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Gooding, Michael

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tel: +44 1970 62 2400

email: is@aber.ac.uk

CENTENARY REVIEW

Decimal growth stages for precision wheat production in changing environments?

H.M. Barber¹, J. Carney¹, F. Alghabari² & M.J. Gooding³

¹ School of Agriculture Policy and Development, University of Reading, Berkshire, UK

² Department of Arid Land Agriculture, King Abdulaziz University, Jeddah, Saudi Arabia

³ Institute of Biological, Environmental and Rural Sciences, University of Aberystwyth, Ceredigion, UK

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Correspondence

Prof. M.J. Gooding, Institute of Biological, Environmental and Rural Sciences, University of Aberystwyth, Gogerddan, Aberystwyth, Ceredigion SY23 3EE, UK. Email: mig21@aber.ac.uk

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Abstract

The utility of the decimal growth stage (DGS) scoring system for cereals is reviewed. The DGS is the most widely used scale in academic and commercial applications because of its comprehensive coverage of cereal developmental stages, the ease of use and definition provided and adoption by official agencies. The DGS has demonstrable and established value in helping to optimise the timing of agronomic inputs, particularly with regard to plant growth regulators, herbicides, fungicides and soluble nitrogen fertilisers. In addition, the DGS is used to help parameterise crop models, and also in understanding the response and adaptation of crops to the environment. The value of the DGS for increasing precision relies on it indicating, to some degree, the various stages in the development of the stem apex and spike. Coincidence of specific growth stage scores with the transition of the apical meristem from a vegetative to a reproductive state, and also with the period of meiosis, is unreliable. Nonetheless, in pot experiments it is shown that the broad period of booting (DGS 41–49) appears adequate for covering the duration when the vulnerability of meiosis to drought and heat stress is exposed. Similarly, the duration of anthesis (61–69) is particularly susceptible to abiotic stresses: initially from a fertility perspective, but increasingly from a mean grain weight perspective as flowering progresses to DGS 69 and then milk development. These associations with DGS can have value at the crop level of organisation: for interpreting environmental effects, and in crop modelling. However, genetic, biochemical and physiological analysis to develop greater understanding of stress acclimation during the vegetative state, and tolerance at meiosis, does require more precision than DGS can provide. Similarly, individual floret analysis is needed to further understand the genetic basis of stress tolerance during anthesis.

Introduction

Cereal plants mature from seed germination to harvest via distinct but integrated developmental phases, typical of annual grasses. It is clear that the effects of agronomic inputs and the environment on crops interact greatly with developmental stage (Klepper *et al.*, 1982; Kirby & Appleyard, 1987; Entz & Fowler, 1988; Landes & Porter, 1989; Slafer & Rawson, 1994; Frank *et al.*, 1997; Sylvester-Bradley *et al.*, 2008; Leather, 2010; Thomas,

2014). This journal has, therefore, been at the forefront of describing and furthering the use of growth stage descriptions for the benchmarking and definition of experimental treatments and for the interpretation of cereal crop responses (Tottman, 1977; Tottman *et al.*, 1979; Tottman, 1987; Lancashire *et al.*, 1991; Vahamidis *et al.*, 2014). Here we review the utility and application of the most widely used growth stage scoring system: that of Zadoks *et al.* (1974b) as further illustrated and defined by Tottman *et al.* (1979), with commendation from Zadoks (1985) and

Tottman (1987). The combined citations in the academic literature to the original score and subsequent illustrations and amendments are, so far, well over 5000. Further citations are to very closely related scales that owe much of their development to Zadoks *et al.* (1974*b*), including the BBCH scale that has been widely applied and extended to use with both monocotyledon and dicotyledon plant species (e.g. Hess *et al.*, 1997; Arcila-Pulgarín *et al.*, 2002). The scale of Zadoks *et al.* (1974*b*) has a decimal format (Table 1), so henceforth the scale and the scores within it will be referred to as the decimal growth stage, that is DGS. We provide an overview of the DGS and its common uses, before assessing the extent to which DGS does reflect physiological development, and therefore the extent to which DGS can be used to assess crop adaptation.

