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Yield physiology of short-statured sunflower

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Summary

This paper reviews the information on the yield physiology of dwarf sunflower to assess if the yield advantage achieved by the development of short-statured (dwarf) cultivars in cereals is transferable to sunflower. It is concluded that aspects of the resistance to crop collapse should be directly transferable but in view of the great importance of stem-stored assimilate to yield in sunflower, it is probable that, without further selection, dwarfing will result in smaller and more variable yield, especially in terminally-stressed environments. This is despite observations that dwarf crops explore the same soil depth and use similar amounts of water as taller cultivars. Avenues for investigation are identified. Of importance are anatomical studies to identify the characteristics that determine stem strength and physiological studies to determine the role of stem-stored assimilate to seed set, seed-filling and to stem strength itself.

Introduction

The widespread commercial acceptance of short-statured (dwarf) cereal cultivars results from their agronomic advantage over their taller predecessors. Dwarf cultivars produce greater yield and are also physically less prone to collapse and consequent loss during harvest. The yield advantage derives from the production of more seed per unit area, a result of reduced competition for assimilate between developing inflorescence and stem during the period of major vegetative growth prior to anthesis. More seed then exert greater demand for assimilate on the canopy which responds in production although those issues of assimilate interaction between source (canopy) and sink (seed) are poorly understood. At the agronomic level, increased seed yield (g) is also seen as greater harvest index (HI), an effect that is assisted by any reduction in vegetative biomass (v) since HI = g/((g+v).

By analogy, the breeding of dwarf cultivars is a seemingly appropriate route for cultivar improvement in sunflower. To the present, however, progress in the release of dwarf cultivars has been limited due to problems of infertility that are now being overcome. Given that, the purpose of this paper is to assess the transferability to sunflower of the yield advantages well established in dwarf cereals. Comparisons are drawn particularly with wheat and special attention is given to the effect of water stress because it is a feature of many environments where sunflower is grown.

Stem height

The genetics of expression of stem height are relatively well understood in sunflower (Berreta and Miller, 1985; Moutous and Roath, 1985; Miller and Hammond, 1991). Dwarfing reduces internode length rather than node number and, as recorded in other crops, the effect is greatest at the lower internodes. Sadras *et al.* (1991) measured a reduction of 50% in stem length below the fourth internode and 26% above it.

Crop collapse

There are two distinct causes of crop collapse, *viz.* lodging and stem breakage. Both are related to stem height, stem strength, and size of capitulum. Predisposing factors are weather conditions (principally wind and rain), damage by pests and disease, morphological defects, and physiological change, particularly during seed filling. Lodging occurs when the mechanical moment exerted by the stem-capitulum combination exceeds the lateral support of the root system. Capitula of a given mass exert greater force on tall than short stems so that tall crops are less able to withstand extreme conditions of rain, strong winds and low soil strength. Stem breakage, by contrast, occurs when the mechanical moment of the capitulum exceeds stem strength under conditions when the root system holds firm. It occurs most commonly at the base of the stem or close to the capitulum. For capitula of given mass, stem breakage near the stem base is more likely on tall than short stems.

Focus of breeding to date has been on decreasing stem height and at least maintaining stem diameter which, not surprisingly, has improved resistance to lodging (see Miller and Hammond, 1991 for summary). There has not, however, been any separate assessment of the relationship between stem height and stem breakage. While selection for short stems is a sensible place to start for resistance to both problems, it is itself, an insufficient basis for continuing crop improvement.

Anatomical studies of sunflower stems are required to define the nature of stem strength in sunflower and its relationship to dwarfism, environment and nutrition. It has been shown, for example, that boron deficiency causes brittle stems (Fernandez et al. 1985) but little is known of the comparative boron nutrition of sunflower cultivars. The stem comprises a cylindrical annulus of structurally strong material enclosing a soft pith, which, it seems, may contribute significantly to stem strength by turgidity achieved by osmotic relationships. The separate identification of the nature and role of these two components is critical to progress because overall stem diameter need not be the best indicator of stem strength. This distinction becomes particularly important during seed filling when the pith first withdraws from the stem outer annulus and then gradually disintegrates at a time when the load on stems from developing capitula increases. Little is known of the importance of this physiological change to stem strength, the variation between cultivars, the effect of environmental conditions and stresses, and the relationship to the mobilization of assimilates for seed filling.

