficient argument for a re-evaluation of these issues. At a deeper level, we also need to progress beyond description to the identity and 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 (Hay and Ellis, 1998) and *Arabidopsis* (Martínez-Zapater et al. , 1994; Weigel, 1995) are complex and may involve a number of genes and their interactions. Studies such as that of León et al. (2000), represent a useful first step for sunflower. 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.

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.) and de la Vega (unpubl.) indicate that photoperiod extension from V5 or earlier onwards, 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 (Slafer and Rawson, 1997) and quinoa (Bertero et al., 2000)). Partial reversion of primordium fate after differentiation in response to photoperiod (e.g. Martínez-Zapater et al., 1994, Bertero et al., 1999a) could be involved in determining the stable leaf number at flowering.

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. López Pereira et al., 2000). Some understanding of the underlying genetics has also been achieved (e.g. León et al.,1995). Because hull growth is completed while kernel mass is still increasing, and deposition of reserve lipids commences after the start of rapid increase in kernel mass (Villalobos et al., 1996), terminal stresses are likely to affect final grain oil proportion simply through changes in the rates and durations of embryo and oil increases (e.g. Hall et al., 1985). 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 by Mantese (2000) 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. Her 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 (Fig. 2).

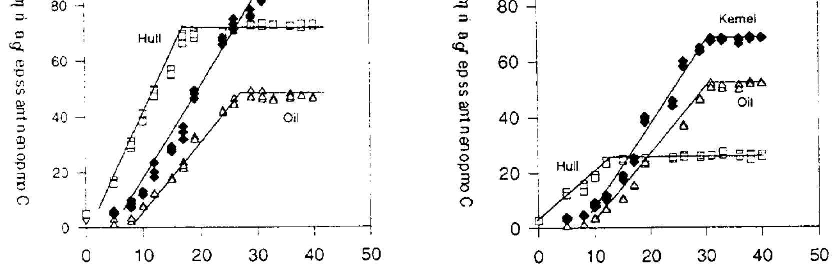

Fig. 2. Dynamics of mass increase for grain components in hybrids of low (ca. 30 %,left) and high (ca. 58%, right) final oil proportion in grain. Data of Mantese (2000).

Research by Villalobos et al. (1994) and by Dosio (1998) and his associates (Dosio et al., 2000; Nolasco et al., 2000) has pointed up an interesting contrast in grain oil proportion responses to the timing of resource availability (Fig. 3). Villalobos et al. (1994) clearly showed that final grain oil proportion shows a positive response to plant population density (i.e. to decreasing

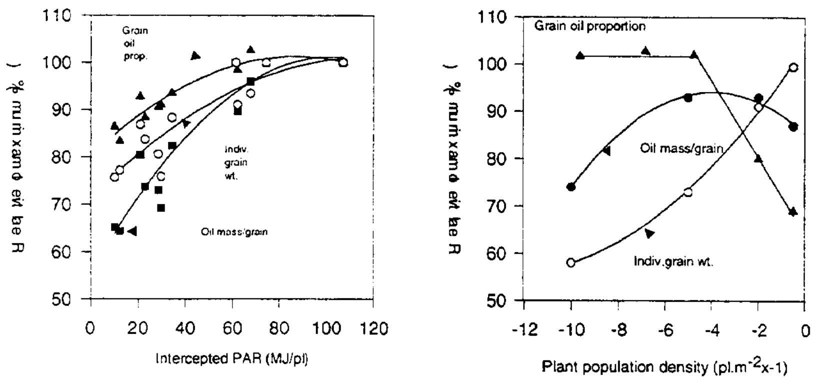

Fig. 3. Responses (relative to maxima) of grain oil proportion, individual grain mass and oil mass/grain to variations in resource availability determined by thining and shading treatments (responsive hybrid only, Dosio et al., 2000, left) or by variations in plant population density (mean of four hybrids, Villalobos et al., 1994, right). Note reversed x-axis in right-hand panel.

seasonal resource availability). In contrast, Dosio et al. (2000) 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.] , Nolasco et al., 2000). 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 (Dosio, 1998).

