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OPINION PAPER

# Heterosis, stress, and the environment: a possible road map towards the general improvement of crop yield

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## Abstract

**Contemporary plant breeding is under pressure to improve crop productivity at a rate surpassing past achievements. Different research groups dealing with this issue reached similar conclusions that the solution lies in improved biomass production by way of enhanced light capture and use efficiency, modified photosystem biochemistry, and improved partitioning of assimilates to the economic part of the plant. There seems to be a consensus of sorts. This 'opinion paper' calls attention to the phenomenon of heterosis, as expressed in maize, sorghum, and other crops where, depending on the case and the trait, larger biomass and greater yield have been achieved without a change in growth duration, photosystem biochemistry, or harvest index. This discussion maintains that there is no consensus about the genetics or the genomics of heterosis in regulating yield under diverse environments. Therefore, in a search for the basis of heterosis in yield and adaptation, the discussion bypasses the genetics and searches for answers in the phenomics of heterosis. The heterotic phenotype in itself provides challenging and important hints towards improving the yield of open-pollinated crops in general. These hints are linked to the homeostasis of photosynthesis with respect to temperature, the photobiology of the plant as mediated by phytochrome, the architectural foundations of the formation of a large sink, and the associated hormones and signals in controlling sink differentiation and source–sink communication. This discussion does not lay out plans and protocols but provides clues to explore within and beyond the current thinking about breeding for high yield.**

**Key words:** Biomass, flowering, heterosis, hormones, hybrids, light, maize, phytochrome, photosynthesis, plant breeding, plant competition, sorghum, source–sink, stress, temperature, yield.

## Introduction

Plant breeding has been successfully increasing major crop yields at mean historical rates of ~1% per annum, depending on the crop, the environment, and the specific study. Much has been achieved by increasing the harvest index (HI) and less has been achieved by increasing basic plant productivity in terms of converting solar irradiation into biomass. The route for improving yield by increasing the HI in the cereals is approaching its end.. Breeders are still extracting yield increases from the available germplasm, but the future for raising plant production and potential yield is under serious debate.

It is no surprise, therefore, that this subject, combined with worries about global climate change and population increase, compel the scientific establishment to seek a solution. A popular direction is an intervention in the biochemistry of photosynthesis, as the foundation of plant carbon assimilation and biomass growth. Two major ambitious routes are noted: attempts at modifying $C_3$ metabolism of rice (*Oryza sativa*) into $C_4$ (von Caemmerer *et al.*, 2012) and modifying the biochemistry of photosynthesis and assimilate use efficiency in $C_3$ wheat (*Triticum aestivum*) (Reynolds *et al.*, 2009; Parry *et al.*, 2011). Both endeavours are important, but the results are not close at hand. Alternatives and additions to this major thrust should not be overlooked.

Heterosis has been used to obtain impressive steady increases in crop yields for >90 years (e.g. Duvick, 2005), and research to understand this enigmatic phenomenon followed suit. This 'opinion paper' suggests that certain phenotypic, physiological, and agronomic manifestations of heterosis offer interesting if not exciting hints for possible ways to improve crop yield, not necessarily by way of heterosis and hybrid production *per se*. As has been the case for other problem-solving matters in plant breeding, the solution sometimes rests within the interdisciplinary domain rather than with the unique expertise, be it molecular, physiological, or genetic.

Thus, in order to derive hints and clues, one must first recognize in a very concise manner what is known about heterosis, not as a (huge) collection of experimental data and opinions but as a consensus, if at all.

