Decimal growth stages for precision wheat production in changing environments?

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Cereal growth stages for precision agriculture in changing environments

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Abstract

Developmental growth stages in wheat play an important role in agronomic decision making, as well as identifying periods of growth susceptible to environmental stresses. Different developmental scales have been reviewed, with a particular focus on the Zadoks growth scale. The role of DGS in identifying the effect of environmental stresses was also reviewed. It was concluded that although DGS aren't always consistent across genotypes, they provide a good framework to broadly identify optimal agronomic timings as well as identifying susceptible developmental timings to environmental stresses when combined with a more detailed view of the physiological stage the plant has reached.

Growth stage scores defining cereal development

Cereal plants mature from seed germination to harvest by passing through distinct, but integrated developmental phases typical of annual grasses. It is important to define the developmental stage of a crop because: responses and appropriate benchmarking of crops to agronomic and environmental conditions depend on stage of development; genotypic adaptation can be better understood to facilitate crop improvement; and calendar date or days from sowing are unreliable predictors of developmental stage (Kirby & Appleyard, 1987; Landes & Porter, 1989; Sylvester-Bradley *et al.*, 2008; Leather, 2010). Schemes for defining crop growth stage have, therefore, been devised and divided into those relying on assessing the exterior morphology of the plants with the naked eye, and those that need dissection of the shoot apex and some level of magnification (Landes & Porter, 1989). Of the exterior schemes, the decimal growth stage (DGS) of Zadoks, Chang & Konzak is the

most widely and frequently used. The DGS was first published in *Eucarpia Bulletin* (Zadoks *et al.*, 1974a), followed by *Weed Research* (Zadoks *et al.*, 1974b), *Annual Wheat Newsletter* (Zadoks *et al.*, 1975a) and *Cereal Rusts Bulletin* (1975b). Zadoks (1985) also commended the subsequent illustrations of the DGS in this journal by Tottman *et al.* (1979) as being 'excellent', and further detail and revision is provided in Tottman (1987). The combined citations in the academic literature to the original score and subsequent illustrations and amendments are, so far, well over 5000. Zadoks (1985) promotes the scale as: covering all stages from seed sown to seed harvested; providing a recording system for development stages as they can be readily observed in the field; being a two-digit, computer-compatible, easy-to-memorize, numerical code; and to becoming a readily accepted, official standard for many international organisations. Tottman (1987) also highlights the benefits of the DGS in allowing detailed descriptions of individual plants, and also for different parts of the code to be used concurrently (e.g. leaf production and tiller production).The reader is referred to Tottman (1987) for the detailed scoring system with precise definitions and illustrations but Table 1 gives a summary. Landes & Porter (1989) and Harrell *et al.* (1993; 1998) provide equivalent scores between DGS and other systems. Landes & Porter (1989) compare DGS with six other 'exterior' scales: Feekes (1941), Keller & Baggiolini (1954), Woodford & Evans (1965), Chancellor (1966), Kuperman (1973), Waldren & Flowerday (1979); but use the DGS as standard because of the greater range and detail of plant development described. Acevedo *et al.*, (2002) consider the DGS to be '*the most comprehensive and easiest to use*' scale. Thomas (2014) reasons that it was the detailed descriptions of key growth stages in Tottman (1987) that have been particularly influential in practical cereal agronomy because of the clarity in definition of important development phases for the optimal application of fertilizers and agrochemicals in crop production. The response of wheat to the timing of plant growth regulators (Kettlewell *et al.*, 1983; Bodson & Durdu, 1996; Gandee *et al.*, 1997, 1998; Rajala & Peltonen-Sainio, 2002; Hussain & Leitch, 2007; Wiersma *et al.*, 2011), herbicides (Wilson & Cussans, 1978; Tottman, 1982; Martin *et al.*, 1990; Leaden *et al.*, 2007; Pageau & Lajeunesse, 2008; Kong *et al.*, 2009; Robinson *et al.*, 2013); insecticides (Carter *et al.*, 1989; Mann *et al.*, 1991; Oakley *et al.*,1996); fungicides (Guy *et al.*, 1989; Goulds & Fitt, 1990; Duczek & Jonesflory, 1994; Nicolas, 2004; Wiersma & Motteberg, 2005; Marroni *et al.*, 2006; Edwards & Godley, 2010;

Wegulo *et al.*, 2011); and nitrogen application (Darwinkel, 1983; Powlson *et al.*, 1989; Sylvester-Bradley *et al.*, 1987; Flowers *et al.*, 2001; Weisz *et al.*, 2001; Efretuei *et al.*, 2014); are all commonly interpreted with reference to DGS. Of particular importance is in identifying when inputs are: most likely to have a desired response such as the stem shortening effect of plant growth regulators (Gandee *et al.*, 1997, 1998); safe to use on crops so as to avoid damaging effects such as can occur with mistimed application of hormonally-based herbicides (Tottman, 1982); applied to allow optimal resource capture such as nitrogen applied for canopy formation (Sylvester-Bradley *et al.* 1987); and used to protect important yield components such with fungicides applied to maintain the life of the flag leaf and therefore grain filling (Dimmock & Gooding, 2002).

As with other scores, however, caution is required when using DGS for comparative and statistical purposes. Except for when all scores are within categories 1, 2, 4, 5 or 6 (Table 1) the arithmetic mean of a sample of scores has no ready interpretation. Categories of the DGS or divisions within them do not necessarily reflect relative durations or agronomic importance (e.g. Fig. 1). Finally, as acknowledged by both Tottman (1987) and Zadoks *et al.* (1974b), DGS can be an unreliable predictor for physiological development as defined by the status of the meristems. It is the developmental stage of the meristem and growing spike that plays the crucial role in defining shoot vulnerability, patterns of dry matter partitioning (Craufurd & Cartwright, 1989) and yield components likely to be influenced by genetic, agronomic and environmental factors (Slafer *et al.*, 2009; Reynolds *et al.*, 2012). The potential disparity between DGS and the internally-defined stages of physiological development could, therefore, limit further precision of timing of inputs based on DGS, and wider application of the DGS for understanding crop adaptation. Here we first assess the extent to which DGS does reflect the status of meristems, and then address relationships between DGS and adaptive traits.

