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CENTENARY REVIEW

Decimal growth stages for precision wheat production in changing environments?

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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.* (1974b), 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.* (1974b) 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.*, 1974a), followed by *Weed Research* (Zadoks *et al.*, 1974b), *Annual Wheat Newsletter* (Zadoks *et al.*, 1975a) and *Cereal Rusts Bulletin* (Zadoks *et al.*, 1975b). 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; Maidl *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.* (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 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.* (1974b) 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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References

- Acevedo E., Silva P., Silva H. (2002) Wheat growth and physiology. In *Bread Wheat Improvement and Production*, pp. 39–70. Eds B.C. Curtis, S. Rajaram and H. Gómez Macpherson. Rome, Italy: FAO.
- Addisu M., Snape J.W., Simmonds J.R., Gooding M.J. (2010) Effects of reduced height (*Rht*) and photoperiod insensitivity (*Ppd*) alleles on yield of wheat in contrasting production systems. *Euphytica*, **172**, 169–181.

- Alghabari F., Lukac M., Jones H.E., Gooding M.J. (2014) Effect of *Rht* alleles on the tolerance of wheat grain set to high temperature and drought stress during booting and anthesis. *Journal of Agronomy and Crop Science*, **200**, 36–45.
- Anon (2009) *Cereal Growth Stages – A Guide for Crop Treatments*. Stoneleigh, UK: Home-Grown Cereals Authority.
- Arcila-Pulgarín J., Buhr L., Bleiholder H., Hack H., Meier U., Wicke H. (2002) Application of the extended BBCH scale for the description of the growth stages of coffee (*Coffea* spp.). *Annals of Applied Biology*, **141**, 19–27.
- Asseng S., Ewert F., Rosenzweig C., Jones J.W., Hatfield J.L., Ruane A.C., Boote K.J., Thorburn P.J., Rotter R.P., Cammarano D., Brisson N., Basso B., Martre P., Aggarwal P.K., Angulo C., Bertuzzi P., Biernath C., Challinor A.J., Doltra J., Gayler S., Goldberg R., Grant R., Heng L., Hooker J., Hunt L.A., Ingwersen J., Izaurralde R.C., Kersebaum K.C., Muller C., Naresh Kumar S., Nendel C., O’Leary G., Olesen J.E., Osborne T.M., Palosuo T., Priesack E., Ripoche D., Semenov M.A., Shcherbak I., Steduto P., Stockle C., Stratonovitch P., Streck T., Supit I., Tao F., Travasso M., Waha K., Wallach D., White J.W., Williams J.R., Wolf J. (2013) Uncertainty in simulating wheat yields under climate change. *Nature Climate Change*, **3**, 827–832.
- Bányai J., Karsai I., Balla K., Kiss T., Bedő Z., Láng L. (2014) Heat stress response of wheat cultivars with different ecological adaptation. *Cereal Research Communications*, **42**, 413–425.
- Barnabas B., Jäger K., Feher A. (2008) The effect of drought and heat stress on reproductive processes in cereals. *Plant, Cell and Environment*, **31**, 11–38.
- Beed F.D., Paveley N.D., Sylvester-Bradley R. (2007) Predictability of wheat growth and yield in light-limited conditions. *Journal of Agricultural Science*, **145**, 63–79.
- Bennett M.D., Smith J.B., Kemble R. (2011) The effect of temperature on meiosis and pollen development in wheat and rye. *Canadian Journal of Genetics and Cytology*, **14**, 615–624.
- Bodson B., Durdu M.-H. (1996) Study of the possibilities of use of chlormequat chloride at different development stages of winter wheat. *Mededelingen Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen Universiteit Gent*, **61**, 1129–1135.
- Carter N., Powell W., Wright A.F., Ashby J.E. (1989) Effectiveness of different insecticides applied at various growth stages to control aphids on winter wheat. *Crop Protection*, **8**, 271–276.
- Chancellor R.J. (1966) A note on the definition of cereal growth stages. *Weed Research*, **6**, 172–178.
- Cook R.J., Hayward C.F. (1988) Effect of fungicide and spray timing on control of *Septoria tritici* on wheat. *Tests of Agrochemicals and Cultivars*, No. 9, *Annals of Applied Biology*, **112**, Supplement, 42–43.