## The genetic basis of heterosis in plants: is there a consensus?

The orthodox conventional long-term argument has been that heterosis is controlled by dominance and/or overdominance gene actions (Lippman and Zamir, 2007; Birchler *et al.*, 2010; Sanghera *et al.*, 2011; Kaeppler, 2012; Schnable and Springer, 2013). Debates on the universal validity of this explanation are still ongoing. Over time and depending on the specific study and the crop, epistasis has been identified as part of the control of heterosis, mainly in rice. This was especially true for complex characters such as yield. For example, Yu *et al.* (1997) found in rice that dominance and overdominance had little effect on heterosis for yield and its components, while epistasis was found to have a major effect in this respect. Epistasis was found to be important in rice heterosis also in the control of simpler traits such as heading date and plant height (Yu *et al.*, 2002). In their theoretical framework for the resolution of epistasis, dominance, and overdominance effects on heterosis, Melchinger *et al.* (2007) referred to the epistasis effect by the term 'augmented dominance effect'. Birchler *et al.* (2010) tended to conclude that where the effect of these three gene actions is considered, the relative role of each might be related to the trait in question.

In theory, overdominance heterosis can and should be expressed also on a single gene basis. Evidence for plants has been obtained in two cases. The *Ma* gene of sorghum (*Sorghum bicolor*) controls photoperiod sensitivity and flowering time. Using nearly perfect isogenic lines, Quinby and Karper (1946) demonstrated heterosis in the *Mama* genotype which was expressed as a greater plant size for the same growth duration. This was interpreted as heterosis in cell number due to an enhancement of the rate of cell division. This explanation of heterosis has been an undercurrent in ongoing discussions from 1936 (East, 1936) to the present time (e.g. Birchler *et al.*, 2010). In a second case for single gene heterosis, Krieger *et al.* (2010) provided evidence for heterosis due to heterozygosity for two tomato (*Solanum lycopersicum*) mutant alleles of the SFT (SINGLE FLOWER TRUSS) gene. Heterosis was expressed in the brix yield of fruit. It is interesting that in the case of both sorghum and tomato, single gene heterosis involved genes which directly or indirectly regulate flowering. Gene expression profiling in *Arabidopsis thaliana* (Ni *et al.*, 2009) suggested that genes involved in circadian rhythm, such as LHY (LATE ENLONGATED HYPOCOTYL) and CCA1 (CIRCADIAN CLOCK ASSOCIATED 1), both MYB-like transcription factors, were associated with heterosis

On the other hand, a rather simple mechanistic explanation of heterosis of complex traits such as yield is defined as 'component complementation' or 'multiplicative heterosis'. Grafius (1959) was among the first to discuss component complementation for grain yield. For example, heterosis in the hybrid is expressed in grain yield, where one parent contributes a high grain number per spike and the other parent contributes a high number of spikes per plant. Melchinger *et al.* (1994) later reiterated this for the case of *Vicia faba* and developed a theoretical framework for multiplicative heterosis. Lippman and Zamir (2007) discussed the apparent need for dealing with the components of a complex trait such as yield in order to resolve gene action and multiplicative heterosis.

Molecular tools are widely considered to hold promise for the dissection of heterosis in grain yield and other complex traits. For example, earlier work by Stuber *et al.* (1992) evaluated 76 molecular markers over 3168 plots (nearly 100 000 plants) grown in three US states. Hybrid grain yield was found to be associated mainly with overdominance effect quantitative trait loci (QTLs). On the other hand, a more recent detailed study in maize by Frascaroli *et al.* (2012) underlined the importance of the dominance effect for QTLs that were associated with agronomic traits.

Kaeppler (2012) reviewed past attempts to develop a unifying theory of the genetic basis of heterosis, from the early dominance theory to more recent genome-wide molecular investigations. His convincing conclusion is that there are many and diverse molecular mechanisms that translate DNA into phenotype and it is the combination of all these mechanisms across many genes that produces heterosis in complex traits such as yield. This conclusion is compatible with many previous questions raised about the complex nature of heterosis when viewed across the plant kingdom. With the emerging evidence for epigenetic regulation of heterosis (Tsaftaris and Kafka, 1997; He *et al.*, 2011), the genetics of heterosis seem to be more complex as the biological tools for its dissection become more sophisticated. Recent genomic research is attempting to dissect heterosis by first resolving gene expression in hybrids as being different from that in parents. This route has been defined by Birchler *et al.* (2010) as 'ambiguous as to whether any observed changes (in gene expression in hybrids) are correlative, causative, or predictive of heterosis'.

