The importance of grain or kernel number in wheat: A reply to Sinclair and Jamieson

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Abstract

This paper is a response to Sinclair and Jamieson [Sinclair, T.R., Jamieson, P.D., 2006. Grain number, wheat yield, and bottling beer: an analysis. Field Crops Res. 98, 60–67] who propose that bulk carbon and nitrogen accumulation are fundamental to grain yield determination in wheat (*Triticum aestivum* L.), while challenging the common approach to yield through the separate processes of grain number determination, followed by grain filling, as governed by source–sink balance then. The response focuses on yield determination under potential conditions for which genetic and agronomic progress is clearly associated with increased grain number, herein abbreviated to KNO (kernels m^{-2}). It argues that grain yield in modern cultivars is still limited by post-anthesis sink (KNO) and that understanding KNO determination is therefore useful for predicting physiological routes to higher yield. KNO determination appears to be strongly related to dry matter accumulation in spikes at anthesis (g m^{-2}), governed by events in the last 20–30 days before anthesis, while some modern cultivars show higher grain number per unit spike weight. Post-anthesis photosynthesis and crop dry weight accumulation have increased as KNO has increased with breeding. There is no evidence for effects of N on KNO apart from those operating via dry matter accumulation, or for grain N demand limiting post-anthesis photosynthesis. Beyond this simple model, several other linkages that might exist between the pre- and post-anthesis periods are explored. Such linkages could help maintain the balance between the post-anthesis sink and the source required to fill the sink, and constitute common underlying processes which to some extent reconcile the model of Sinclair and Jamieson (2006) with current mainstream thinking about grain yield in wheat. Reports of an increasing amount of pre-anthesis carbohydrate reserves in the crop with breeding progress is a good example, but overall it is concluded that at least under potential conditions, the commonly accepted approach to grain yield determination is not invalidated by Sinclair and Jamieson (2006).
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1. Introduction

Sinclair and Jamieson (2006) recently proposed that grain number (hereafter referred to as kernel number, KNO, with units of m^{-2}) does not determine wheat grain yield (GY, g m^{-2}), but is rather the consequence of yield, which along with KNO, is the consequence of the crop's ability to gather resources. They used the analogy of a brewery to illustrate this view: the bottle supply represents grain number, and is seen not to limit brewery capacity, representing grain yield, for the brewery simply orders up bottles to match beer production. More significantly, they argue that the strong KNO versus GY associations, commonly reported in studies of the effect on grain yield of agronomic factors and of breeding progress, are not useful in predicting the way forward. It is important to consider this challenge to those many crop physiologists who have concluded otherwise in their attempts to assist yield improvement.

Briefly summarizing the Sinclair and Jamieson (2006) paper, the first section, on the pre-anthesis period, concludes that bulk resource capture is the key in setting up yield possibilities, and that this may involve not only acquisition of reduced carbon (C) but also reduced nitrogen (N). Discussion in the next, post-anthesis section, brings forth examples when there is not enough assimilate or C to fill more grains (e.g., post-anthesis water stress), with the implication that this is a general situation, and may involve N as a co-limiting post-anthesis resource. The critical role of N pre- and post-anthesis is pursued further in the third section of the paper, where it is argued that high early N accumulation is essential to prevent "self

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destruction'' of the photosynthetic machinery during grain filling as N is translocated to the growing grains; this is strengthened *inter alia* by some unsupported assumptions on N accumulation and reported genetic progress in Mexico building on the results of Sayre et al. (1997). Finally the paper uses a wheat data set, with variation in location, cultivar, and water and N supply, to show that grain yield can be modelled satisfactorily without even considering KNO. This comes from a model (Sinclair and Amir, 1992) in which ''crop mass and nitrogen accumulation are simply partitioned to bulk grain during the grain growth period'', these becoming the critical processes for yield.