- Cook R.J., Hims M.J., Vaughan T.B. (1999) Effects of fungicide spray timing on winter wheat disease control. *Plant Pathology*, **48**, 33–50.
- Craufurd P.Q., Cartwright P.M. (1989) Effect of photoperiod and chlormequat on apical development and growth in a spring wheat (*Triticum aestivum*) cultivar. *Annals of Botany*, **63**, 515–525.
- Craufurd P.Q., Vadz V., Jagadish S.V.K., Prasad P.V.V., Zaman-Allah M. (2013) Crop science experiments designed to inform crop modelling. *Agricultural and Forest Meteorology*, **170**, 8–18.
- Darwinkel A. (1983) Ear formation and grain-yield of winter wheat as affected by time of nitrogen supply. *Netherlands Journal of Agricultural Science*, **31**, 211–225.
- De Melo Sereno M.J.C., Fernandes M.I.D., Zanettini M.H. (1981) Effects of pesticides, fungal diseases and pests on the meiotic behavior of wheat. *Revista Brasileira de Genética*, **4**, 593–610.
- Dimmock J.P.R.E., Gooding M.J. (2002) The effects of fungicides on rate and duration of grain filling in winter wheat in relation to maintenance of flag leaf green area. *Journal of Agricultural Science*, **138**, 1–16.
- Dorion S., Lalonde S., Saini H.S. (1996) Induction of male sterility in wheat by meiotic-stage water deficit is preceded by a decline in invertase activity and changes in carbohydrate metabolism in anthers. *Plant Physiology*, **111**, 137–145.
- Duczek L.J., Jones-Flory L.L. (1994) Effect of timing of propiconazole application on foliar disease and yield of irrigated spring wheat in Saskatchewan from 1990 to 1992. *Canadian Journal of Plant Science*, **74**, 205–207.
- Edwards S.G., Godley N.P. (2010) Reduction of Fusarium head blight and deoxynivalenol in wheat with early fungicide applications of prothioconazole. *Food Additives and Contaminants Part A: Chemistry Analysis Control Exposure & Risk Assessment*, **27**, 629–635.
- Efretuei A., Gooding M., White E., Spink J., Hackett R. (2015) Effect of nitrogen fertilizer timing on nitrogen use efficiency and grain yield of winter wheat. *Irish Journal of Agricultural and Food Research*, in press.
- Entz M.H., Fowler D.B. (1988) Critical stress periods affecting productivity of no-till winter wheat in Western Canada. *Agronomy Journal*, **80**, 987–992.
- Evans L.T., Wardlaw I.F., Fischer R.A. (1975) Wheat. In *Crop Physiology*, pp. 101–150. Ed. L.T. Evans. London, UK: Cambridge University Press.
- Fábián A., Jaeger K., Barnabás B. (2013) Developmental stage dependency of the effect of drought stress on photosynthesis in winter wheat (*Triticum aestivum* L.) varieties. *Acta Agronomica Hungarica*, **61**, 13–21.
- Feekes W. (1941) *De Tarwe en haar milieu*, pp. 560–561. Verslagen van de Technische Tarwe Commissie, 17 Groningen: Hoitsema
- Ferris R., Ellis R.H., Wheeler T.R., Hadley P. (1998) Effect of high temperature stress at anthesis on grain yield and biomass of field-grown crops of wheat. *Annals of Botany*, **82**, 631–639.

- Fischer R.A. (1985) Number of kernels in wheat crops and the influence of solar radiation and temperature. *Journal of Agricultural Science*, **105**, 447–461.
- Flowers M., Weisz R., Heiniger R. (2001) Remote sensing of winter wheat tiller density for early nitrogen application decisions. *Agronomy Journal*, **93**, 783–789.
- Foulkes M.J., Sylvester-Bradley R., Worland A.J., Snape J.W. (2004) Effects of a photoperiod-response gene *Ppd-D1* on yield potential and drought resistance in UK winter wheat. *Euphytica*, **135**, 63–73.
- Fowler D.B., Limin A.E. (2007) Progress in breeding wheat with tolerance to low temperature in different phenological developmental stages. In *Wheat Production in Stressed Environments*, pp. 301–314. Eds H.T. Buck, J.E. Nisi and N. Salomón. Dordrecht, the Netherlands: Springer.
- Frank A.B., Cardwell V.B., Ciha A.J., Wilhelm W.W. (1997) Growth staging in research and crop management. *Crop Science*, **37**, 1039–1040.