Therefore, there is still no scientific consensus on the genetic basis of heterosis in plants. In this respect, it remains an enigma. Consequently, in a search for the basis of the advantage of heterosis in yield and adaptation, this analysis bypasses the genetics and genomics of heterosis and looks for answers in the phenomics of heterosis.

## The metabolic/physiological expression of heterosis in plants: is there a consensus?

Heterosis has been phenotypically expressed in numerous and various metabolic and physiological traits (e.g. McDaniel and Frankel, 1986; Stuber, 1994; Tsaftaris and Kafka, 1997; Coors and Pandey, 1999; Goff, 2010). Various and different suggestions were offered as physiological explanations of the heterotic phenotype, ranging from hybrid enzymes to energy efficiency. The impression a reader will receive from the different reviews is that a consensus is not agreed upon.

It might be useful to look first for answers at the whole-plant level. The typical and general heterotic plant phenotype is large in size (i.e. 'hybrid vigour'), as compared with its parents or common open-pollinated varieties. This size advantage is expressed in greater biomass, commonly for the same growth duration as the parent materials. Convincing metabolic, physiological, or molecular arguments must first explain this large phenotype. Without such a link, explanations of heterosis remain episodic or dependent on the case studied. 'Hybrid enzymes', 'mitochondrial metabolism', 'metabolic flux', or 'metabolic balance' might have explained certain feature of heterosis depending on the specific study or the review, but without a link to the basically large heterotic phenotype a consensus cannot be reached.

Larger size as a typical heterotic phenotype is mainly attained via a greater cell number rather than a greater cell size, as suggested by various studies, since that of Quinby and Karper (1946) to the more recent reviews (e.g. Birchler *et al.*, 2010). In most cases of heterosis in crop plants, and even in *Arabidopsis* (Meyer *et al.*, 2004), the seedling is already larger than its parents. Therefore, heterosis in the rate of cell division is set very early with the seed embryo, sometimes expressed even several days after fertilization (Meyer *et al.*, 2007). There is therefore a base level of heterosis in cell numbers which is set very early, followed by a compounding effect in cell division and organ differentiation, towards a final large plant and/or organ size or organ numbers (such as flowers). The formation of a large plant by way of a high rate of cell division and differentiation also depends on plant energy resources and assimilation. Here is where certain suggested metabolic enhancements by heterosis (e.g. Goff, 2010) can materialize into an effect towards a large-sized plant or organ.

Cause and effect should be carefully considered when heterosis is explained on metabolic and physiological grounds, with careful attention to the whole system. Observed metabolic and physiological expression in the hybrid can be taken as an explanation for heterosis or sometimes the results thereof. For example, the large root and associated greater water use in maize (*Zea mays*) hybrids is not so much driving heterosis (Araus *et al.*, 2010) as rather being the result of heterosis (Blum *et al.*, 1977; Hoecker *et al.*, 2006), which indeed may confer an advantage to the hybrid under certain growing conditions. Similarly, increased assimilate partitioning to the grain is considered as a partial explanation of heterois in maize (Tollenaar *et al.*, 2004; Tollenaar and Lee, 2006). However, increased partitioning can also be taken as a result of the basic heterosis in grain number, which constitutes a demand that drives assimilates to the grain (Zamski and Schaffer, 1996; Bihmidine *et al.*, 2013).

A consensus heterotic physiological phenotype should therefore be based on an inherent high rate of cell division (and organ differentiation) by which a large sink is created together with metabolic and physiological traits which constitute an effective source to sustain cell division and fill up the large sink. Photosynthesis and the availability of a carbohydrate pool must be considered as crucial in this respect.

The central role of the sink–source relationship in regulating the grain yield of crop plants has long been under constant discussion (Zamski and Schaffer, 1996). It is accepted now that the sink regulates source activity by signals which are not yet fully resolved (Bihmidine *et al.*, 2013). Sink demand can even kill the source (Thomas, 2013). The regulation involves both the current source activity and plant reserve mobilization to the sink.