Growth stage scores defining cereal development

Schemes for defining crop growth stage have been 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). The DGS is an exterior scheme, first published in *Eucarpia Bulletin* (Zadoks *et al.*, 1974*a*), followed by *Weed Research* (Zadoks *et al.*, 1974*b*), *Annual Wheat Newsletter* (Zadoks *et al.*, 1975*a*) and *Cereal Rusts Bulletin* (Zadoks *et al.*, 1975*b*). 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-memorise, 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 and Porter (1989) compare DGS with six other 'exterior' scales: Feekes (1941), Keller and Baggiolini (1954), Woodford and Evans (1965), Chancellor (1966), Kuperman (1973), Waldren and 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) purports 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 fertilisers and agrochemicals in crop production (e.g. Anon., 2009). 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; Huberman *et al.*, 2014; Peng *et al.*, 2014), 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; Kennedy & Connery, 2012), fungicides (Nelson & Sutton, 1987; Cook & Hayward, 1988; Guy *et al.*, 1989; Goulds & Fitt, 1990; Duczek & Jones-Flory, 1994; Cook *et al.*, 1999; 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.*, 1997; Maird *et al.*, 1998; Sticksel *et al.*, 1999, 2000; Flowers *et al.*, 2001; Weisz *et al.*, 2001; Efreteui *et al.*, 2015) are all commonly interpreted with reference to DGS. Similarly, the responses to other agronomic decisions, such as sowing density, can be interpreted with reference to canopy formation and architecture at particular DGS (Whaley *et al.*, 2000). 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.*, 1997); 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.* (1974*b*), DGS can be an unreliable predictor for physiological development as defined by the status of the meristems. It is the developmental stage of the stem apex 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

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

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

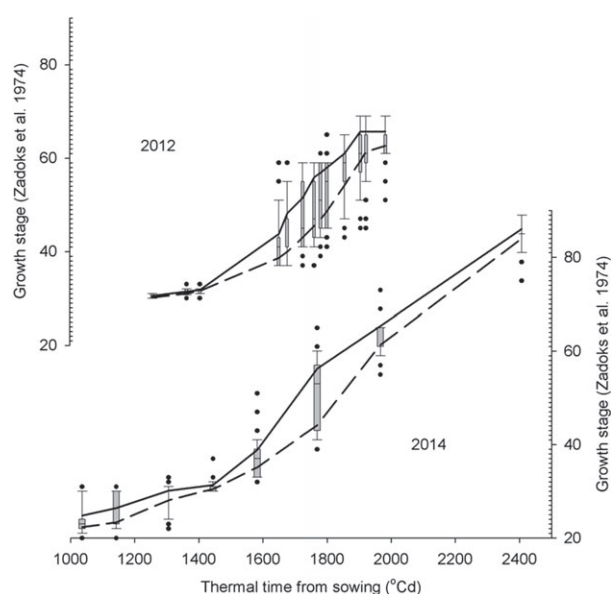


Figure 1 Distribution of decimal growth stage (DGS) for 64 doubled haploid progeny of Renesansa and Savannah when field grown in the UK in two seasons. Boxes are limited by 25 and 75 percentiles, whiskers by 10 and 90 percentiles; points are outliers beyond 10 and 90 percentiles, and the line within 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).

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.

Crop development and coincidence with the DGS

The development of the shoot apex and its role in the origin of leaves, tillers, stem and ear is described by Kirby and Appleyard (1987) and reviewed by McMaster (1997). 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 1.5–4 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 soil surface. 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 at 10 mm above the crown (but which could still be below the soil surface). Indeed, in the definitions of Tottman (1987), an apex above 10 mm could still be described as at DGS 30 as long as the first internode was less than 10 mm long. Mulholland *et al.* (1997) for one site and genotype found terminal spikelet to coincide with *late* DGS 31. Late DGS 31 could involve the apex being 30 mm above the crown (Tottman, 1987). Overall, therefore, the ear being 10–30 mm above, the crown would normally encompass the terminal spikelet stage, coinciding with DGS 31–32, 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 20–25 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 leaf sheaths as the developing ear expands within them. Tottman (1987) associates meiosis with DGS 37, that is the appearance of the flag leaf. Zadoks *et al.* (1974*b*) state that meiosis in wheat occurs in the early booting *stage*, that is 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 1–2 days at 20–15°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 phases. In work on the effects of drought on photosynthesis, Fábíán *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 5 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 (DGS 51) of the main stems (Westgate *et al.*, 1996; Subedi *et al.*, 1998; Alghabari *et al.*, 2014).