In discussing the paper, remarks here are confined to potential growing conditions, with water and N non-limiting, but with one small diversion into N deficiency and nitrogen's role. Potential conditions are perhaps a subset of what the authors have embraced, but none the less an important subset, for example over 50% of the developing world's wheat production comes from irrigated conditions approaching potential ones. This is also an easier domain to discuss and a logical starting point for understanding situations with water and N limitation (see also Slafer et al., 2005). Nor are modelling approaches considered here: parsimonious models are to be applauded if they work well, and they often do where a single factor like water or nitrogen is limiting, but genetic (and agronomic) advance in yield potential appears to be more complex.

Man's interest in a crop is to maximize the production of filled grains at as many grain sites as possible, and to do so, the crop must optimize its use of limited resources in both building and filling these sites. The statement that KNO ''can be considered more as a consequence of yield than a determinant'' (Sinclair and Jamieson, 2005, Abstract), implying that both KNO and GY are limited by the crops ability to gather C and N resources, is difficult to comprehend. KNO is largely determined before yield itself: extra grains cannot be called up during grain filling (but see later) if post-anthesis resources are abundant, nor discarded if resources falter. In terms of the analogy, the brewery must produce the bottles, and do so largely before filling them, different and possibly competing processes, which must be optimized to give maximum grain production. It is obvious from the literature that increased KNO has proved a necessary, if not sufficient, condition for improvement in yield potential in the hands of breeders and agronomists over the last 50 years. Two questions can then be fairly asked of this approach, as do Sinclair and Jamieson: (1) whether greater KNO is a sufficient condition for further yield increases (can more grains be filled other things during the post-anthesis period remaining equal), and (2) whether understanding the determination of KNO can help? This paper will deal with the second question first, as it arises earlier in the development of the crop, and because it will then be argued that the answer to the first question is affirmative.

2. Determination of kernel number

Sinclair and Jamieson (2006) have presented a limited picture of research on KNO determination, and are unclear on the supposed link to bulk C and N resource accumulation. However in the last 30 years or so, a great deal has been published on the subject in wheat, certainly much more than these authors care to cite:

(a) Early studies focussed on the numerical components of kernel number (number of plants, spikes, spikelets, florets per spikelet and grains/floret (grain set)), but they did do not indicate any unique path to greater KNO. Championed by the writings of Donald (e.g., Donald, 1963), crop physiologists quickly learnt that component variation needed to be studied in the field crop where competition for resource supplied on an area basis was the key factor, and meaning that treatments, whether agronomic (e.g. high seeding density) or genetic (e.g. heavy tillering or branched spike genotypes) aiming for a large KNO, usually fail to deliver more kernels.

(b) Total dry weight at anthesis, as an index of resource accumulation, does not always correlate well with KNO, or yield, even when there is adequate water. The simple comparison of spring and winter wheats in southern Australia (Gomez-McPherson and Richards, 1995), each set planted so as to flower at the same date in the spring, indicated greater mass with the longer cycle varieties in each case, but no greater KNO. Short-term environment manipulation, such as treatments with shading and thinning, CO_2 fertilization, and temperature and photoperiod change, applied to field crops, as well as natural variation in radiation and temperature, are a more powerful tool for understanding the timing of KNO determination. It was found that, rather than the total growth period from seedling emergence to anthesis, the much shorter period immediately preceding anthesis is most critical for KNO determination in the wheat crop (e.g., Willey and Holliday, 1971; Fischer, 1975; Evans, 1978; Wall, 1979; summarized in Fischer, 1985). This corresponds to the last 20 or 30 days before anthesis, commencing at penultimate leaf emergence, and ending very soon after 50% spikes showing first anthesis, a period when >95% of the spike growth occurs.