If source activity is insufficient for complying with sink demand for assimilates, the sink might regulate its size to fit the reduced source. Breeders were known to create plants which have very large sinks and thus expected a yield increase. However, without a parallel increase in source effectiveness, such sinks did not meet their expectations. A classical case is the uniculm Gigas wheat lines which have an impressively large spike carrying a large number of florets (Atsmon and Jacobs, 1977). Under the conditions of a plant population, yield per unit area of the Gigas genotype was lower than that of standard wheat due to floret abortion (Atsmon *et al.*, 1986*b*). The reason for abortion was at least due to the normal rate of leaf photosynthesis in the Gigas plant (Atsmon *et al.*, 1986*a*).

It is therefore unreasonable to accept that a large hybrid plant with its large sink can realize high yield without an advantage in photosynthesis over its parents or over open-pollinated varieties. Certainly, heterosis for maximum rate or potential rate of photosynthesis has been expected and envisaged but not confirmed in all experiments as a universal expression of heterosis. Results varied with the specific study, crop species, or environment. In maize, for example, heterosis was seen in crop assimilation after grain set due to delayed leaf senescence and/or erect leaf configuration in the canopy (Tollenaar *et al.*, 2004), but not due to an inherent advantage in maximum leaf photosynthetic rate.

The question is, therefore, whether with the current state and the known boundaries of photosynthesis biochemistry there may be a universal expression of heterosis in photosynthesis which might explain a consistent strength of the source to support a large hybrid sink.

## The case of sorghum hybrids for source and sink strength

Sorghum hybrids might be just one of many other cases of heterosis. However, sorghum is an excellent model plant for the study of yield heterosis: it expresses a high rate of heterosis for yield; it is well studied in terms of physiology and the genetics of ontogeny; and it is a determinate open-pollinated plant lacking any inbreeding depression.

Heterosis in sorghum (reviewed by Blum, 2004) is expressed in biomass production, with little or no effect on HI. Biomass increases in the hybrid, with very little change in plant height and even with some reduction in growth duration, as compared with the parents. Thus heterosis is generally expressed as a high plant or crop growth rate. Leaf area per plant and leaf area index (LAI) show initial heterosis during the early growth stages, but this heterosis is not sustained during and after flowering. It appears that the larger developing panicle in the hybrid competes with the growth expansion of the last 3–4 leaves which tend to limit the expansion of LAI towards panicle exertion. The initial plant vigour is already seen in seedling shoot and root size. Thus, the greater biomass and dry matter accumulation in the hybrid is at least partly a compounding result of the initial seedling vigour and its large leaf area, up to about the boot stage. Subsequently, most growth heterosis is invested in the panicle. The larger root is largely a function of heterosis in the growth rate of crown roots.

Heterosis for grain yield of sorghum is expressed exclusively in a large number of grains per panicle. Furthermore, progress in hybrid yield improvement over 30 years materialized exclusively through a larger panicle (Miller and Kebede, 1984). A large number of flowers or fruit per plant is the typical if not the common yield component affected by heterosis as expressed on the basis of the single plant and the population. The sorghum panicle consists of axial whorls of branches which carry the spikelets. Heterosis in the number of grains per panicle is largely expressed in the basal whorls of the panicle (Blum, 1970). The differentiation of branch whorls and spikelets proceeds acropetaly. When panicle differentiation was studied in a heterotic sorghum hybrid and its two parents (Blum, 1977), it was found that the hybrid had a time lapse of 4 d between the termination of the differentiation of panicle branches and the onset of spikelet initiation on the branches, while no lapse was seen in either parent. As suggested by Lee *et al.* (1974), such a time lapse allowed more spikelets to be formed, especially at the basal panicle branches. Furthermore, the hybrid had a larger apical dome at the onset of panicle initiation, as compared with its parents (Blum, 1977). However, the larger apical dome in the hybrid was not a result of a longer vegetative period. The duration of the vegetative period in the hybrid was even slightly shorter than that in both parents. The larger apical dome could therefore be traced to a larger seedling in the hybrid, indicating that at least part of the potential for panicle size is already determined at the seedling growth stage and most probably in the seed embryo. Thus, yield heterosis in sorghum involves an initial advantage in the seed embryo and the emerging seedling, followed by compounded growth and programmed differentiation of the apical meristem leading to a large panicle of many spikelets, florets, and grains within less time than in the parents. This indeed can be defined as 'magic' (Lippman and Zamir, 2007; Sanghera *et al.*, 2011).