Heading date is often recorded when assessing genotypes, for example Pask *et al.* (2014) and Lopez *et al.* (2014) define heading date as when 50% of ears have fully emerged, that is when 50% of ears are at DGS 59. The adaptive significance of heading date is principally because of 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. Of some concern is that peduncle extension can sometimes be insufficient, particularly in short cultivars under stress, such that anthesis can sometimes occur without full ear emergence. 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 2–5 days, while over a whole plant or crop may extend over 5–10 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 development can be described as proceeding in three phases (Jenner *et al.*, 1991), which can be roughly demarcated by reference to water fluxes (Pepler *et al.*, 2006). 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 fertilisation. 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 continues a near linear increase in grain dry matter, accumulation while mass of water per grain 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) stage (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 and Wych (1982) also associate physiological maturity with senescence, 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. Mulholland *et al.*, 1997; Sanna *et al.*, 2014). 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 parameterise models (M.A. Semenov, personal communication). Gillett *et al.* (1999) present a model describing the growth and senescence of the canopy, and relate fitted parameters to specific DGS as observed in the field: maximum green area index occurred between DGS 55 and 61 in 10 out of 12 cases. 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). It should be acknowledged, however, that discrepancies between model predictions of DGS and field observations do occur (Kirby & Weightman, 1997; Weightman *et al.*, 1997). There has been little work attempting to quantify how specific environmental factors influence the coincidence between DGS and spike development, or how they contribute to discrepancies between model performance and field observations.

The DGS 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 utilisation efficiencies, such as by increasing radiation-use and harvest indices that are 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. Beed *et al.* (2007) investigate how light limitation during specific growth stages defined by DGS influence yield and yield components. The power of DGS analysis for interpreting and predicting effects on grain yield, however,

depends on the following: 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 (vernalisation) and day length (photoperiod). The vernalisation requirement is particularly influenced by alleles at the *Vrn-1* loci, located on each of the long arms of the group 5 chromosomes, that is *Vrn-A1*, *Vrn-B1* and *Vrn-D1*, and their regulation by minor vernalisation genes (Loukoianov *et al.*, 2005; Reynolds *et al.*, 2012). Wheats with a significant vernalisation requirement (winter wheats) are maintained in a vegetative state until the requirement has been met. Acevedo *et al.* (2002) found spring wheats to require 7–18°C for 5–15 days for floral initiation, while winter wheats required 0–7°C for 30–60 days. Development can also be accelerated by exposure to long days, that is 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, that is *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 14 days earlier than photoperiod-sensitive genotypes in typical UK field conditions (Snape *et al.*, 2001; Fig. 1), mostly associated with time to DGS 31, rather than the duration from DGS 31 to 61 at this latitude (Foulkes *et al.*, 2004).

Even when vernalisation 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, vernalisation 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 (Slafer & Rawson, 1994). Fig. 1 shows the wide distribution of growth stages attained in 64 doubled haploid progeny of *Renesansa* and *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 vernalisation 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 vernalisation and the exposure of photoperiod-sensitive varieties to short days helps maintain plants in the vegetative state and thereby better able to acclimatise 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 Melo Sereno *et al.*, 1981) and abiotic stresses such as cold (Subedi *et al.*, 1998; Tang *et al.*, 2011), heat (Saini & Aspinall, 1982; Barnabas *et al.*, 2008; Jaeger *et al.*, 2008; Omid *et al.*, 2014) and drought (Saini & Aspinall, 1981; Dorion *et al.*, 1996; Lalonde *et al.*, 1997a,b; Barnabas *et al.*, 2008; Jaeger *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 5 days, it should be possible to broadly map susceptibility to abiotic stresses occurring during periods reasonably demarcated by DGS. Fig. 2 are results from a complete factorial replicated pot experiment (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 timing of stress or irrigating to field capacity). Environment treatments were imposed by transferring pots to matched growth cabinets at 15:30 h GMT for three 16 h day, 8 h night cycles (8°C below day temperature) before returning to the original, completely randomised, position outside. Each main stem 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. 2A), a weakness that is further exacerbated by the imposition of high temperatures (Fig. 2B and 2C). In contrast, mean grain weight in this experiment was largely unaffected by drought imposed during booting (Fig. 2D), and when just heat was considered high temperature stress at booting resulted in heavier grains (Fig. 2E) in partial compensation for the poor grain set (Fig. 2B). 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, for example 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 main stem 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. 3e versus 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