Crop development and coincidence with the Decimal Growth Stage

The development of the shoot apex, and its role in the origin of leaves, tillers, stem and ear is described by Kirby & Appleyard (1987). The apical meristem is initially *vegetative*, giving rise to leaves, tillers and adventitious roots while the apex often remains below ground level. Leaves

originate as primordia which are attached at nodes on the stem. Tillers develop from buds in the axils where the leaf joins the stem. The *reproductive* development of the meristem begins as it elongates from 0.1 to 0.3 mm with the appearance of primordia as single ridges. At this stage the stem apex is still close to ground level. The buds in the axils of the apex ridges are spikelet primordia and, with their leaf initials form *double ridges* as the developing spike elongates to between 0.8 and 1 mm. It does not seem possible to assign, precisely, the start of reproductive development or double ridges to a DGS: Tottman (1987) recognised that DGS 30 usually occurred after double-ridges but Hay (1986) failed to find a correlation between double ridges and leaf or tiller number, or when considering different reports, leaf sheath lengths. After double ridges the spike continues to elongate and as it does so the central spikelets swell while additional double ridges are formed acropetally until the *terminal spikelet* is formed at the apex. At this stage the embryonic spike may be 1.5 to 4 mm long and Tottman (1987) says it can be broadly coincident with DGS 31. Hay (1986), however, found the terminal spikelet stage to commonly occur when the developing ear was 10 mm above the crown, i.e. possibly earlier than DGS 31. Tottman (1987) only conceded that '*the apex will be beyond the double ridge stage and floret initiation is likely to be in progress*' when the apex was 10 mm above the soil surface. In some environments, therefore, the ear being 10 to 30 mm above ground level would normally encompass the terminal spikelet stage, coinciding with DGS 31 to 32, although this also depends on variety (Wibberley 1989). Despite the slight apparent divergence of opinion, the 'ear above 10 mm' is still used as the timing of terminal spikelet formation in studies of wheat development (e.g. Sanna *et al.*, 2014), and given the speed of stem elongation thereafter (Craufurd & Cartwright, 1989) discrepancies may be small.

Differentiation of the spikelets continues, having started before the terminal spikelet stage and being most advanced in the lower midpart of the spike. The florets differentiate from primordia in the axils of floret bracts. The floret apex, surrounded by the carpel, develops into the ovule. A single egg (megaspore) mother cell is formed from one archesporial cell in each ovule and undergoes *meiosis*. Each anther contains many archesporial cells, each forming four pollen mother cells which each undergo meiosis while the anthers are green and apparently about 1 mm long (Kirby & Appleyard, 1981) and when the ear is 20 to 25 mm long (Tottman, 1987). The structures of the ear

develop as it is simultaneously elevated through the leaf sheaths of the canopy by the extending stem. Booting describes the swelling of the sheath of the ultimate leaf, the flag leaf, as the developing ear expands within it. Tottman (1987) associates meiosis with DGS 37, i.e. the appearance of the flag leaf. Zadoks *et al.* (1974b) state that meiosis in wheat occurs in the the early booting *stage*, i.e. DGS 41 but concede that coincidence is likely to be strongly influenced by environment. It should also be noted that meiosis within a single floret can last for about 1 to 2 days (at 20°C to 15°C respectively; Bennett *et al.*, 2011), but within an ear meiosis in different florets may be separated by three or more days (Saini & Aspinall, 1982) and the asynchrony can be expected to be greater between ears, particularly between tillers of different ages. In work on the effects of drought on photosynthesis Fábián *et al.* (2013) detect the start of meiosis in the middle third of the spike with cytology, but correlate this with the position of the spike within the leaf sheath and consider the meiotic period of whole plants to last for five days. Booting is soon followed by emergence of the ear above the flag leaf and, when applying stresses broadly targeted at meiosis, authors have imposed treatments for a duration lasting several DGS: from at least as early as the flag leaf ligule visible stage (DGS 39) until ear emergence (DGS51) of the main stems (Subedi *et al.*, 1998; Westgate *et al.*, 1996; Alghabari *et al.*, 2014).

Heading date is often recorded when assessing genotypes, e.g. Pask *et al.* (2014) and Lopez *et al.* (2014) define heading date as when 50% of ears have fully-emerged, i.e. when 50% of ears are at DGS 59. The adaptive significance of heading date is principally due to its association with anthesis (Reynolds *et al.*, 2012; Kamran *et al.*, 2014), which commences typically between 3 and 8 days after ear emergence, depending on temperature and variety. Flowering starts in the basal florets of central spikelets and proceeds basipetally and acropetally within the ear, and acropetally within the spikelet. Flowering within a spike is usually complete within 2 to 5 days while over a whole plant or crop may extend over 5 to 10 days due to variations in tiller maturity. The DGS can capture the development of anthesis within a spike although within a field crop the time of flowering is often stated as when half of ears are in flower (Marcello & Single, 1971; Griffiths *et al.*, 2009). It should be noted that the DGS relies on the appearance of the anthers, which is not always precisely coincident with when the stigmas are receptive to pollen (Lukac *et al.*, 2012).

Grain filling with dry matter from anthesis to harvest maturity can often be adequately described with an ordinary logistic function with constant omitted (Gooding *et al.*, 2005). Grain development, can, however, be described as proceeding in three phases (Jenner *et al.*, 1991) which can be roughly demarcated by reference to water fluxes. The first phase is one of grain enlargement as cells multiply and expand with a rapid accumulation of water into the grain (Pepler *et al.*, 2006). Division of the endosperm nucleus occurs within a few hours of fertilization. The first cell walls appear about 3 days later. Rate of cell division slows until a maximum cell number (typically around 10^5) is attained from around 12 days after anthesis (Gao *et al.*, 1992), at about the time when rapid water accumulation stops. The second phase of endosperm development is one of a near linear increase in grain dry matter, starting between 10 and 15 days after anthesis and continuing, depending on genotype and temperature, for 15 to 30 days. Mass of water per grain during this phase is relatively constant (Pepler *et al.*, 2006), and appears to broadly coincide with the period from the milky ripe (DGS 75) to the soft dough (DGS 85) stages (Noda *et al.*, 1994). The third phase describes processes subsequent to the attainment of maximum dry matter per grain. The time of maximum dry matter is often taken as physiological-, rather than harvest-, maturity; and coincides with the start of rapid net water loss from the seed (Pepler *et al.*, 2006), and the acquisition of dormancy. Lopez et al. (2014) take the end of dough development (DGS 89) as being representative of physiological maturity, but assume it to coincide with 100% loss of green tissue on the spike. Hanft & Wych (1982) also associate physiological maturity with senesce, although it is possible to delay flag leaf death until after the end of grain filling in certain field conditions (Pepler *et al.*, 2005).