Setting and filling a large number of grains per plant as well as providing for a large root in the hybrid require extra assimilates. The development of a greater LAI in the hybrid (until the boot stage) cannot fully account for a typical 25% grain yield increase in addition to the larger stover and root biomass in the hybrid over that of the best parent. Thus, hybrids must have more effective assimilation machinery per unit leaf area than parents.

General heterosis for potential or maximum photosynthesis or carbon exchange rate (CER) was not clearly seen in sorghum (Khanna-Chopra, 1982). It appeared that maximum leaf CER in hybrids was largely dependent on the specific cross and the environment (Hofmann *et al.*, 1984; Kidambi *et al.*, 1990).

Sorghum leaf CER was measured over a range of leaf temperatures which were raised from 32 °C to 43 °C in four hybrids and their parents (Blum, 1989). While the optimum temperature for CER was ~36–38 °C, heterotic hybrids expressed heterosis for CER at the optimum temperature as well as at suboptimal or supraoptimal temperatures, depending on the specific hybrid. The integrated CER over the whole range of temperatures measured (i.e. the area under the temperature response curve of CER) was by far larger in the three heterotic hybrids than in their parents. To a large extent, heterosis for CER over different temperatures corresponded (not perfectly) with heterosis for leaf conductance. Homeostatic heterosis for CER over a wide range of leaf temperatures and drought stress conditions was repeated in another study with two heterotic hybrids (Blum *et al.*, 1990). Heterosis for CER was maintained over a wide range of environmental conditions (including variable leaf temperatures and leaf water status) which were expressed in mean CER over all genotypes between 10 μmol $m^{-2}$ $s^{-1}$ and 40 μmol $m^{-2}$ $s^{-1}$. Undoubtedly heterotic sorghum hybrids for yield express homeostatic photosynthesis with respect to temperature which is at least partly associated with enhanced stomatal conductance. Similar results were obtained with cotton (*Gossypium hirsutum*) hybrids where heterosis in net photosynthesis was maintained at high temperatures (Zeng *et al.*, 2011).

Sorghum hybrids also tend to grow better than their parental lines or standard open-pollinated cultivars at low (chilling) temperatures during germination and seedling growth (Pinthus and Rosenblum, 1961; Blum, 1969; Yu and Tuinstra, 2001).

Homeostasis of heterosis with respect to temperatuire in plants has been recognized since the early pioneering work of McWilliam and Griffing (1965) in maize and of Griffing and Zsiros (1971) with *Arabidopsis*. The former study concluded that 'the higher yields of the hybrids were due to the greater phenotypic stability over the entire temperature range'. Evidence for temperature-dependent heterosis was also seen in freezing tolerance of *Arabidopsis* (Rohde *et al.*, 2004), freezing tolerance of wheat hybrids (Parodi *et al.*, 1983), and chilling tolerance of rice hybrids (Kaushik and Sharma, 1986; Kwon *et al*., 2002).

The reduction of photosynthesis at high temperatures is directly linked to the thermal sensitivity of Rubisco activase (Salvucci and Crafts-Brandner, 2004). Tobacco (*Nicotiana tabaccum*) transformed with a Rubisco activase gene inserted in the antisense orientation was compared with untransformed controls (Sharkey *et al.*, 2001). High temperature

(42 °C) reduced photosynthesis in both lines. However, photosynthesis recovered nearly completely in wild-type plants and very little in plants lacking Rubisco activase. Kurek *et al.* (2007) found that thermostable Rubisco activase variants of *Arabidopsis* exhibited higher photosynthetic rates, improved development patterns, greater biomass, and increased seed yields as compared with the lines expressing the wild-type form. Heterosis expressed in superior thermostability of photosynthesis can be enhanced by thermostable variants of Rubisco activase.