(c) It became apparent that the mass of spikes at anthesis (SDWa, g m^{-2}) is often a good predictor of KNO for any given cultivar. A simple illustration of this is that across the large variation in weight per spike between culms within a plot, ranging from huge spikes with many grains found at the plot end facing the equator to small spikes with a few grains belonging to second order tillers within the plot, the same relationship between competent floret number, kernel number, and spike mass, applies, a relationship driven by a cultivar-specific average amount of spike mass per competent floret, a significant dry weight cost for a grain-bearing site, which is approximately 10 mg in the case of the variety Yecora 70 (Fischer, 1984). Bindraban et al. (1998) confirmed the much closer relationship of KNO to SDWa than to biomass accumulation at anthesis across a range of sites, sowings and cultivars. More precise experiments under controlled environments pointed to a tight relationship between spike dry weight accumulation and floret survival (Fischer and Stockman, 1980; Mirralles

et al., 2000). These observations also suggest that those many studies, some cited by Sinclair and Jamieson (2006) such as Whingwiri and Stern (1982) and Sibony and Pinthus (1988), which argue that floret survival is related to fast floret development such that florets reaching a certain size by a given critical relatively early stage of overall spike development will be the survivors, could be more simply interpreted in terms of spike dry weight accumulation (see also Toyota et al., 2001).

(d) Following on the above, a model of KNO determination has been proposed by Fischer (1984) in which:

$$KNO = SDWa \times \frac{K}{SDWa} \qquad (1)$$

and

$$SDWa = Ds \times CGR \times Ps \qquad (2)$$

where K/SDWa is the number of kernels per unit spike weight, Ds is the duration (300 day degrees above 4.5 is suggested in Fischer, 1985) of the spike growth period referred to above, CGR is the rate of accumulation of dry weight then, and Ps, the proportion of this dry matter partitioned to the spike. This relationship is of course only useful if the components are relatively independent and can be measured and understood. Certainly CGR is well understood and the basis of all simulation models of crop growth. And early on with this KNO model, it seemed that environmental effects under potential conditions could be understood largely through effects on CGR (solar radiation) and Ds (temperature and photoperiod), while genetic effects seemed to operate largely through Ps, with semidwarf wheats had higher Ps than tall ones (Brooking and Kirby, 1981; Fischer, 1984; Fischer and Stockman, 1986; Siddique et al., 1989; Youseffian et al., 1992)). More recently in a thorough study of variation amongst short modern Argentine cultivars, differences in KNO were associated largely with differences in K/SDWa (Abbate et al., 1998). There is some evidence that the spike is a preferred sink under shading (Fischer, 1985; Abbate et al., 1997), while one experiment showed remarkable constancy of Ps in one cultivar in the face of simultaneous change in meristematic potential of the spike and assimilate supply (Fischer, 2007). And most recently, there is a suggestion that CGR just before anthesis has improved in the most modern short cultivars, with indirect evidence from Mexican spring wheats (Fischer et al., 1998) and direct evidence for UK winter wheats (Shearman et al., 2005). In this context it is worth noting that recent yield progress in japonica rice (*Oryza sativa* L.) in Japan is associated with more grains, greater CGR just before anthesis, and higher canopy N then (T. Horie, personal communication). Genetic progress in maize (*Zea mays* L.), also associated closely with KNO, is related somewhat to greater CGR at silking, but more so to assimilate partitioning to the inflorescence (Tollenaar and Lee, 2006; Luque et al., 2006).