The imprecise coincidence between DGS and meristem and ear development has led to the latter often being preferentially used within crop models that define development in terms of, for example, double ridges, floral initiation, terminal spikelet, and anthesis (Porter *et al.*, 1987; Jamieson *et al.*, 2007); although observers in the field have still resorted to using particular DGS as assumed equivalents (e.g. Sanna *et al.*, 2014). More latterly, however, a degree of co-ordination between vegetative and reproductive growth (Kirby *et al.*, 1994) has led to models that predict development and DGS through to DGS39 (Jamieson *et al.*, 2007); or conversely, use canopy measurements at specific DGS such as 31, 39 and 61 to parametise models (M. A. Semenov, personal communication).

The DGS is, therefore, deployed when providing parameters and calibration for crop models which are then used to predict crop performance in climate change scenarios (Asseng *et al.*, 2013).

The Decimal Growth Stage and crop adaptation

The effect of light, temperature, water and other environmental aspects on phenological development itself, and also on growth within developmental phases has been reviewed (Evans *et al.*, 1975; Acevedo *et al.*, 2002). It is evident that adaptation of wheat for maximising yield potential in a particular location and environment relies on: ensuring that particularly vulnerable developmental stages (Craufurd *et al.*, 2013) do not coincide with abiotic stresses (Worland *et al.*, 1998) such as cold, heat, drought and nutrient deficiencies; maximising resource (light, water, nutrients) capture, particularly during certain critical developmental periods (Fischer, 1985); and by improving resource utilization efficiencies, such as by increasing harvest indices which is also influenced by developmental periods (Reynolds *et al.*, 2012). It is clear that the phasing of phenological development (Slafer *et al.*, 2009), and therefore potentially DGS, can help in understanding crop adaptation and yield potential in a particular environment. The power of DGS analysis for interpreting and predicting effects on grain yield, however, depends on: the degree of compensation and plasticity in response between different yield components; the developmental synchrony of different plants and stems within a crop; and as mentioned previously the coincidence between DGS and phenological development.

The rate of wheat development depends largely on variety, temperature, the need for a cold period (vernalization) and day length (photoperiod). The vernalization requirement is particularly influenced by alleles at the Vrn-1 loci, located on each of the long arms of the group 5 chromosomes, i.e. Vrn-A1, Vrn-B1 and Vrn-D1, and their regulation by minor vernalization genes (Loukoianov *et al.*, 2005; Reynolds *et al.*, 2012). Wheats with a significant vernalization requirement (winter wheats) are maintained in a vegetative state until the requirement has been met. Acevedo *et al.*, (2002) found spring wheats to require 7 to 18^{o}C for 5 to 15 days for floral initiation while winter wheats required 0 to 7 ^{o}C for 30 to 60 days. Development can also be accelerated by exposure to long days, i.e. photoperiod sensitive varieties are quantitative long day plants. Major genes controlling

photoperiod sensitivity in wheat are found on the short arms of group 2 chromosomes, i.e. Ppd-D1, Ppd-B1 and Ppd-A1, with dominant (notated a) alleles conferring plants with insensitivity to photoperiod. Presence of Ppd-D1a has, for instance, been associated with plants flowering up to fourteen days earlier than photoperiod sensitive genotypes in typical UK field conditions (Snape *et al.*, 2001; Fig. 1).

Even when vernalization and photoperiod requirements are fully met developmental rates still vary between varieties. These differences can be ascribed to variations in earliness *per se*. Because varieties vary in their response to temperature, vernalization and photoperiod, in the extent to which these factors interact, and in relative sensitivity to them at different growth stages (Sanna *et al.*, 2014), varieties vary, apparently continuously, in their rates of maturation, thus contributing to the wide adaptation and distribution of wheat in world agriculture. Fig. 1 shows the wide distribution of growth stages attained in 64 doubled haploid progeny of Renesansa x Savannah (Simmonds *et al.*, 2006) when grown in the UK (Addisu *et al.*, 2010). Savannah had high yield potential in NW Europe as listed for the UK in 1998 while Renesansa had high yield potential in southern Europe and listed in 1995. The large effect of *Ppd-D1a* deriving from Renesansa is clearly evident, as is much variation that cannot be solely attributed to this source of photoperiod insensitivity.

Avoidance and tolerance of abiotic stresses

The yields of wheat crops are at risk of abiotic stresses throughout plant development, until physiological maturity. Varieties can vary in their tolerance of stresses applied for ranges of DGS (Bányai *et al.*, 2014). It is evident that some growth stages are particularly sensitive to the environment (Craufurd *et al.*, 2013). Much adaptation involves the deployment of genetic resources and agronomic intervention such that: the crop's tolerance of stress is improved; and/or markedly sensitive periods of development do not coincide with particularly inclement conditions. With extreme weather events predicted to become more frequent in climate change scenarios (Semenov *et al.*, 2014) a greater understanding of how stresses at specific growth stages influence yield and yield

stability is required. Whether the DGS is adequate to describe developmental status in this context needs to be addressed.

Winter hardiness and cold tolerance

The requirement for vernalization and long days can delay the onset of floral initiation and this in itself may contribute to the avoidance of cold damage if reproductive development is not initiated until after the harshest weather has passed. However, Vrn-1 genes are closely linked to, and also interact with, other genes conferring cold tolerance (Reddy et al 2006), and therefore, survival over winter. The requirement for vernalization and the exposure of photoperiod sensitive varieties to short days helps maintain plants in the vegetative state and thereby better able to acclimatize to low-temperature; ability largely lost once the plants have moved to the reproductive state, defined here as approximating to double ridges (e.g. Mahfoozi *et al.*, 2000; Limin & Fowler, 2006; Fowler & Limin, 2007). The inability for DGS to delineate the double ridge stage remains a weakness of this and other externally-based scores.