Homeostatic heterosis for photosynthesis was also observed for chilling temperatures. Hybrid maize had a more stable photosystem II than its parents when subjected to chilling stress (Kočová *et al.*, 2009). Maize hybrids subjected to moderate chilling stress showed positive heterosis particularly in the volume density of granal thylakoids of mesophyll chloroplasts (Kutík *et al.*, 2004). Maize heterosis under chilling stress was found for the Hill reaction (Körnerová and Holá, 1999) and for the Hill reaction and photosystem I of isolated mesophyll chloroplasts (Holá *et al.*, 1999).

## The case of maize hybrids and plant competition

Heterosis for yield is expressed on the basis of a plant population. Plants growing in a typically dense population are subjected to stress which has been defined as ‘high plant density stress’, ‘high plant competition stress’, or ‘crowding stress’.

The classical crop response to increased plant density and crowding is expressed in a typical optimum curve. Population yield increases while yield per plant decreases to a given plant density of maximum yield, after which the continued reduction in yield per plant with the increased density begin to reduce population yield. Thus, maximum yield is achieved with a population of undersized stressed plants. The primary strain under crowding stress is considered to be shading. Plants in a dense population try to avoid shading by investing energy and resources in modifying growth and shape (Aphalo *et al.*, 1999).

Single hybrid plants have a relatively large leaf area, intercept more light, and assimilate more than their parents. This relative advantage is diminished as plants are crowded towards mutual shading (Wells *et al.*, 1989). It is therefore expected that the inherently larger maize or sorghum hybrid plant would be more sensitive to plant competition than its smaller sized parents. However, it was found in maize that the rate of heterosis for grain yield and HI increased with the increase in plant density (Liu and Tollenaar, 2009*a*). Furthermore, modern superior maize hybrids were found to yield more under high plant density than older ones, thus being defined as resistant to high density stress (Tollenaar and Wu, 1999). As maize hybrids were selected for higher yield by way of improved parents and heterosis, they were genetically shifted towards greater adaptation to crowding, despite being inherently large in size.

Maize heterosis in these studies was ascribed to greater LAI, better light interception (due to more erect leaf configuration), and delayed leaf senescence (Tollenaar *et al.*, 2004). The increase in HI was also used as an explanation, but HI is a calculated end-result rather than a true physiological explanation. Plant density tolerance has also been ascribed to reduced interplant variability, which reduces competition and thus promotes the productivity of the population as a whole. Indeed, a population of non-competitive plants has long been recognized as conducive to high yield (Reynolds *et al.*, 1994). The shorter dwarf cereal plant ideotype as associated with the ‘green revolution’ may have contributed to greater crowding tolerance. This is not compatible with the crowding tolerance of the basically large hybrid maize plant. What is the strain caused by crowding stress and what imparts crowding tolerance to the plant?

In an experiment at a plant density of four plants $m^{-2}$ it was found that maize heterosis for grain yield increased with shading treatments during the pre-silking and silking growth stages (Liu and Tollenaar, 2009*b*). It is not clear why heterosis increased with shading. The expression of heterosis in photosynthesis was found to be greater at high than at low irradiance in maize (Li *et al.*, 2007), cotton (Zeng *et al.*, 2011), and *Arabidopsis* (Meyer *et al.*, 2004; Fujimoto *et al.*, 2012). The advantage of an improved high-yielding wheat variety over older ones was especially prominent under high irradiance (Blum, 1990).

Shading and high density in the maize experiments as discussed above must have modified the quality of light within the population. Plants in a community are subjected to photobiological signals besides the level of solar irradiance and the interception of photosynthetically active radiation. These signals as sensed and modulated by the phytochrome complex are crucial in regulating plant response to crowding in terms of plant morphology and function (e.g. Smith, 2000; Sawers *et al.*, 2005; Carvalho *et al.*, 2011; Casal 2013*a*, *b*).