(e) Sinclair and Jamieson (2006) cite Abbate et al. (1995) to support the notion that grain number bears a stronger relationship to spike N content (g m^{-2}) than to spike mass (g m^{-2}); the relationship appears close ($r^2 = 0.74$) but does not pass through the origin, meaning there is no unique amount of spike N per grain, and the relationship is dominated by effects of shading on spike N concentration. Also sampling to determine SDW was at one week after anthesis, when differences in anthesis date can interfere if grains are not removed from spikes. It is useful to look at several more targeted data sets, where in addition N fertilizer amounts and timings have been varied substantially, papers actually cited by Sinclair and Jamieson (Fischer, 1993; Demontes-Meynard et al., 1999; Demontes-Meynard and Jeuffroy, 2004). These show stronger relationships of grain number to spike mass than to spike N. For example with the data set of Fischer (1993), KNO (range 5000–18,000 m^{-2}) was correlated almost as well with spike N content (g m^{-2}, $r^2 = 0.924$) as with SDWa ($r^2 = 0.951$), but this is because SDWa dominates the determination of spike N content. The issue is best revealed by dividing by SDWa, then looking at the relationships between K/SDWa and spike %N. Calculating K/SDWa (range 84–107 g^{-1}), it showed zero correlation ($r^2 = 0.077$) with spike N concentrations at anthesis despite the large range of the latter (1.15–1.81%), such that even in the N-limited crops, there appeared to be no direct effect of N on K/SDWa, but large effects via assimilate supply. The results of Demontes-Meynard et al. (1999) also reveal no relationship between K/SDWa and spike N concentration (range 1.43–2.15%). Similar calculations on the data of Abbate et al. (1995) did show a relationship ($r^2 = 0.433$) but the sampling uncertainties mentioned above remain. Wall (1979) studying this question under potential conditions could show no response in KNO to foliar N applied precisely ahead of and during spike growth. In barley subjected to N and P treatments Prystupa et al. (2004) also confirmed the primary role of spike dry weight. It is concluded that N supply to the spikes is not having a direct effect on KNO, especially under potential conditions when soil N supply is high.

(f) So far this analysis has passed over the issue of the number of grains per competent floret, often referred to as grain set percentage, but by Youseffian et al. (1992) as fertilization ratio. This number is contained within the summary ratio K/SDWa. The number of competent florets or those florets with plump green anthers when the spike first shows anthesis seems to be the component of KNO which is linked to spike mass. Sinclair and Jamieson (2006) have reminded us of interesting early work (Rawson and Evans, 1970) showing that under normal growing conditions some varieties show poor grain set, with only about 70% of the florets competent at anthesis actually producing grains. Evans et al. (1972) suggested that those florets, which are fertilized early inhibit grain set in other competent florets through hormonal influences rather than assimilate competition. Few researchers study grain set these days because it seems that modern wheats are quite efficient in this aspect (values usually >90%: Siddique et al., 1989; Gonzalez et al., 2005, R.A. Fischer, unpublished). It is even possible that the trait has been bred out of modern wheats when the

semi dwarfing genes were introduced. Only one of five cultivars studied by Evans was semidwarf and that cultivar had the best grain set; also Youseffian et al. (1992) found higher grain set in semi dwarf wheats, but Siddique et al. (1989) did not. Fischer (2001) reported values below 90% in some semidwarf durum wheats. Other factors have been found to interfere with grain set in wheat, inducing obvious sterility, for example frost, high temperature, and drought, and in other crops (e.g., low night temperature in rice, high night temperature in cowpea (*Vigna unguiculata* L.)), but such effects are exceptional in wheat grown under potential conditions.

In summary, the above research relates KNO to resource accumulation but indicates that the situation is different to what Sinclair and Jamieson (2006) suggest, pointing to the importance of carbon accumulation and events immediately preceding anthesis. KNO can be dissected into measurable, physiologically meaningful and reasonably independent components, which has improved our understanding of KNO under potential conditions. It also brings us closer to manipulating KNO, and to understanding the possible trade offs. Thus there are some useful leads for increasing KNO through breeding. For example, understanding genetic variation in CGR during the spike growth period, and further selection focussed on related parameters then, is showing promise (Condon et al., in press). Lengthening the duration of the spike growth period (Ds) through changing its photoperiod sensitivity is a plausible approach (Slafer et al., 2001; Gonzalez et al., 2005). Understanding genetic variation in K/SDWa seems another worthwhile avenue to pursue. As well this new understanding reminds us to be wary of the pursuit of over-expressed numerical components of KNO found in some genotypes under spaced planting (heavy tillering, branched spikes, long spikes): when assimilate is limiting as seems inevitable in a crop stand, there may be no KNO advantage. Indeed the acclaimed engineering of cytokinin oxidase in the rice panicle meristem to produce more grains per panicle by Ashikari et al. (2005) may meet the same fate.