- Gallagher J.N., Biscoe P.V. (1978) Radiation absorption, growth and yield of cereals. *Journal of Agricultural Science*, **91**, 47–60.
- Gandee C., Gooding M.J., Davies W.P. (1997) Interactions between nitrogen and growth regulator on bread wheat (*Triticum aestivum*) and spelt (*T. spelta*). Optimising cereal inputs: its scientific basis. *Aspects of Applied Biology*, **50**, 219–224.
- Gandee C., Gooding M.J., Davies W.P. (1998) Nitrogen and growth regulator effects on yield and grain quality of spelt (*Triticum spelta*) and bread wheat (*T. aestivum*). In *European Society for Agronomy, Short Communications 1, Fifth Congress*, pp. 257–258. Eds M. Zima and M.L. Bartosova. Montpellier, France: European Society of Agronomy.
- Gao X.P., Francis D., Ormrod J.C., Bennett M.D. (1992) Changes in cell number and cell-division activity during endosperm development in allohexaploid wheat, *Triticum aestivum* L. *Journal of Experimental Botany*, **43**, 1603–1609.
- García A., Serrago R.A., González F.G., Slafer G.A., Reynolds M.P., Miralles D.J. (2014) Wheat grain number: identification of favourable physiological traits in an elite doubled-haploid population. *Field Crops Research*, **168**, 126–135.
- Gillett A.G., Crout N.M.J., Stokes D.T., Sylvester-Bradley R., Scott R.K. (1999) Simple winter wheat green area index model under UK conditions. *Journal of Agricultural Science*, **132**, 263–271.
- González F.G., Slafer G.A., Miralles D.J. (2003) Grain and floret number in response to photoperiod during stem elongation in fully and slightly vernalized wheats. *Field Crop Research*, **81**, 17–27.
- Gooding M.J., Ellis R.H., Shewry P.R., Schofield J.D. (2003) Effects of restricted water availability and increased temperature on the grain filling, drying and quality of winter wheat. *Journal of Cereal Science*, **37**, 295–309.
- Gooding M.J., Gregory P.J., Ford K.E., Pepler S. (2005) Fungicide and cultivar affect post-anthesis patterns of nitrogen uptake, remobilization and utilization efficiency in wheat. *Journal of Agricultural Science*, **143**, 503–518.
- Goulds A., Fitt B.D.L. (1990) Effects of fungicide timing on the severity of eyespot on winter wheat or winter barley inoculated with w-type or r-type isolates of *Pseudocercospora herpotrichoides*. *Crop Protection*, **9**, 265–270.
- Griffiths S., Simmonds J., Leverington M., Wang Y., Fish L., Sayers L., Alibert L., Orford S., Wingen L., Herry L., Faure S., Laurie D., Bilham L., Snape J. (2009) Meta-QTL analysis of the genetic control of ear emergence in elite European winter wheat germplasm. *Theoretical and Applied Genetics*, **119**, 383–395.
- Guy S.O., Oplinger E.S., Wiersma D.W., Grau C.R. (1989) Agronomic and economic responses of winter wheat to foliar fungicides. *Journal of Production Agriculture*, **2**, 68–73.
- Hanft J.M., Wych R.D. (1982) Visual indicators of physiological maturity of hard red spring wheat. *Crop Science*, **22**, 584–588.
- Harrell D.M., Wilhelm W.W., McMaster G.S. (1993) Scales – a computer-program to convert among 3 developmental stage scales for wheat. *Agronomy Journal*, **85**, 758–763.
- Harrell D.M., Wilhelm W.W., McMaster G.S. (1998) Scales 2: computer program to convert among developmental stage scales for corn and small grains. *Agronomy Journal*, **90**, 235–238.
- Hay R.K.M. (1986) Sowing date and the relationships between plant and apex development in winter cereals. *Field Crops Research*, **14**, 321–337.
- Hess M., Barralis G., Bleiholder H., Buhr L., Eggers T., Hack H., Stauss R. (1997) Use of the extended BBCH scale – general for the descriptions of the growth stages of mono- and dicotyledonous weed species. *Weed Research*, **37**, 433–441.