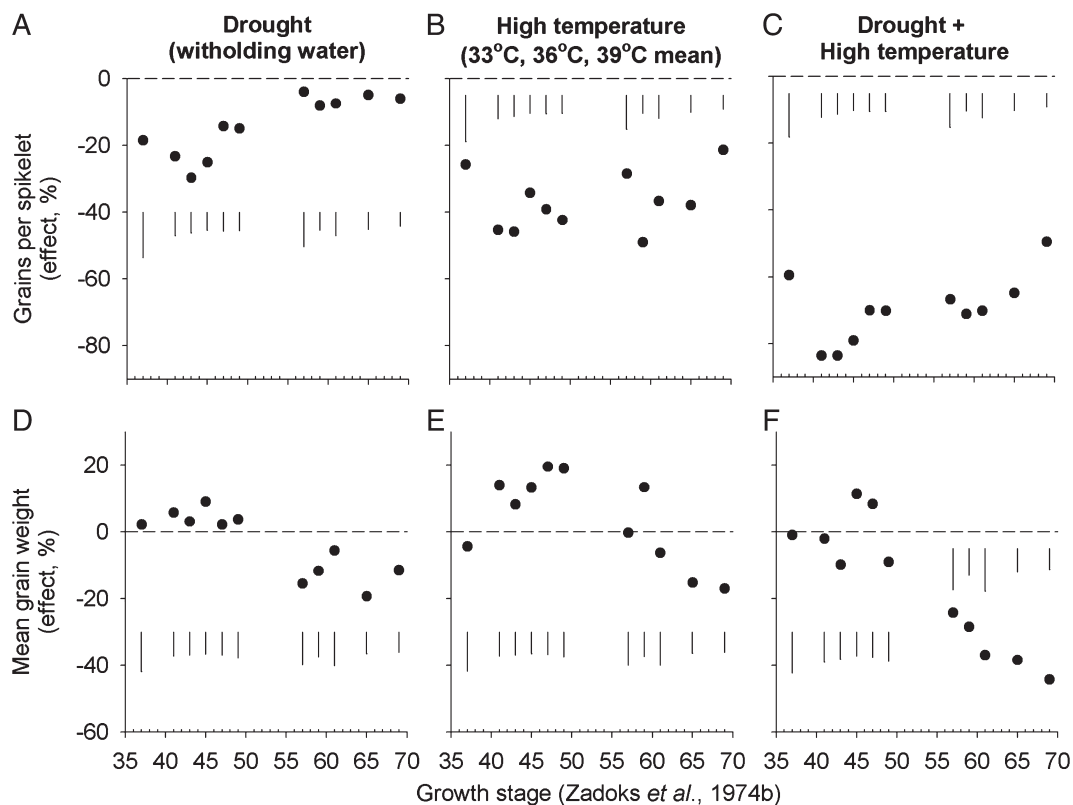


Figure 2 The effect of stem growth stage at the start of 3-day transfers to controlled environment cabinets for the imposition of heat and drought stresses (Alghabari *et al.*, 2014). In each panel, the horizontal dashed line represents the mean result from plants transferred to temperatures 20, 27 and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

particularly marked in Savannah, during a 5-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, 1995*a,b,c*; Wheeler *et al.*, 1996; Ferris *et al.*, 1998; Barnabas *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 that 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 3 days after fertilisation. The earliest flowers on ears assessed as having just completed anthesis at DGS 69 may have been fertilised 4 or 5 days earlier (M. Lukac, personal communication), and hence

beyond the vulnerable growth stage (Saini & Aspinall, 1982; Stone & Nicolas, 1995*a,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