Meiosis

The timing of meiosis appears critical for crop adaptation as it is particularly susceptible to disruption by biotic (De MeloSereno *et al.*, 1981) and abiotic stresses such as cold (Subedi *et al.*, 1998; Tang *et al.*, 2011), heat (Saini & Aspinall, 1982; Barnabäs *et al.*, 2008; Jaeger *et al.*, 2008; Omidi *et al.*, 2014) and drought (Saini & Aspinall, 1981; Dorion *et al.*, 1996; Lalonde *et al.*, 1997a; 1997b; Jaeger *et al.* 2008; Barnabäs *et al.*, 2008); ultimately leading to grain set failure. As described previously, it is not possible to directly relate a single DGS to the onset of meiosis as coincidence is likely to depend on environment and genotype. However, as meiosis within florets, spikes and tillers occurs over a period of up to five days, it should be possible to broadly map susceptibility to abiotic stresses occurring during periods loosely demarcated by DGS. Fig. 2 is a reanalysis with new data from a complete factorial replicated pot (4 litre, four plants per pot) experiment, previously described as Experiment 2 in Alghabari *et al.* (2014). Factors included genotype (11 elite and near-isogenic lines of winter wheat varying for reduced height alleles), day temperature (20, 27, 30, 33, 36, 39°C),

timing of stress (booting or anthesis) and irrigation (withholding water during heat stress or irrigating to field capacity). Environment treatments were imposed by transferring pots to matched growth cabinets at 15:30h GMT for three 16 h day, 8 h night cycles (8°C below day temperature) before returning to the original, completely randomized, position outside. Each mainstem and tiller was scored and tagged for their DGS when the pot was transferred. It is clear that grain set is particularly susceptible to withholding water at the booting DGS (Fig. 2*a*), a weakness that is further exacerbated by the imposition of high temperatures (Fig. 2*b*, *c*). In contrast, mean grain weight in this experiment was largely unaffected by drought imposed during booting (Fig. 2*d*), and when just heat was considered high temperature stress at booting resulted in heavier grains (Fig. 2*e*) in partial compensation for the poor grain set (Fig.2*b*). The effects of heat and drought on grain set are consistent with meiosis being a susceptible period of development and that this coincides with booting. However, any genotype-dependant variation in the coincidence between DGS and meiosis reduces the interpretative certainty from screens of genotypes against stresses applied according to DGS. e.g. an apparently tolerant genotype may have 'escaped' the stress if meiosis occurred at a different DGS to other more 'susceptible' genotypes. A laborious approach to overcoming this issue is to impose shorter duration stresses to different plants on successive days and DGS. Fig. 3 shows the results from this approach. The experimental system was similar to that used for Fig. 2 and comprised 496 pots accommodating two cultivars (Savannah and Renesansa) × two day temperatures (20°C and 35°C) × 31 single day transfers × four randomised blocks. It was hoped that the contrasting target environments of the cultivars would reveal a variation in stress tolerance at and after meiosis. Each mainstem was tagged and scored for growth stage on the day of transfer. Renesansa was clearly earlier maturing than Savannah, consistent with differences in the photoperiod sensitivities of the two lines (Fig. 3*e vs.* 3f). Pots were not watered whilst in the cabinets. Ears of Renesansa and Savannah were harvested at DGS 89. For mean weight per spikelet there were strong interacting effects between temperature and day and between cultivar and day. Both cultivars showed susceptibility to the high temperature treatment during booting (Fig. 3), but this was particularly marked in Savannah, during a five-day period when 80% of the ears were between DGS 37 and 45.

Anthesis

In addition to meiosis, grain set in wheat can be compromised by temperatures above 30°C shortly before and during flowering (Stone & Nicolas, 1995a,b,c; Wheeler *et al.*, 1996; Ferris *et al.*, 1998; Barnabás *et al.*, 2008). Although drought can exacerbate the effect of heat (Fig. 2), drought at moderate temperatures is much less damaging to grain set when it occurs at anthesis, compared with at meiosis (Fig. 2; Saini & Aspinall, 1981; Alghabari *et al.* 2014). In terms of DGS, grain set tends to be more susceptible to heat stress in the earlier stages of flowering: DGS 59-65, compared with DGS 69 (Fig. 2) consistent with observations of stress mid-way through (Mitchell *et al.*, 1993), or shortly before (Wheeler et al., 1996) flowering. It appears that grain set becomes comparatively tolerant of stresses three days after fertilization. The earliest flowers on ears assessed as having just completed anthesis at DGS 69 may have been fertilized four or five days earlier (Lukac, personal communication), and hence beyond the vulnerable growth stage (Saini & Aspinall, 1982; Stone & Nicolas, 1995a,b,c) for grain set. Hence, at GS 69 Semenov *et al.* (2014) still report 1.5 grains per spikelet being set at temperatures as high as 40°C under irrigated conditions. Such grains can, however, be significantly reduced in final mean grain weight (Fig. 2; Semenov *et al.*,2014). As well as heat there is also a large effect of drought shortly after anthesis on final mean grain weight even when subsequent water availability is high before the end of grain growth (Gooding *et al.*, 2003). Renesansa appeared particularly susceptible to the high temperature during a period when over 80% of ears were between GS 59 and 65 (Fig. 3). This early flowering period, however, appeared to be relatively resistant to heat in Savannah. Indeed, when the duration from booting to flowering is considered Renesansa appeared more susceptible to heat than Savannah, confirming previous pot experiments (Semenov *et al.* 2014). This emphasises the likely importance of 'escape' for the adaptation of the S European wheat conferred by more rapid development through photoperiod insensitivity (Worland *et al.*, 1998; Snape *et al.* 2001). Growing Renesansa in the UK out of its intended region of adaptation, however, also resulted in less synchronous development (Fig. 3*e,f*) and it is possible that any consequent reduced co-ordination of reproductive and flowering processes

may have been exacerbated by abiotic challenges. We found no evidence that greater diversity in flowering time improved resilience as suggested by Lukac *et al.* (2012) , rather the reverse.