3. Sufficiency of assimilate to fill grains

Turning now to the other question raised in the Introduction, namely the sources for grain filling, it is difficult to prove experimentally that more grains can be filled if they could be produced and other things were to remain equal (the opposite is easy to establish, for example by applying low levels of gametocide (Fischer et al., 1977)). However there exists good evidence on the increase in the grain filling photosynthetic rate with increased sink strength, such as is likely to occur with increased KNO with breeding progress. Much seems to be overlooked by Sinclair and Jamieson (2006), who cite reductions in wheat in photosynthetic rate during grain filling when the sink is artificially reduced (King et al., 1967), but failed to note that the rate will also increase when the sink demand is increased (e.g., Rawson et al., 1976); Evans (1993) cites many other cases, concluding that differences between

cultivars in photosynthetic activity during grain filling may reflect differences in yield (sink strength and KNO) rather than cause the differences. Studies with tall and semidwarf wheat cultivars, including near isogenic pairs, have shown that the shorter wheat cultivars, which have less biomass at anthesis but larger KNO values because of better partitioning to the spikes, gave clearly higher post-anthesis dry matter accumulation and grain yields (Fischer, 1984; Siddique et al., 1989).

Turning to work within modern short cultivars, yield progress in short Mexican wheats is associated with greater KNO (Sayre et al., 1997), and with higher stomatal conductance and photosynthetic activity during grain filling (Fischer et al., 1998; also Fischer et al., 1981). Under these irrigated potential conditions in Mexico, there is usually no rain during grain filling so total dry weight at maturity can be used to calculate net dry matter accumulation from anthesis fairly accurately. There was a tendency for greater dry weight accumulation after anthesis in higher yielding varieties (R.A. Fischer and K.D. Sayre, unpublished), which could reflect the greater photosynthetic activity but may also derive from delayed senescence, something not very obvious with yield progress in spring wheats but, for example, quite important in progress in maize (e.g., Tollenaar and Lee, 2006). What is clear, however, in these studies, and under irrigation in Australia also (e.g., Fischer, 1993), is that grain yield was always less that net dry weight accumulation during grain filling, being around 0.7–0.9 of the latter, a ratio which shows a tendency to increase with yield progress; such a ratio below one may also be suggestive of adequacy in assimilate supply during grain filling.

Looking specifically at some of the highest yielding cultivars in Mexico, Reynolds et al. (2005) found incorporation of the LR19 *Agropyron* translocation boosted KNO and GY, 15 and 12%, respectively; net dry weight accumulation from anthesis to maturity rose by 13%; leaf photosynthetic activity increased 9% before anthesis and 21% after anthesis, with no obvious changes in stay green. In an even more convincing manipulation experiment by these authors, extra light was given to the two inner rows of plots of a high yielding cultivar only during the 15 days preceding anthesis and was achieved by daytime spreading outwards of the neighbouring rows. The extra light boosted KNO and GY, 22 and 25% respectively, with anthesis to maturity dry weight accumulation increased also by 24% and increases in post-anthesis leaf photosynthesis rate of 10%. Unfortunately Sinclair and Jamieson (2006) failed to notice these results when citing another experiment from Reynolds et al. (2005) in which the multiovary trait increased KNO but not GY, which they attributes to assimilate shortage in grain filling: a more likely explanation of such a response is lingering genetic incompatibilities in these initial efforts to incorporate an exotic gene as is the multiovary trait. Finally, a recent extensive review stated that wheat yield is mainly limited by post-anthesis sink size (Borras et al., 2004). In conclusion, and despite all the progress in KNO, it seems that grain filling and grain yield in wheat, particularly in spring wheats from which the Mexican data was derived, still remains significantly sink limited.