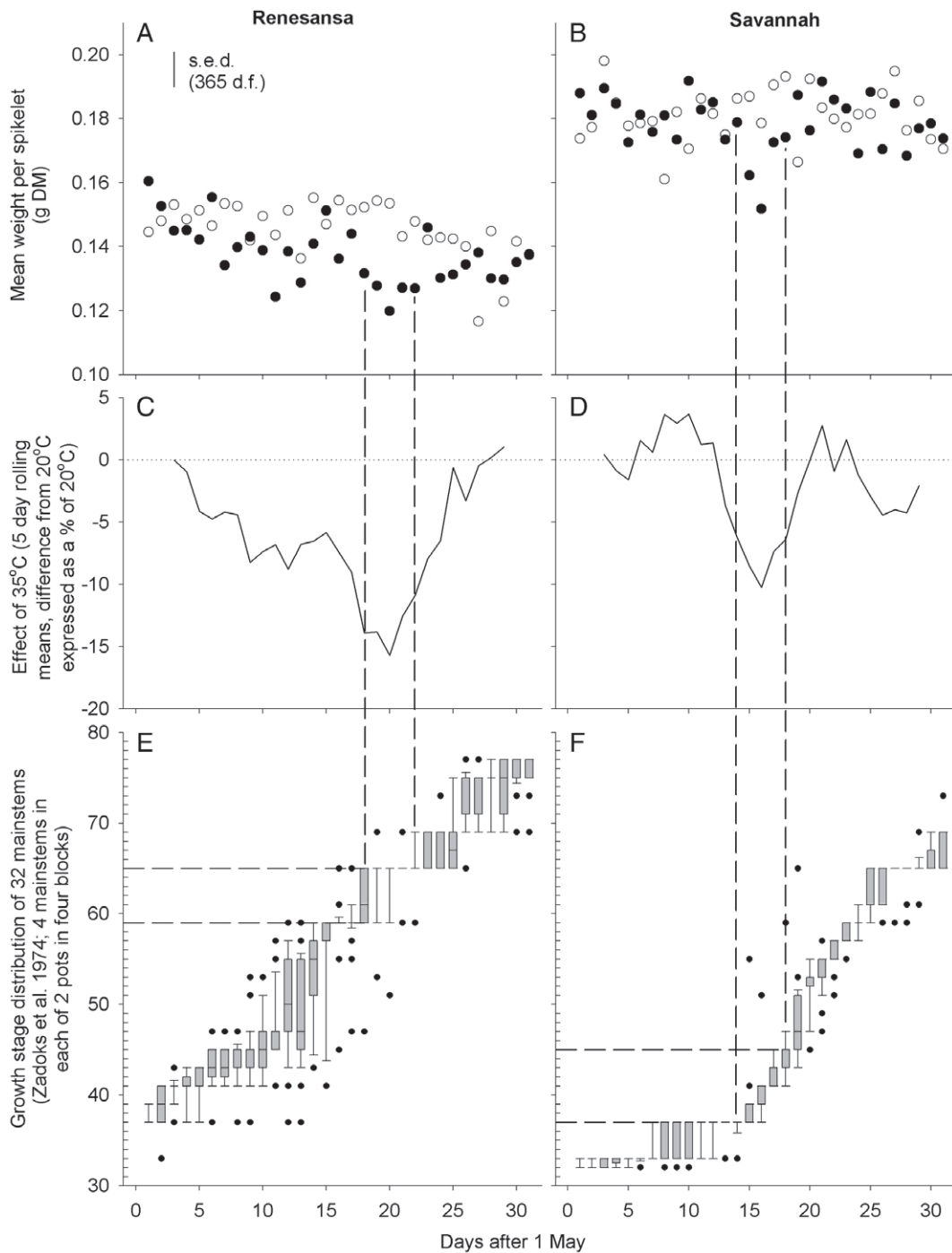


Figure 3 Effects of wheat cultivar and successive 1-day transfers to controlled environment cabinets at 20/12 (O) and 35/27°C (●) day/night temperature (16 h day) on mean weight per spikelet of main stems. (E) and (F) give the growth stage distributions of the main stems at the time of transfer in to 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). SED 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. Median growth stages for when plants were removed from the cabinets are given in Fig. 4.