Maximizing resource capture and dry matter partitioning

Figs 4 and 5 show results from the Renesansa x Savannah doubled haploid population averaged over the 2007/08 (as described in Addisu *et al.*, 2010), 2011/12 and 2013/14 field growing seasons in the UK. Accumulated light interception from sowing until DGS89 is clearly important for production of above ground biomass (Fig. 5*a*; Gallagher & Biscoe, 1978). Extending the growing season in clement and high light availabilty conditions, and as rotational system factors allow, can therefore increase yields, particularly when light interception is increased late in the season (Fig. 4*a*, 5*d*; Sylvester-Bradley *et al.*, 2005; Gooding *et al.*, 2005). Early season growth, however, may be less important, particularly if it is at the expense of harvest index (Figs. 4*f*, 5*f*). Extending the duration and/or light interception during particular stages of development can, therefore, have a disproportionate effect on yield because of influences on specific yield components, dry matter partitioning, and radiation-use efficiency (Figs. 4, 5; Slafer *et al.*, 2009; Reynolds *et al.*, 2012). For example grain number per unit area is often the major yield component, and still limits yield in many areas of the world. It is necessary to increase this yield component to improve yields to satisfy future demand. Grain number per unit area is often positively related to light interception and radiation-use efficiency during the so-called critical period when the spikes are actively growing during the stem elongation phase until immediately after anthesis. Increasing light interception during this phase can increase the number of florets that become fertile and avoid floret death (Reynolds *et al.*, 1999; Miralles *et al.*, 2000; Gonzalez *et al.*, 2003), and also increase the number of tillers per unit area and reduce the numbers that die. Fischer (1985) initially defined the critical period for the effects of light interception on grain number determination as being from when the penultimate leaf had emerged until anthesis. The stem-elongation phase has, however, also been defined as from DGS 31 to DGS 65 (Garcia *et al.*, 2014). In the Renesansa x Savannah population grain yield was positively associated with light interception in the stem elongation phase up to around 275 MJ PAR/m^2 (Fig. 5*b*). As light interception increased further, grain yields decreased

because here increasing PAR was achieved with excessive delays in anthesis and a consequential reduction in harvest index (Fig. 4*g*).

Conclusions

To conclude, DGS provides a simple, useable framework that can help to optimise agronomic applications as well as identify vulnerable stages of plant development to environmental stresses. The Zadoks scale is the most widely used due to its simple, yet effective layout. However, care must be taken when assessing certain phases of crop development using DGS as timings can differ depending on genotype and environment. Although DGS are an excellent tool for optimising agronomic timings, they fail to identify in detail key reproductive stages, such as the double ridge stage and meiosis. This is largely due to the influence environment and genotypic factors can have on the timing of these physiological stages relative to external DGS. Despite this, DGS can still be used as a broad marker when assessing for the effect of environmental stresses. DGS has also been used in phenotypic trials to help identify relationships between light interception between different DGS and the effects this has on various yield components.

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Figure Legends

Fig.1. Distribution of DGS for 64 doubled haploid progeny of Renesansa x Savannah when field grown in the UK in two seasons. Boxes are limited by 25 and 75 percentiles, whiskers by 10 and 90 percentiles; points are outliers beyond 10 and 90 percentiles, and the line within the box is the median where appropriate. Heavy solid line connects median for progeny carrying the marker for *Ppd-D1a* (photoperiod insensitive); dashed line is for *Ppd-D1b* (photoperiod sensitive).

Fig. 2. The effect of stem growth stage at the start of 3 day transfers to controlled environment cabinets for the imposition of heat and drought stresses (Alghabari *et al.*, 2014). In each panel the horizontal dashed line represents the mean result from plants transferred to temperatures 20, 27 and 30°C, irrigated to field capacity. Vertical bars are S.E.D. for comparison between the points and the dashed line.

Fig. 3. Effects of wheat cultivar and successive 1-day transfers to controlled environment cabinets at 20/12 and 35/27°C day/night temperature (16h day) on mean weight per spikelet of main stems. *e* and *f* give the growth stage distributions of the mainstems at the time of transfer in to the cabinets (boxes are limited by 25 and 75 percentiles, whiskers by 10 and 90 percentiles; points are outliers beyond 10 and 90 percentiles, and the line within the box is the median where appropriate). S.E.D. in *a* is for comparing temperatures within day and cultivar for both *a* and *b*. Dashed lines correspond to days and growth stages denoting the most susceptible 5-day period to 35°C for each cultivar.

Fig. 4. Durations between different decimal growth stages (Zadoks *et al.*, 1974*b*) of 64 doubled haploid progeny of Renesansa x Savannah and associations with radiation use efficiency (RUE), and dry matter accumulated and partitioned by harvest. Points are means of two replicate field-grown plots in each of three growing seasons. Error bars are S.E.D. for comparing points. Fitted lines are incorporate polynomial effects when significant (P<0.05).

Fig. 5. Interception of photosynthetically active radiation between different decimal growth stages (Zadoks *et al.*, 1974*b*) of 64 doubled haploid progeny of Renesansa x Savannah and associations with radiation use efficiency (RUE), and dry matter accumulated and partitioned by harvest. Points are means of two replicate field-grown plots in each of three growing seasons. Error bars are S.E.D. for comparing points. Fitted lines are incorporate polynomial effects when significant (P<0.05).

Table 1. Summary of the decimal growth stage (DGS) scoring system (Zadoks *et al.*, 1974b; Tottman, 1987).

DGS	Abbreviated description
0*n*	**Germination** (*n* indicates pre-leaf emergence development from dry seed (*n*=0) to first leaf at coleoptile tip (*n*=9))
1*n*	**Leaf production (seedling growth)** on the main stem (*n*=number of leaves unfolded to the extent that the ligule is visible, to maximum of 9)
2*n*	**Tiller production** (*n*=number of tillers per plant to maximum of 9)
3*n*	**Stem elongation** (*n*=0 refers to 'pseudostem erect' when the ear is at least 10mm above where the lowest leaves are attached; for *n*= 1–6, *n* = number of nodes detectable, to maximum of 6; then *n*=7 for flag leaf just visible, and *n*=9 flag leaf ligule visible).
4*n*	**Booting** (*n* indicates degree of swelling)
5*n*	**Ear emergence** (*n* indicates proportion of ear emerged)
6*n*	**Anthesis** (*n* indicates degree of completion)
7*n*	**Grain expansion (milk development)** (i.e. grain fluid exuded when caryopsis squeezed changes from watery (*n*=1) to milky (*n*=7))
8*n*	**Dough development** (i.e. no droplet exuded from squeezed caryopsis, thumbnail imprint not retained (*n*=3) to thumbnail imprint retained (*n*=5+)
9*n*	**Ripening** (describes harvest ripeness (*n*=2), to seed with no primary dormancy (*n*=7)).