Sinclair and Jamieson (2006) would argue that increases in post-anthesis dry weight accumulation, if they occurred, must have come about because of greater N accumulation at anthesis. We know that extra grain yield needs extra crop nitrogen accumulation if grain protein concentration is to be maintained (approximately 20 kgN/ha per extra ton of grain). It is also possible that the extra photosynthetic activity may also need more N in the canopy, although there is a little evidence for this in flag leaf %N data at anthesis in Fischer et al. (1998) when stomatal conductance increase explained about half of the photosynthesis activity increase with breeding. Grain N accumulation in wheat seems not to be the rigid driver of self destruction of the canopy during grain filling as is implied by Sinclair and Jamieson (2006). Wheat grain N% can vary widely when yield approaches an N response plateau (e.g., Fischer et al., 1993), and wheat nitrogen harvest index can also vary (Fischer, 1993), under potential conditions falling below the fixed value of 80% assumed by Sinclair and Jamieson (2006). Besides uptake of soil N after anthesis is possible if soil moisture is favourable (Cassman et al., 1992; Fischer, 1993). Thus it is not clear that N accumulation is the critical limiting factor post-anthesis as claimed by Sinclair and Jamieson (2006). Meeting the N accumulation demands of any extra grain at reasonable protein levels may be sufficient to meet those for the necessary extra post-anthesis photosynthesis, and is likely accommodated by management not genetics (but see also below).

4. Reconciliation

The approach to grain yield described above suggests a sequence of events: firstly the formation of grains, a process ending soon after anthesis, then the filling of these grains to some fraction of their potential size, usually a substantial fraction but a function of the ratio of post-anthesis source to sink. It thus assumes an independence of KNO and kernel weight (KW), linked only by the fact that KNO determines post-anthesis sink size, with possible negative consequences for KW if source is scarce. In reality, the yield potential progress which this model attempts to describe has been driven by empirical yet effective selection by breeders seeking higher yield, often with greater inputs, while making sure that grains are plump (adequate hectolitre weight, low screenings%) and protein concentration is maintained in a useful range (9–13%). This will unwittingly place pressures upon a crop's physiology: it may mean that the above sequence is simplistic, and that the breeding selection has favoured other physiological linkages between KNO, KW and GY, other underlying common causes, as Sinclair and Jamieson (2006) appear to be suggesting. These underlying mechanism(s) could lie in processes which bridge the pre-anthesis and post-anthesis periods, thereby permitting grain filling to keep up with increases in KNO, or KNO to be adjusted downwards at the last moment to meet expected short falls in source. This notion is explored here briefly in an attempt at reconciliation with the contentions of Sinclair and Jamieson (2006):

(a) A clear example is provided by water soluble carbohydrate (WSC) reserves accumulated in the crop by anthesis (mostly in stems) and contributing to the grain carbon via post-anthesis translocation to the grain. Conditions which favour more reserves could also obviously favour more grains. Indeed WSC at anthesis has increased substantially with yield progress in UK winter wheats (Shearman et al., 2005) and also in Western Australian spring wheats (Van Herwaarden and Richards, 2002). The UK data indicate about 20 mg more WSC reserves for every extra grain added by breeding, about 40% of the source needed to fill the extra grains, and incidentally, meaning that grain yield clearly exceeds post-anthesis net dry matter accumulation (Shearman et al., 2005), in contrast to spring wheat in Mexico.