The earliest signal of light quality modification upon crowding is a reduction of the red:far-red light ratio (R:FR), caused by far-red light reflection from neighbouring plants. Plants sense this change through their phytochrome photoreceptors which regulate a signal transduction cascade also involving biosynthesis and transport of the plant hormone auxin (Keuskamp and Pierik, 2013). Auxin is deeply involved in the phyllotaxis of the stem apical meristem (Sassi and Vernoux, 2013) which can determine inflorescence size.

Upon sensing the proximal photobiological signal in a dense population, plants invest resources in coping with crowding, which can affect the productivity of the population. The R:FR light ratio signalling of plant proximity in a population can be an early warning signal which precedes a situation of low irradiance for photosynthesis and thus an insufficient plant carbon pool for setting seed—the latter being the target of plant evolution. This early warning system is comparable with root abscisic acid (ABA) signalling which causes stomatal closure and even reduced fertility before leaf water status has been affected by the drying soil (Davies *et al.*, 2005). Reducing the signal or the sensitivity of the plant to the signal might perhaps improve productivity (in both cases). For example, divergent selection for leaf ABA content in maize indicated that low leaf ABA content was associated with higher yield (Landi *et al.*, 2001).

It is therefore not surprising that phytochrome and R:FR light ratio manipulations were found to affect crop yield. A low R:FR light ratio reaching the stem reduced grain yield in sunflower (*Helianthus annuus*) (Libenson *et al.*, 2002). Increased phytochrome B alleviated plant density effects on tuber yield of field potato crops (Boccalandro *et al.*, 2003). Light-regulated overexpression of an *Arabidopsis* phytochrome A gene in rice altered plant architecture and increases grain yield (Garg *et al.*, 2006). Phytochrome B mRNA expression enhances biomass yield and physiology of cotton plants (Rao *et al.*, 2011). Sawers *et al.* (2005) pointed out that phytochrome manipulation results can be quite different depending on the specific plant architecture in question.

Whereas phytochrome is also involved in mediating photoperiodism and flowering (Jackson, 2009), it is interesting to note here that the only cases of a single gene heterosis for yield were observed for genes which regulate flowering in sorghum and tomato (see above). It might not be a coincidence perhaps that the high yield achieved in most green revolution crop plants involved a change towards dwarfing and photoperiod insensitivity, which again might be linked to phytochrome biology. Another interesting clue towards this issue is the Gigas wheat which had a very large ear under short days but lost this phenotype and became stunted under long days (Atsmon *et al.*, 1986*a*).

## Synthesis and conclusion: hints towards crop yield improvement

The thesis discussed above is based on old and new research results spanning over some 40–50 years. When taken together, they lead to certain conclusions and even speculations. These can be justly debated and challenged, hopefully with the benefit of improving crop yield.

The preceding discussion indicates that there is no consensus about the genetic basis of heterosis, especially in regulating a complex trait such as yield. It was therefore proposed here to examine the phenomics of heterosis with respect to yield and its improvement in different environments and crops.

Stress is the norm. Optimum conditions rarely occur for an extended time during the season or even during the same day. ‘At the end of the day’ the heterotic hybrid will most probably assimilate more than its parents over the natural range of daily change in temperature, light, and photobiological signals, notwithstanding other cues such as soil moisture, wind, or low atmospheric vapour pressure deficit which can affect leaf temperature and thus assimilation.

Recent advocates for achieving significant yield improvement in our crops understandably address the need to intervene in basic biochemistry of photosynthesis, targeting maximum potential capacity (see above). The lesson learned from heterosis under environmental change in the field points to the homeostasis of photosynthesis over a broad range of environmental conditions as the basis for a strong source. Response to ambient temperature seems to be a prime factor. Plans for improving wheat yield already consider the need to stabilize photosynthesis at high temperatures by tweaking Rubisco activase towards improved heat tolerance (Parry *et al.*, 2011), but heterosis also indicates the importance of stable assimilation at suboptimal temperatures. This is an important consideration in breeding for homeostatic photosynthesis of warm season crops (Long and Spence, 2013). Current efforts to tweak photosynthesis biochemistry towards a higher rate at optimum temperature should consider the hazardous possibility that such modifications might reduce photosynthesis at non-optimal temperatures, beyond the present normal levels.