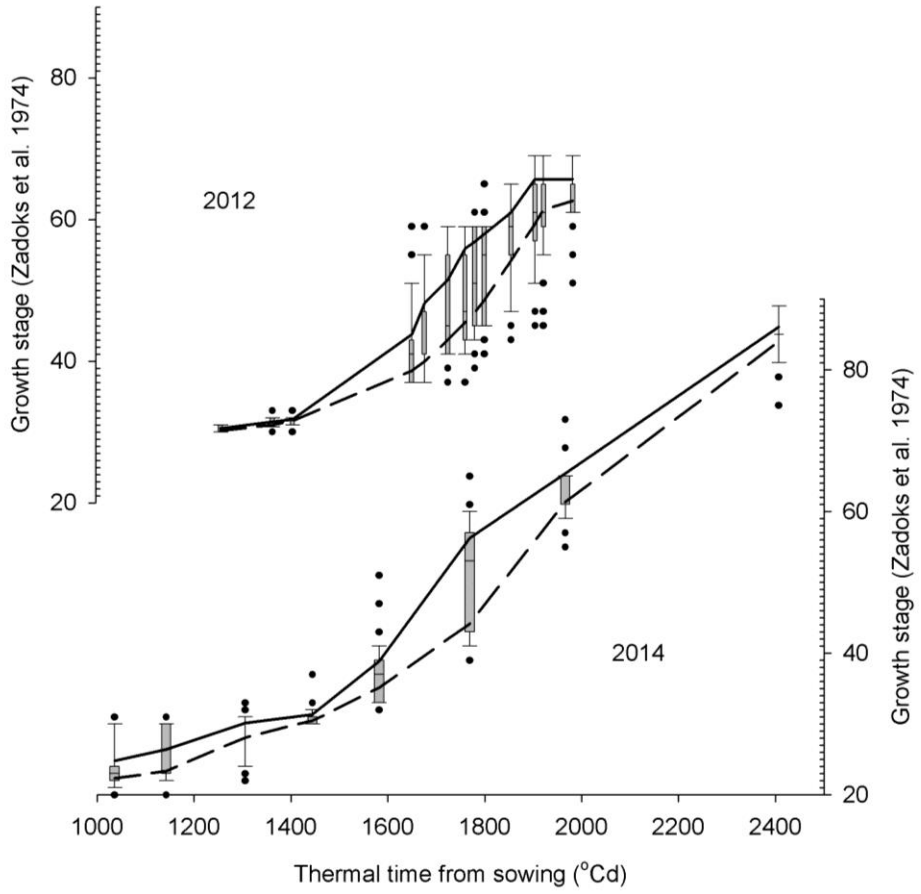
Growth stage (Zadoks et al. 1974)
80
60
40
20
2012
2014
1000
1200
1400
1600
1800
2000
2200
2400
Thermal time from sowing (°Cd)

Fig. 1

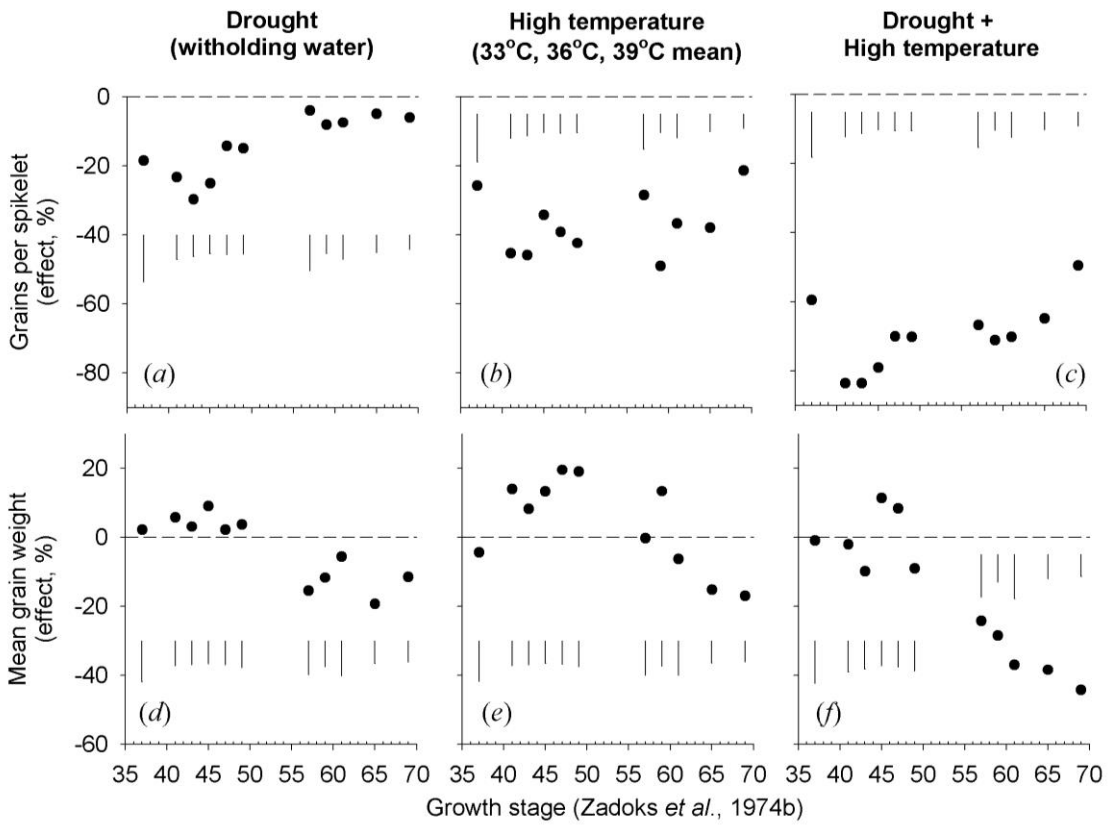
Drought
(witholding water)
High temperature
(33°C, 36°C, 39°C mean)
Drought +
High temperature
Grains per spikelet
(effect, %)
Mean grain weight
(effect, %)
0
-20
-40
-60
-80
20
0
-20
-40
-60
(a)
(b)
(c)
(d)
(e)
(f)
35 40 45 50 55 60 65 70
Growth stage (Zadoks et al., 1974b)

Fig. 2.