It is noted here that resistance to collapse is a trait that enables the more complete harvest of crop yield. In contrast, the following issues relating stem height to yield concern the nature and efficiency of seed-production itself.

Canopy structure

Stem height changes the pattern of leaf insertion and hence of foliage density and display. Sadras *et al.* (1991) described this in terms of an index of leaf overlap. They showed that 50% reduction in stem length below the fourth node was associated with a threefold-increase in the leaf area per unit stem length in the lower part of the canopy. A difference of at least 100% was maintained from there to the top of the canopy. This compression of the canopy affects the interception of radiation and the aerodynamic conductance of the canopy which are important in both photosynthesis and transpiration. In general, one could hypothesize that dwarf canopies, would experience smaller photosynthesis and transpiration per unit leaf area due to less well illuminated canopies and a greater aerodynamic resistance to gaseous transfer within the canopy. The magnitude of the differences, although likely to be less than 5%, are unknown. As a first approximation, it would seem that any tendency for dwarf cultivars to have shallower root systems and hence more restricted access to soil water would be of greater importance to their water relationships and productivity, particularly in rainfed systems.

There have been few studies of these issues. Schneiter *et al.* (1988) reported similar behaviour of tall and dwarf cultivars as measured by total water use, water-use efficiency and harvest index. Of great significance, they found no relationship between plant height and depth of activity of root systems. In a further comparison of the water relations of tall and dwarf cultivars, Sadras *et al.* (1991) similarly recorded no difference in total water use or the fraction of it that was transpired by the crop. They did, however, record that the two types achieved similar partition of water use by different routes. The dwarf cultivar, with greater LAI, had smaller transpiration per unit leaf area than the tall cultivar. At an early stage of development (20 days after sowing, DAS20), the reduction was 50% relative to the tall cultivar but declined rapidly as the canopy expanded, falling to zero from DAS50. This is consistent with the proposition that the canopy of the dwarf cultivar is less well ventilated than that of the tall cultivar.

Stem biomass

Dwarf cultivars will contain less biomass than tall cultivars unless reduced height is offset by greater stem thickness. Stem thickness is inherited independently of height (Miller and Hammond 1991) so the possibility exists for a wide range in the partition of biomass to stem in dwarf cultivars. In the comparison reported by Sadras *et al.* (1992), stems of a dwarf cultivar weighed 30% of those of a tall cultivar. This was the basis in their study of the difference in partition of biomass between the two morphological types.

Reduced stem growth has important implications for the yield forming processes and for response to stress. These will be discussed in two steps. First the relationship between stem growth and the development of yield potential (seed number) at anthesis. Second, the role of stem-stored assimilate in seed filling and the realization of potential yield.

Yield potential

During the phenophase from bud (star) visible to anthesis, stem, leaf, root and capitulum grow strongly. It is reasonable to hypothesize that during this period there is less competition for assimilate between capitulum and stem in dwarf cultivars so that the development of the inflorescence might be less susceptible to assimilate shortage induced by stress. Relationships between floret number and biomass at anthesis are one way to study the efficiency of growth in establishing yield potential. A characteristic of dwarf cereals is the greater ratio of kernel number to biomass at anthesis than in tall cultivars but there are no comparisons of this relationship for tall and dwarf sunflower cultivars. Such investigations are urgently required to improve understanding of the source-sink relationships in sunflower and its response to stress.

In cereals, seed number is related to assimilate supply during the period from floral initiation to anthesis as shown by experiments of the type in which crops are shaded for successive periods of seven to 10 days. In the case of wheat, Fischer (1985) showed a strong effect on seed number during the 3-week period prior to 50% anthesis. Chimenti and Hall (1992) have performed similar experiments with sunflower and also shown significant reductions in seed number. However, they established that the period of susceptibility is longer, covering six weeks centred on 50% anthesis. The difference may reflect the comparative anatomy of flower formation in the two crops. In cereals, flowers are formed along an axis of small biomass whereas in sunflower the capitulum is a relatively massive structure whose expansion requires considerable assimilate presenting greater competition with the developing seed.