(b) Almost all the photosynthetic area for the post anthesis period is built before anthesis, and is the main source of assimilate immediately before as well as after anthesis. This could be a strong underlying common cause, akin the C and N resource accumulation of Sinclair and Jamieson (2006). However under yield potential management, modern cultivars always have sufficient leaf area for full (>95%) radiation interception; indeed they may have excessive leaf area such that removing substantial amounts of leaf area in the crop at anthesis may have no effect on grain yield (e.g., Aggarwal et al., 1990). Longevity of the photosynthetic machinery could be more important for grain filling, and possibly depends also on N accumulation, but under potential conditions the N status is such that flag leaf loss of green in wheat usually follows grain maturity. More attention however needs to be given to the possibility of differences in functional leaf senescence, found to be critical to yield progress in maize (Tollenaar and Lee, 2006).

(c) Most root growth occurs pre-anthesis but clearly these same roots are alive in the post-anthesis period and could play various as yet undiscovered roles controlling KNO and grain filling.

(d) Much crop N is accumulated pre-anthesis and can contribute to grain N (but under potential or irrigated conditions if there is available soil mineral nitrogen, substantial post-anthesis uptake (and contribution) can occur (Cassman et al., 1992; Fischer, 1993)). Nitrogen has been discussed above and is considered to have a passive role, rather than that of a direct controlling factor in yield determination of wheat under potential conditions, but more work is warranted (and suggested by T. Horie's recent observations on progress in Japonica rice mentioned earlier).

(e) KNO and KW determination are not separated in time as clearly as the discussion so far has suggested. Kernels can abort at a small size after fertilization and simply disappear (this should not be confused with loss of small kernels in mechanical harvesting, leading to under-estimates of KNO, and sometimes confusion). As well the potential kernel weight at given floret positions can be influenced by events as early as one week before anthesis

(e.g., Calderini and Reynolds, 2000; Duggan and Fowler, 2006). So with this overlap, there is possibly further scope for simultaneous adjustment in grain number and size to future conditions as signalled by those around flowering. Similarly the mechanism by which grain set can fall below 90%, seen in the earlier quoted studies of L.T. Evans, perhaps exists to reduce KNO from its potential at anthesis if assimilate shortages loom. From the appearance of the spikes of modern wheats (grain set normally >90%) it does not seem to be operating any longer in them, but this also needs further explicit study.

(f) One further observation links KNO and KW. The key genotypic parameter, namely the number of kernels per unit of spike dry weight (K/SDWa) shows a clear negative relationship to potential kernel weight given unlimited source (Fischer and HilleRisLambers, 1978; P.E. Abbate, personal communication), such that spikes with high mass per floret and grain have large potential kernel weights. This would seem to be of the nature of an allometric relationship. A few modern varieties (e.g., Baviacora 92 in Mexico (Sayre et al., 1997) and its progeny) have followed the route of large, and necessarily fewer kernels, to reach similar yield levels as their much more common smaller kernel weight contemporaries.

5. Conclusion

Through the various mechanisms outlined above, the wheat crop could be changing with breeding progress to help maintain the grain filling source–sink balance. The mechanisms do not appear to add up to enough in themselves to alter the earlier conclusion that yield has increased because of more assimilate reaching, and being used more efficiently in, the growing spike. This has led to increased KNO, which has been accompanied by, and maybe has helped, post-anthesis photosynthetic activity to increase. It would be unwise to abandon this path in the search for further yield progress, but the above possible complicating mechanisms, in particular the quantity of WSC accumulated by anthesis, needs to be studied in more detail. The physiologist-breeder can try to model the situation, either conceptually or mathematically, but should take advantage of all that is known, something not evident in the Sinclair and Jamieson (2006) conclusion. Finally, however, and guided by the modelling, physiologists must push the wheat phenotype genetically (and agronomically) in promising directions to see what happens; no amount of modelling is likely provide definitive answers on something as complex as grain yield potential. It is worth adding that functional genomics, so much in fashion now, is also confronted by this uncertainty: genetic engineering for higher yields can surely only proceed if the physiological mechanisms of grain yield determination are understood, such that bottlenecks in key yield processes can be relieved without incurring costly hidden trade offs, a point made by T.R.Sinclair himself (Sinclair et al., 2004).

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