Interestingly, oil mass per grain (mg oil/grain) in the Villalobos et al. (1994) results tended to remain constant within the 0.5 to 5 pl/m^2 range of population densities, contrasting with a continuous fall in individual grain weight over the same range. Above 5 pl/m^2, both variables

fell together as resource availability decreased, showing a response similar to that found by Dosio et al. (2000) 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 when resource availability is only varied during grain filling, this effect may not be expressed. Additional, genotype-dependent, factors presumably apply , as seen by the contrast between hybrids found by Dosio et al. (2000). 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) 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, and suggest 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 (Dosio et al., 2000) . 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 (de la Vega, unpubl.). There were significant genotype by environment (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, 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 predominantly in the direction that would reduce oil proportion, contributed little to the observed behaviour (Fig. 4). 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. The effects on grain oil proportion found by de la Vega may therefore be allied to the responses to shading during grain-filling reported by Dosio (1998). Other factors may also play a part: extending the photoperiod for crops sown late did not alter the tendency of grain oil proportion to fall in most of the hybrids, but did induce significant increases with respect to late crops grown under natural photoperiods in a few hybrids (de la Vega, unpubl.).

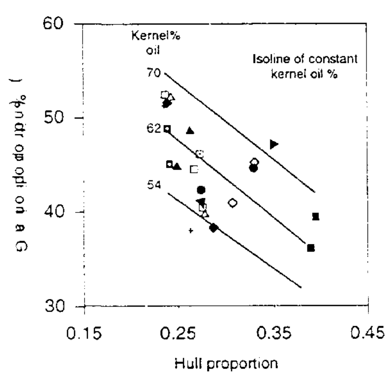

Fig. 4. Final oil proportion as a function of proportion of hull for a set of 10 hybrids sown early (S1) and late (S2) and late in the season. For each hybrid (different symbol), the higher y-value is the S1 result, the lower S2 (the change between S1 and S2 is exemplified by arrow for hybrid 6). Diagonal isolines represent response to hull proportion expected with the indicated constant kernel oil proportions. Unpublished data of de la Vega.

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 the results of Villalobos et al. (1994), 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 (Donovan and Lee, 1977), 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. Somerville and Somerville, 1999) will probably serve to guide research on similar processes in sunflower.

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. Cukadar-Olmedo and Miller, 1997). Significant time of sowing (normal vs. late) and GxE interactions were exhibited by the dynamics of the intercepted fraction of incident radiation in crops of a set of ten reference sunflower hybrids (de la Vega and Hall, 2000). Oil yield in these experiments was associated with the integral of fractional interception for the flowering to physiological maturity phase (Fig. 5) 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, i.e. 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 (Thomas and Smart, 1993).

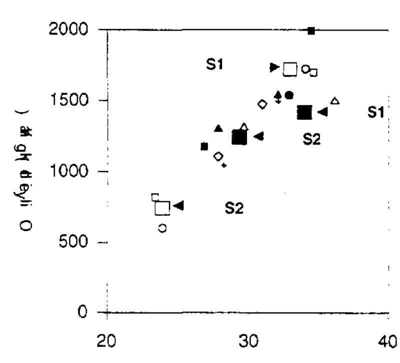

Fig. 5. Oil yield as a function of the integral of daily fractional radiation interception for a set of 10 hybrids (different symbol) sown early (S1) and late (S2) and late in the season.Highest values for each hybrid on both axes are S1 data, lower ones S2 data. Oversize symbols exemplify for two hybrids the nature of GxE interactions observed in these experiments. Unpublished data of de la Vega

Rousseaux et al.(2000)studied the relationships beween leaf colour and photosynthetic capacity on the one hand, and leaf colour and specific leaf nitrogen on the other. They were interested in pre-anthesis senescence in sunflower canopies, but their observations pose important questions for post-anthesis senescence and stay green. 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.1400 µmoles 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 (Fig. 6). In other experiments, specific leaf nitrogen, a variable strongly linked to leaf photosynthetic capacity (Connor et al., 1993), also showed a concave curvilinear relationship with chlorophyll content, 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 (Rousseaux et al., 2000).

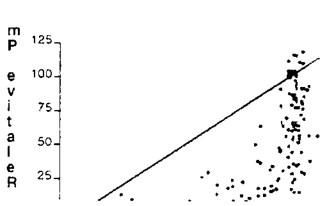

Fig. 6. Relative (to maxima) photosynthetic rates at ca. 1400 µmoles m^{-2} s^{-1} as a function of relative chlorophyll content for sunflower leaves at the base of the canopy during senescence. Data of

In other crop species it has also been found that 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 (Guiamet and Giannibelli, 1996), and tends to retain its colour 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 (Guiamet et al., 1990).

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. Nevertheless, 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.

Conclusions

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.

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