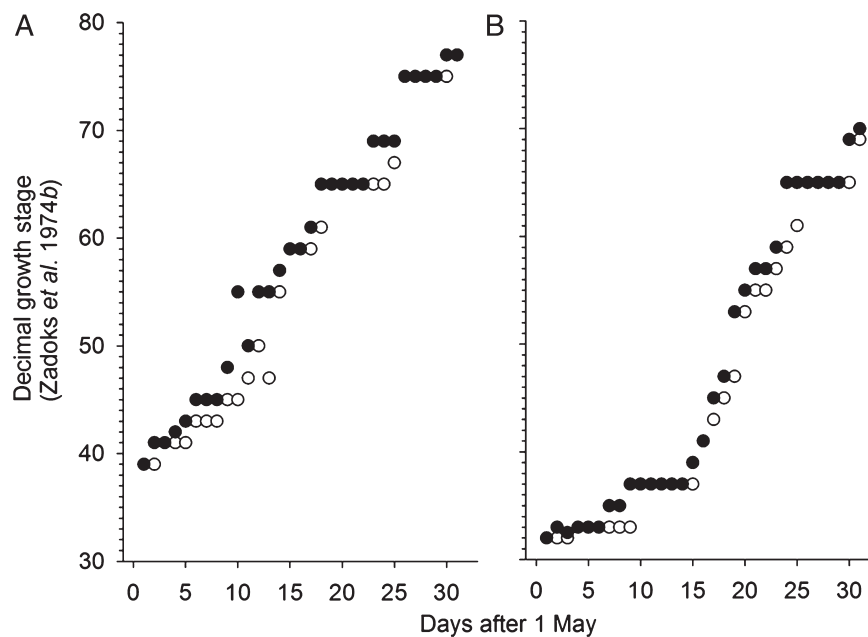


Figure 4 Effect of cultivar [(A) Renesansa; (B) Savannah] and day of transfer to controlled environment cabinets at 20/12 35/27°C day/night temperature (16 h day) on the median growth stage when transferred (O), and when removed from the cabinet (●) 24 h later.

UK out of its intended region of adaptation, however, also resulted in less synchronous development (Fig. 3E and 3F), and it is possible that any consequent reduced co-ordination of reproductive and flowering processes may have been exacerbated by abiotic challenges (Lukac *et al.*, 2012). These pot experiments do not allow for certain adaptations that might be conferred in the field such as more efficient root architectures (Semenov *et al.*, 2014), or acclimatisation as a drought develops, but we found no evidence that greater diversity in flowering time improved resilience as suggested by Lukac *et al.* (2012), rather the reverse.

Maximising resource capture and dry matter partitioning

Figs 5 and 6 show results from the Renesansa and 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. 6O; Gallagher & Biscoe, 1978). Extending the growing season in clement and high light availability conditions, and as rotational system factors allow, can therefore increase yields, particularly when light interception is increased late in the season (Figs 5O and 6D; Gooding *et al.*, 2005; Sylvester-Bradley *et al.*, 2005). Early season growth, however, may be less important, particularly if

it is at the expense of harvest index (Figs 5F and 6F). 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 (RUE; Figs 5 and 6; 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 RUE during the so-called critical period when the spikes are actively growing during the stem elongation phase until immediately after anthesis (Reynolds *et al.*, 2012). Increasing light interception during this phase can increase the number of florets that become fertile and avoid floret death (Kirby, 1988; Reynolds *et al.*, 1999; Miralles *et al.*, 2000; González *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 (García *et al.*, 2014). In the Renesansa and Savannah population, grain yield was positively associated with light interception in the stem elongation phase up to around 275 MJ PAR m⁻² (Fig. 6B). As light interception increased