- Huberman M., Riov J., Goldschmidt E.E., Apelbaum A., Goren R. (2014) The novel ethylene antagonist, 3-cyclopropyl-1-enyl-propanoic acid sodium salt (CPAS), increases grain yield in wheat by delaying leaf senescence. *Plant Growth Regulation*, **73**, 249–255.
- Hussain Z., Leitch M.H. (2007) The effect of sulphur and regulators on growth characteristics and grain yield of spring sown wheat. *Journal of Plant Nutrition*, **30**, 67–77.
- Jaeger K., Fábíán A., Barnabás B. (2008) Effect of water deficit and elevated temperature on pollen development of drought sensitive and tolerant winter wheat (*Triticum aestivum* L.) genotypes. *Acta Biologica Szegediensis*, **52**, 67–71.
- Jagadish S.V.K., Muthurajan R., Oane R., Wheeler T.R., Heuer S., Bennett J., Craufurd P.Q. (2010) Physiological and proteomic approaches to address heat tolerance during anthesis in rice (*Oryza sativa* L.). *Journal of Experimental Botany*, **61**, 143–156.
- Jamieson P.D., Brooking I.R., Semenov M.A., McMaster G.S., White J.W., Porter J.R. (2007) Reconciling alternative models of phenological development in winter wheat. *Field Crops Research*, **103**, 36–41.

- Jenner C.F., Ugalde T.D., Aspinall D. (1991) The physiology of starch and protein deposition in the endosperm of wheat. *Australian Journal of Plant Physiology*, **18**, 211–226.
- Kamran A., Iqbal M., Spaner D. (2014) Flowering time in wheat (*Triticum aestivum* L.): a key factor for global adaptability. *Euphytica*, **197**, 1–26.
- Keller C., Baggolini M. (1954) Les stades repères dans la végétation du blé. *Revue Romande d'Agriculture, Lausanne*, **10**, 17–20.
- Kennedy T.F., Connery J. (2012) Control of barley yellow dwarf virus in minimum-till and conventional-till autumn-sown cereals by insecticide seed and foliar spray treatments. *Journal of Agricultural Science*, **150**, 249–262.
- Kettlewell P.S., Whitley E.A., Meredith W.S., Sylvester-Bradley R. (1983) Effects of early application of chlormequat on tillering and yield of winter wheat. *Journal of Agricultural Science*, **100**, 735–738.
- Kirby E.J.M. (1988) Analysis of leaf, stem and ear growth in wheat from terminal spikelet stage to anthesis. *Field Crops Research*, **18**, 127–140.
- Kirby E.J.M., Appleyard M. (1981) *Cereal Development Guide*. Stoneleigh, UK: National Agricultural Centre.
- Kirby E.J.M., Appleyard M. (1987) Development and structure of the wheat plant. In *Wheat Breeding: Its Scientific Basis*, pp. 287–311. Ed F.G.H. Lupton. London, UK: Chapman & Hall.
- Kirby E.J.M., Weightman R.M. (1997) Discrepancies between observed and predicted growth stages in wheat. *Journal of Agricultural Science*, **129**, 379–384.
- Kirby E.J.M., Appleyard M., Simpson N.A. (1994) Coordination of stem elongation and Zadoks growth stages with leaf emergence in wheat and barley. *Journal of Agricultural Science*, **122**, 21–29.
- Klepper B., Rickman R.W., Peterson C.M. (1982) Quantitative characterization of vegetative development in small cereal grains. *Agronomy Journal*, **74**, 789–792.
- Kong L.G., Si J.S., Feng B., Li S.D., Wang F.H., Sayre K. (2009) Differential responses of two types of winter wheat (*Triticum aestivum* L.) to autumn- and spring-applied mesosulfuron-methyl. *Crop Protection*, **28**, 387–392.
- Kuperman F.M. (1973) *Morfofiziologija rastenij*. Moscow, Russian Federation: Vysšaja Škola, 225 pp.
- Lalonde S., Morse D., Saini H.S. (1997a) Expression of a wheat ADP-glucose pyrophosphorylase gene during development of normal and water-stress-affected anthers. *Plant Molecular Biology*, **34**, 445–453.
- Lalonde S., Beebe D.U., Saini H.S. (1997b) Early signs of disruption of wheat anther development associated with the induction of male sterility by meiotic-stage water deficit. *Sexual Plant Reproduction*, **10**, 40–48.