Heterosis for carbohydrate metabolism also offers an additional clue for improving assimilate availability for sink development. An example is the case for enhanced leaf sucrose phosphate synthase activity observed in heterotic maize hybrids (Causse *et al.*, 1995). Carbohydrate metabolism is part of the engine for enhancing assimilate availability to the sink or a storage mechanism for supporting the sink without photosynthesis. Carbohydrate storage and its remobilization is a crucial component of breeding for source strength under stress such as high temperature (Blum *et al.*, 1994). Starch or fructan metabolism in support of grain yield is now receiving more attention (e.g. Zhang *et al.*, 2009), but not as much as needed.

An important contribution to the strength of the photosynthetic source in hybrids is initial leaf area growth which develops into effective light interception machinery. In hybrids, a large leaf area is a compounded effect beginning with seedling vigour. Seedling vigour as a major component of heterosis in maize, sorghum, and other plants points at three important yield-supporting traits expressed in their size: leaf area per plant, root size, and sink size. Seedling vigour most probably begins with the seed embryo. If it begins with the embryo, then all these three components trace back to a high rate of cell division, which again is a major secret of heterosis. The cases of sorghum, maize, tomato, and other crops indicate that a large sink in terms of flowers per plant is basically an advantage in ontogeny, differentiation, and morphogenetics. In determinate plants such as the cereals, the stem apical meristem (which is the foundation of heterosis for sink size) develops into a large inflorescence through an exact design of phyllotaxis proceeding from leaves to the inflorescence. This design is regulated by the hormone auxin on one hand (Sassi and Vernoux, 2013) and gibberellic acid (GA) on the other (Foster *et al.*, 1994), with the intervention of phytochrome (Reed *et al.*, 1996).

A large sink is not just a matter of reducing flower abortion, but it is a matter of basic structural architecture, as seen in how the large heterotic panicle is formed in sorghum on one hand and the case of the Gigas wheat plant on the other. This brings one to hope that researchers move on to understand the metabolic and physiological basis of sink architecture.

Turning to the greater expression of maize heterosis under high competition brings up the possible role of phytochrome in controlling plant size under crowding stress. A link between photobiology and hormones such as GA in affecting sink size can be suspected, beyond what is already known about GA, semidwarfism, and the high yield of modern photoperiod-insensitive cereals. Intervention in the phytochrome complex and the signalling network is a potential lead towards dense high-yielding plant populations. It is interesting to note here a news item released by Stine Seed Company (Adel, IA, USA) in 2013 announcing the deployment of high plant density agronomy in their maize and soybeans breeding programmes (http://www.stineseed.com/about-stine/news-releases). The work by Tollenaar and associates must have been the impetus in this respect.

Certainly specific abiotic stress resistance is important in constructing a stable high-yielding genotype, and information on the subject is growing exponentially, if not exploding. Still the most crucial impact of stress is the direct hit upon a potentially large sink which reduces fertility of flowers, florets, and pods due to stress temperatures and ABA produced in response to other stresses such as water deficit or various soil impediments. The interaction between ABA and carbohydrates can be important for maximizing grain setting (e.g. Setter and Parra, 2010). The reduction in plant ABA content (Landi *et al.*, 2001) or reduced ABA sensitivity might also hold promise as sites for intervention.

This ‘opinion paper’ does not draw an exact and detailed road map towards yield improvement but offers some thoughts and hints pointing at roads which might lead to that destination. The heterotic crop phenotype can serve as a compass, irrespective of its undecided genetic control. Therefore, the design of a high-yielding crop plant is an integrated venture beginning with the seed embryo, through plant morphogenesis, homeostatic photosynthesis, and the photobiological sensory regulation of the plant, from its basic individuality to its compatibility with a dense population. The issue here is coping with the normal everyday stress conditions in the field in terms of sink design and a homeostatic source capacity.

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