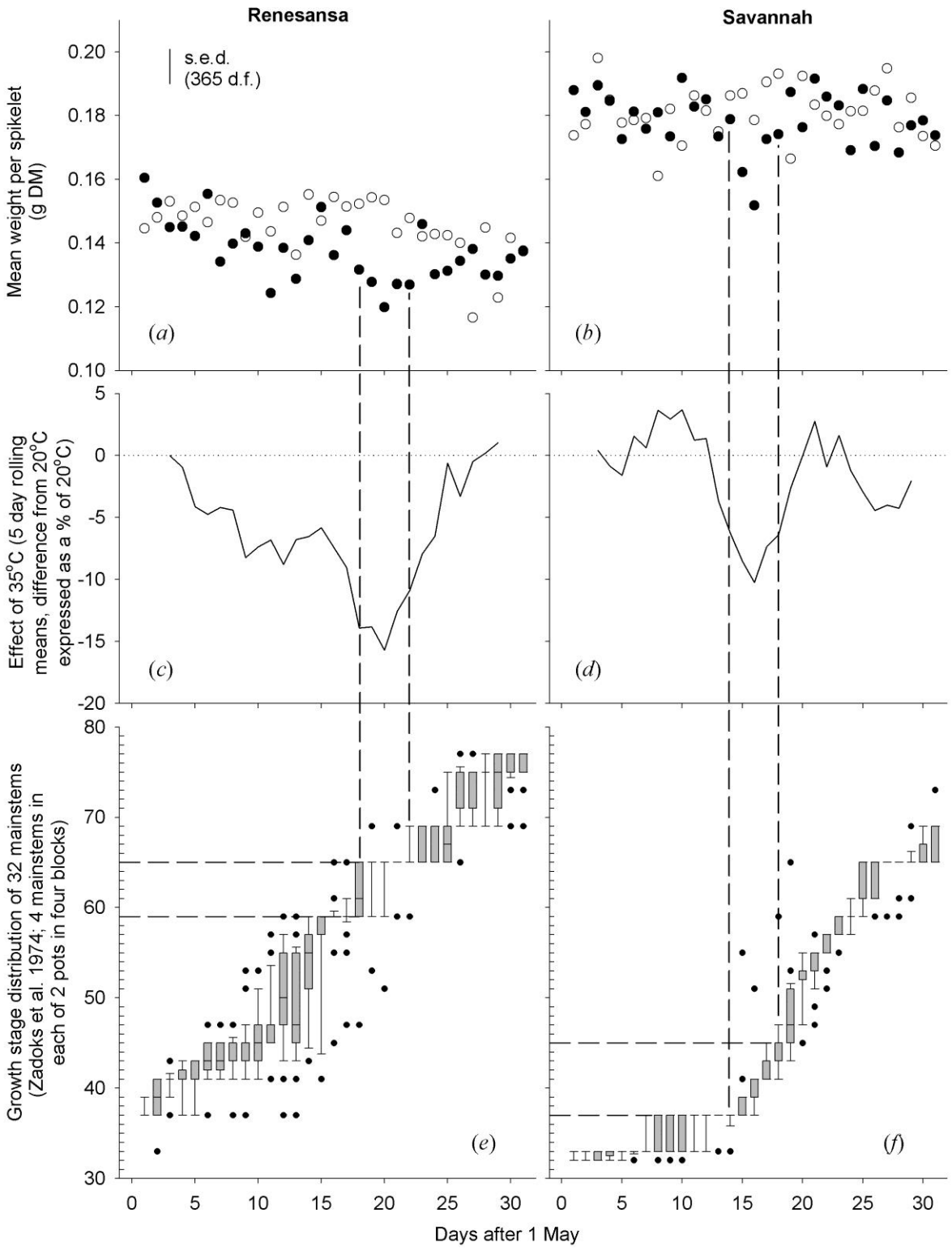
Renesansa
Savannah
s.e.d.
(365 d.f.)
Mean weight per spikelet (g DM)
0.20
0.18
0.16
0.14
0.12
0.10
(a)
(b)
Effect of 35°C (5 day rolling means, difference from 20°C expressed as a % of 20°C)
5
0
-5
-10
-15
-20
(c)
(d)
Growth stage distribution of 32 mainstems (Zadoks et al. 1974; 4 mainstems in each of 2 pots in four blocks)
80
70
60
50
40
30
(e)
(f)
0
5
10
15
20
25
30
Days after 1 May

Fig. 3.