- Lancashire P.D., Bleiholder H., Vandenboom T., Langeludde P., Stauss R., Weber E., Witzenger A. (1991) A uniform decimal code for growth stages of crops and weeds. *Annals of Applied Biology*, **119**, 561–601.
- Landes A., Porter J.R. (1989) Comparison of scales used for categorising the development of wheat, barley, rye and oats. *Annals of Applied Biology*, **115**, 343–360.
- Leaden M.I., Lozano C.M., Monterubbianesi M.G., Abello E.V. (2007) Spring wheat tolerance to DE-750 applications at different growth stages. *Weed Technology*, **21**, 406–410.
- Leather S.R. (2010) Precise knowledge of plant growth stages enhances applied and pure research. *Annals of Applied Biology*, **157**, 159–161.
- Limin A.E., Fowler D.B. (2006) Low-temperature tolerance and genetic potential in wheat (*Triticum aestivum* L.): response to photoperiod, vernalization, and plant development. *Planta*, **224**, 360–366.
- Lopez M.S., Saglam D., Ozdogan M., Reynolds M. (2014) Traits associated with winter wheat grain yield in Central and West Asia. *Journal of Integrative Plant Biology*, **56**, 673–683.
- Loukoianov A., Yan L.L., Blechl A., Sanchez A., Dubcovsky J. (2005) Regulation of *VRN-1* vernalization genes in normal and transgenic polyploid wheat. *Plant Physiology*, **138**, 2364–2373.
- Lukac M., Gooding M.J., Griffiths S., Jones H.E. (2012) Asynchronous flowering and within-plant flowering diversity in wheat and the implications for crop resilience to heat. *Annals of Botany*, **109**, 843–850.
- Mahfoozi S., Limin A.E., Hayes P.M., Hucl P., Fowler D.B. (2000) Influence of photoperiod response on the expression of cold hardiness in wheat and barley. *Canadian Journal of Plant Science*, **80**, 721–724.
- Maidl F.X., Sticksel E., Retzer F., Fischbeck G. (1998) Effect of varied N-fertilization on yield formation of winter wheat under particular consideration of mainstems and tillers. *Journal of Agronomy and Crop Science: Zeitschrift für Acker und Pflanzenbau*, **180**, 15–22.
- Mann B.P., Wratten S.D., Poehling M., Borgemeister C. (1991) The economics of reduced-rate insecticide applications to control aphids in winter wheat. *Annals of Applied Biology*, **119**, 451–464.
- Marcello H., Single W.V. (1971) Quantitative responses of wheat to photoperiod and temperature in the field. *Australian Journal of Agricultural Research*, **22**, 343–351.
- Marroni M.V., Viljanen-Rollinson S.L.H., Butler R.C., Deng Y. (2006) Fungicide timing for the control of *Septoria tritici* blotch of wheat. *New Zealand Plant Protection*, **59**, 160–165.
- Martin D.A., Miller S.D., Alley H.P. (1990) Spring wheat response to herbicides applied at three growth stages. *Agronomy Journal*, **82**, 95–97.
- McMaster G.S. (1997) Phenology, development, and growth of the wheat (*Triticum aestivum* L.) shoot apex: a review. *Advances in Agronomy*, **59**, 63–118.
- Miralles D.J., Richards R.A., Slafer G.A. (2000) Duration of the stem elongation period influences the number of fertile florets in wheat and barley. *Australian Journal of Plant Physiology*, **27**, 931–940.

- Mitchell R.A.C., Mitchell V.J., Driscoll S.P., Franklin J., Lawlor D.W. (1993) Effects of increased CO₂ concentration and temperature on growth and yield of winter wheat at two levels of nitrogen application. *Plant, Cell and Environment*, **16**, 521–529.
- Mulholland B.J., Craigen J., Black C.R., Stokes D.T., Zhang P., Colls J.J., Atherton J.G. (1997) Timing of critical developmental stages and leaf production in field-grown spring wheat for use in crop models. *Journal of Agricultural Science*, **129**, 155–161.
- Nelson K.E., Sutton J.C. (1987) Fungicides, fungicide timing and sowing date in relation to eyespot incidence in Ontario winter wheat. *Phytoprotection*, **68**, 111–120.
- Nicolas H. (2004) Using remote sensing to determine of the date of a fungicide application on winter wheat. *Crop Protection*, **23**, 853–863.