Sadras *et al.* (1992) have investigated the effect of water stress on the competition for assimilate between stem and inflorescence in tall and dwarf cultivars of sunflower during the period from bud visible to anthesis. They hypothesized that dwarf cultivars should be less susceptible to stress than tall cultivars because of a smaller demand for *assimilate by the stem. However, they did not show this to be the case.* Rather, the reduction in seed number that resulted from water shortage could not be explained by decreased assimilate supply. Assimilate concentration in the developing inflorescence increased in both types under water stress, indicating that growth was more restricted than was assimilate supply. Individual cultivars showed variable responses which the authors suggested could be related to differences in nitrogen nutrition or hormonal relationships.

Seed yield

There are two sources of assimilate for seed filling in determinate species such as sunflower and cereals. The first is assimilate stored in the vegetative parts at anthesis, dominantly in stem and tap root. The second is assimilate produced by photosynthesis concurrently with seed growth.

The relative contribution of the two sources is well studied in cereals where preanthesis assimilate is known to play a minor role (max. 10%) in crops of moderate to high yield. Whether similar results might be obtained in sunflower depends on two significant differences between the crop types. First, the contribution of stem-stored assimilate to yield is greater in sunflower than in cereals, and second, the high oil content of sunflower seed places an additional demand on assimilate supply to provide the respiratory substrate for metabolism.

Hall *et al.* (1989; 1990) have shown that translocation of preanthesis-stored assimilate contributes more to seed yield in sunflower than in cereals. They measured the contribution at 600 kg C ha^{-1} which is around three times that in cereals. Given the size of this contribution, it seems possible that dwarf cultivars of sunflower would respond *differently to cereals especially during terminal drought when the relative importance of* stored assimilate is greater. Sadras *et al.* (1992) have studied the proposition that the yield of dwarf cultivars of sunflower would be more susceptible to terminal stress than tall cultivars. Their work supports the importance of stem-stored assimilate to yield stability in sunflower established by Hall *et al.* (1989; 1990) but established no clear relationship between stem height and the contribution of assimilate from stem to seed.

Discussion

The advantage to increased yield of dwarf cereals is achieved by greater physiological efficiency in the formation of yield and by more complete harvest resulting from greater resistance to crop collapse. Available information suggests that these advantages will transfer unequally to sunflower.

Dwarf sunflower should benefit from increased resistance to crop collapse. It has been shown that resistance to lodging is greater in dwarf than tall sunflower cultivars but there has been no separate analysis of stem breakage. Selection of improved cultivars requires studies of the stem anatomy to identify the features that determine stem strength and the nutritional and physiological factors that predispose stems to breakage.

The root systems of dwarf and tall cultivars explore the same soil depth and crops of both types use similar amounts of water, although the partition between transpiration and soil evaporation may be different. There is some evidence that the more compact canopies of dwarf cultivars have greater water-use efficiency than the more open canopies of taller cultivars but the effect is small and restricted to the early part of the cycle.

Physiological studies have shown that the production of florets in dwarf cultivars is equally susceptible to water stress before anthesis as in tall cultivars, but the effect of stress during that period is incompletely understood. The partition of biomass between stem and capitulum during the phenophase bud visible to anthesis requires further study. An important aspect of this work should be to establish cultivar-environment relationships between biomass at anthesis or growth during some earlier period and floret production.

During seed filling, the relative importance of stem-stored assimilate in sunflower compared with cereals is a possible basis for smaller yield of dwarf cultivars. The magnitude of that contribution is such as to question the yield stability of dwarf sunflower in terminally stressed environments. However, research has demonstrated variation within dwarf cultivars in their capacity to export assimilate from stem to seed so that this difference between sunflower and cereals may be overcome provided ideotype definition can be improved by further research.

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