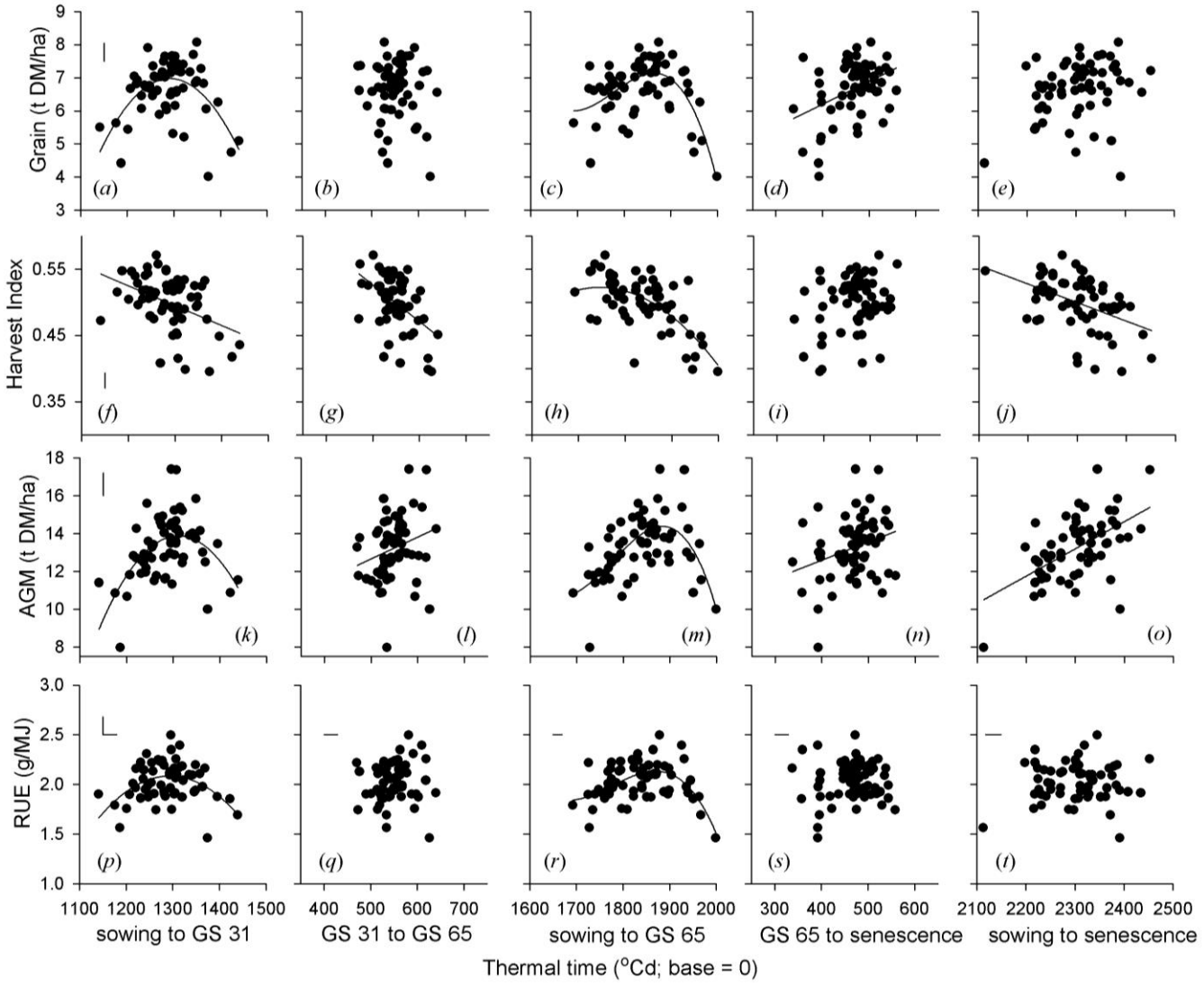
Grain (t DM/ha)
Harvest Index
AGM (t DM/ha)
RUE (g/MJ)
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)
(n)
(o)
(p)
(q)
(r)
(s)
(t)
1100 1200 1300 1400 1500
sowing to GS 31
400 500 600 700
GS 31 to GS 65
1600 1700 1800 1900 2000
sowing to GS 65
300 400 500 600
GS 65 to senescence
2100 2200 2300 2400 2500
sowing to senescence
Thermal time (°Cd; base = 0)

Fig 4.,

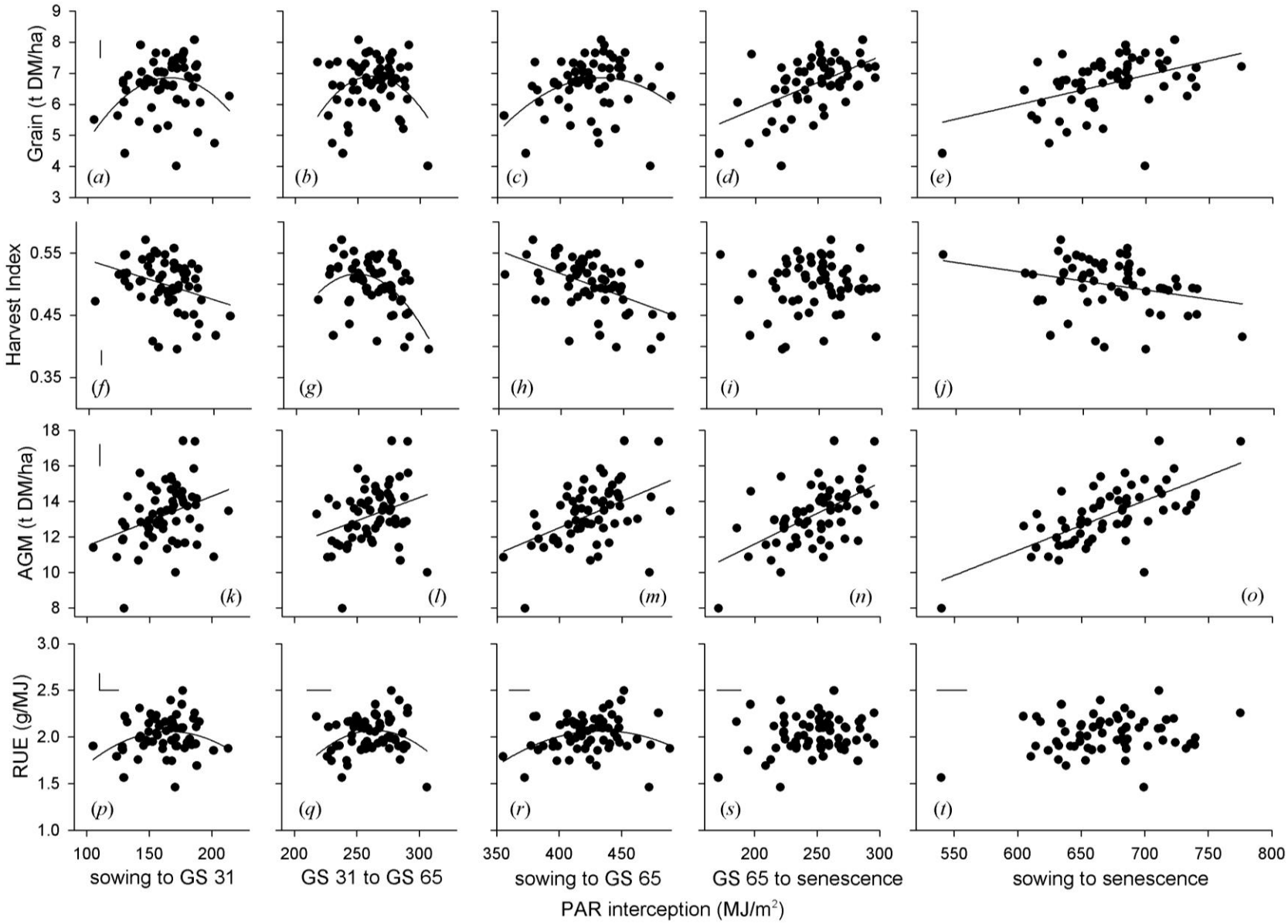
Grain (t DM/ha)
Harvest Index
AGM (t DM/ha)
RUE (g/MJ)
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)
(n)
(o)
(p)
(q)
(r)
(s)
(t)
sowing to GS 31
GS 31 to GS 65
sowing to GS 65
GS 65 to senescence
sowing to senescence
PAR interception (MJ/m²)

Fig. 5