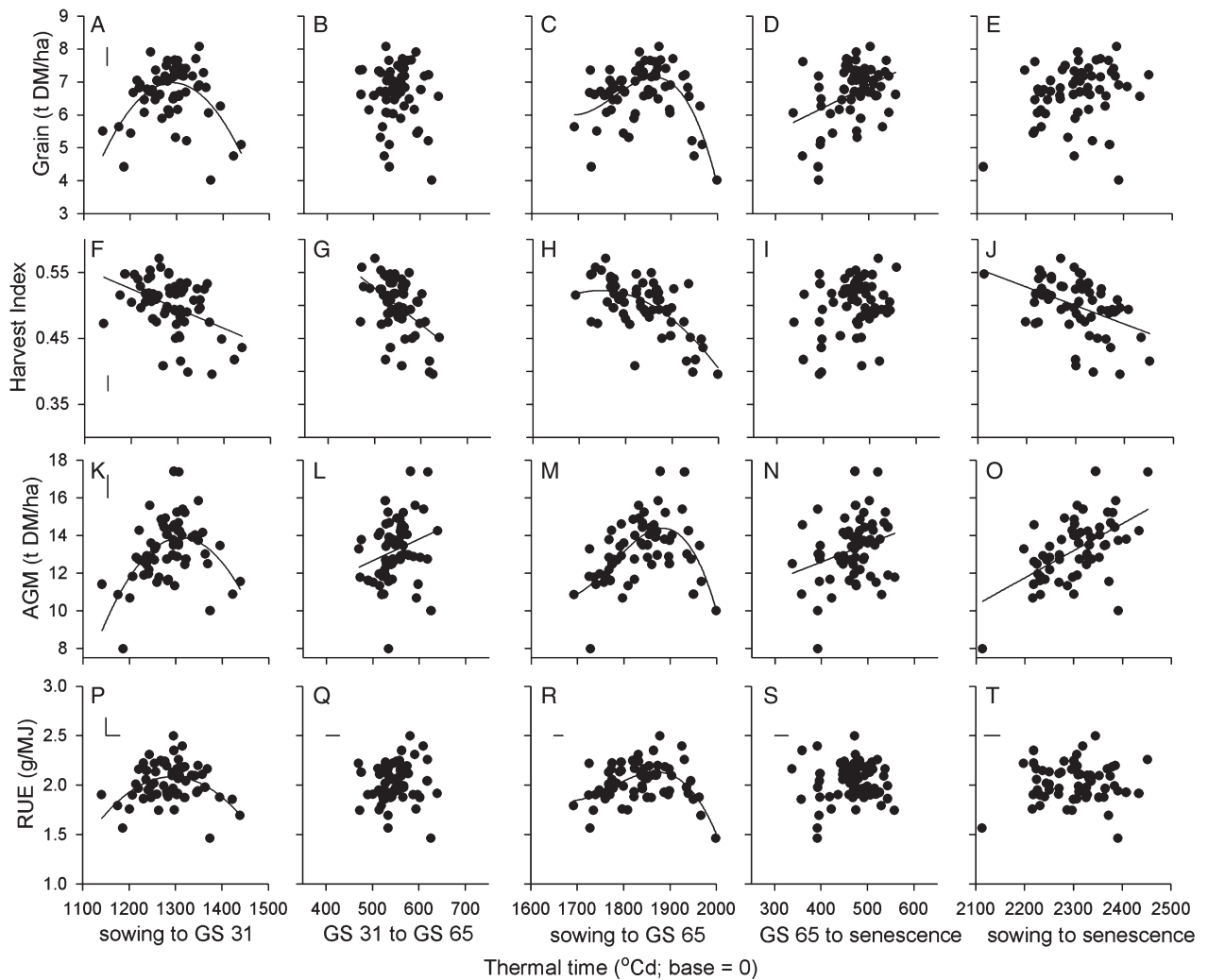


Figure 5 Durations between different decimal growth stages (DGS; Zadoks *et al.*, 1974b) of 64 doubled haploid progeny of Renesansa and Savannah and associations with radiation-use efficiency (RUE), above ground mass (AGM), and harvest index. Points are means of two replicate field-grown plots in each of three growing seasons. Error bars are SED for comparing points. Fitted lines are polynomial effects when significant ($P < 0.05$).

further, grain yields decreased because here increasing PAR was achieved with excessive delays in anthesis and a consequential reduction in harvest index (Fig. 5G).

Conclusions

Being able to assess and record the developmental stage of a crop is essential for optimising inputs, benchmarking crop performance and understanding crop adaptation. The Zadoks *et al.* (1974b) scale and as illustrated and further defined by Tottman *et al.* (1979) and Tottman (1987) has been widely adopted because of its comprehensive coverage from germination to harvest maturity, its ease of use and clarity of interpretation, the ability to describe individual plants or spikes as well as a community of

plants and its use as an official standard. Decimal growth stage can be broadly mapped on to the development of the stem apex and spike, although there are weaknesses particularly with regard to the transition of the growing point from vegetative to reproductive states, and also for the start of meiosis. Despite lack of precision in defining certain developmental phases, the DGS has been proved sufficiently robust for widespread use in commercial cereal production for directing agrochemical and fertiliser application. In terms of understanding crop adaptation, and for parameterising crop models, the important period from the start of stem extension until the start of grain filling appears to be captured by DGS: many assume DGS 31 to broadly signify the start of rapid stem extension and reasonable coincidence with terminal spikelet stage. Booting

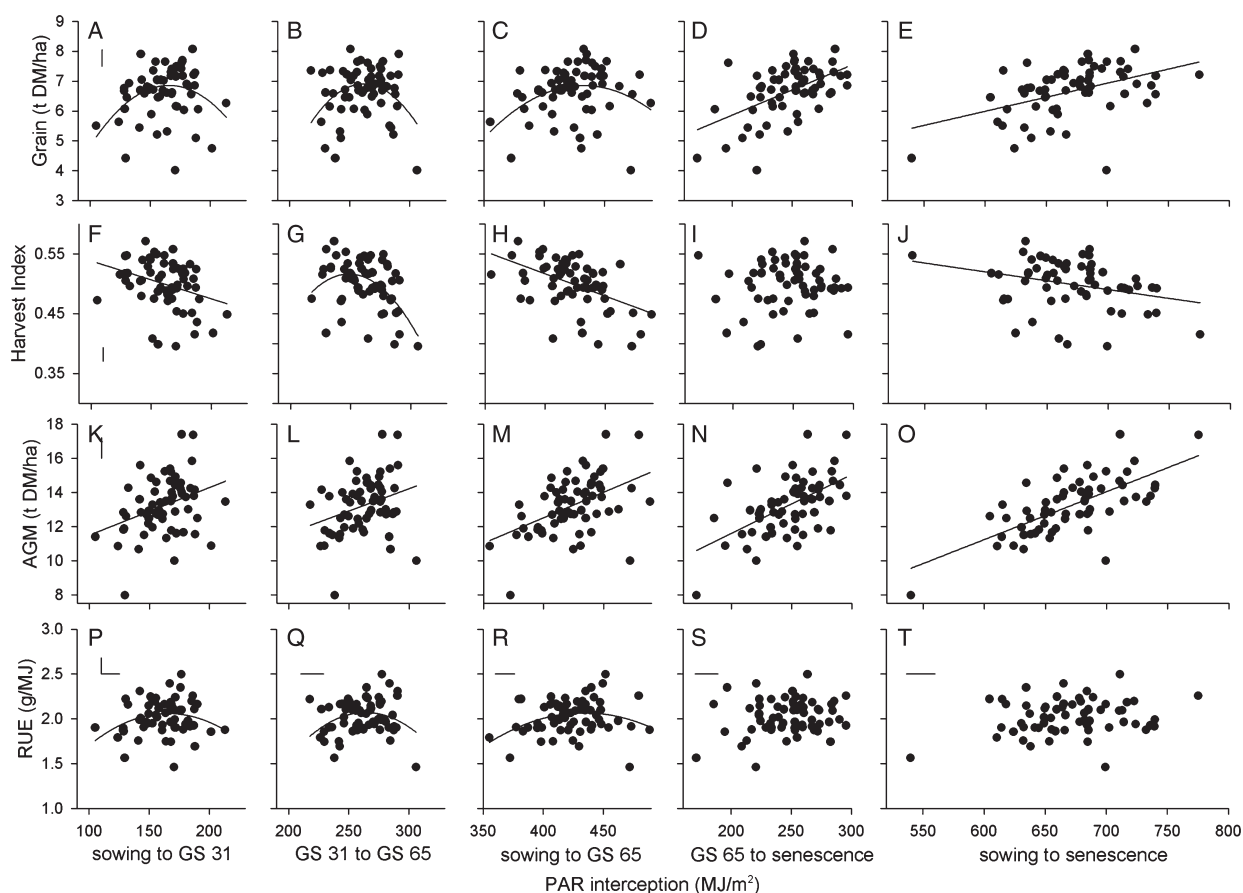


Figure 6 Interception of photosynthetically active radiation between different decimal growth stages (DGS; Zadoks *et al.*, 1974b) of 64 doubled haploid progeny of Renesansa and Savannah and associations with radiation-use efficiency (RUE), above ground mass (AGM) and harvest index. Points are means of two replicate field-grown plots in each of three growing seasons. Error bars are SED for comparing points. Fitted lines are polynomial effects when significant ($P < 0.05$).

appears adequate for defining the period during which the vulnerability of meiosis is exposed. However, genetic, biochemical and physiological analysis to develop greater understanding of stress tolerance at meiosis does require more precision than DGS can provide. Similarly, anthesis is particularly susceptible to abiotic stresses: initially from a fertility perspective, but increasingly from a mean grain weight perspective as flowering progresses to DGS 69 and then milk development. The vulnerability of anthesis is, therefore, captured by DGS, but individual floret analysis may be needed to further understand the genetic basis of tolerance (Jagadish *et al.*, 2010; Lukac *et al.*, 2012; Steinmeyer *et al.*, 2013). Emerging phenotyping technologies should be assessed for ability in defining growth stages; further assistance in the non-destructive determination of the start of the reproductive stage, and for meiosis would be particularly welcomed.

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