- Noda K., Kawabata C., Kanzaki K. (1994) Re-classification of developmental stage of wheat grain. *Breeding Science*, **44**, 115–120.
- Oakley J.N., Walters K.F.A., Ellis S.A., Green D.B., Watling M., Young J.E.B. (1996) Development of selective aphicide treatments for integrated control of summer aphids in winter wheat. *Annals of Applied Biology*, **128**, 423–436.
- Omidi M., Siahpoosh M.R., Mamghani R., Modarresi M. (2014) The influence of terminal heat stress on meiosis abnormalities in pollen mother cells of wheat. *Cytologia*, **79**, 49–58.
- Pageau D., Lajeunesse J. (2008) Control of volunteer canola in barley: effect of three herbicides applied at different cereal growth stages. *Canadian Journal of Plant Science*, **88**, 247–255.
- Pask A., Joshi A.K., Manès Y., Sharma I., Chatrath R., Singh G.P., Sohu V.S., Mavi G.S., Sakuru V.S.P., Kalappanavar I.K., Mishra V.K., Arun B., Mujahid M.Y., Hussain M., Gautam N.R., Barma N.C.D., Hakim A., Hoppitt W., Trethowan R., Reynolds M.P. (2014) A wheat phenotyping network to incorporate physiological traits for climate change in South Asia. *Field Crops Research*, **168**, 156–167.
- Peng D.L., Chen X.G., Yin Y.P., Lu K.L., Yang W.B., Tang Y.H., Wang Z.L. (2014) Lodging resistance of winter wheat (*Triticum aestivum* L.): lignin accumulation and its related enzymes activities due to the application of paclobutrazol or gibberellin acid. *Field Crops Research*, **157**, 1–7.
- Pepler S., Gooding M.J., Ford K.E., Ellis R.H. (2005) A temporal limit to the association between flag leaf life extension by fungicides and wheat yields. *European Journal of Agronomy*, **22**, 365–376.
- Pepler S., Gooding M.J., Ellis R.H. (2006) Modelling simultaneously water content and dry matter dynamics of wheat grains. *Field Crops Research*, **95**, 49–63.
- Porter J.R., Kirby E.J.M., Day W., Adam J.S., Appleyard M., Ayling S., Baker C.K., Beale P., Belford R.K., Biscoe P.V., Chapman A., Fuller M.P., Hampson J., Hay R.K.M., Hough M.N., Matthews S., Thompson W.J., Weir A.H., Willington V.B.A., Wood D.W. (1987) An analysis of morphological development stages in Avalon winter wheat crops with different sowing dates and at ten sites in England and Scotland. *Journal of Agricultural Science*, **109**, 107–121.
- Powlson D.S., Poulton P.R., Moller N.E., Hewitt M.V., Penny A., Jenkinson D.S. (1989) Uptake of foliar-applied urea by winter wheat (*Triticum aestivum*): the influence of application time and the use of a new ¹⁵N technique. *Journal of the Science of Food and Agriculture*, **48**, 429–440.
- Rajala A., Peltonen-Sainio P. (2002) Timing applications of growth regulators to alter spring cereal development at high latitudes. *Agricultural and Food Science in Finland*, **11**, 233–244.
- Reddy L., Allan R.E., Campbell K.A.G. (2006) Evaluation of cold hardiness in two sets of near-isogenic lines of wheat (*Triticum aestivum*) with polymorphic vernalization alleles. *Plant Breeding*, **125**, 448–456.
- Reynolds M.P., Rajaram S., Sayre K.D. (1999) Physiological and genetic changes of irrigated wheat in the post-green revolution period and approaches for meeting projected global demand. *Crop Science*, **39**, 1611–1621.
- Reynolds M., Foulkes J., Furbank R., Griffiths S., King J., Murchie E., Parry M., Slafer G. (2012) Achieving yield gains in wheat. *Plant, Cell and Environment*, **35**, 1799–1823.
- Robinson M.A., Cowbrough M.J., Sikkema P.H., Tardif F.J. (2013) Winter wheat (*Triticum aestivum* L.) tolerance to mixtures of herbicides and fungicides applied at different timings. *Canadian Journal of Plant Science*, **93**, 491–501.
- Saini H.S., Aspinall D. (1981) Effect of water deficit on sporogenesis in wheat (*Triticum aestivum* L.). *Annals of Botany*, **48**, 623–633.
- Saini H.S., Aspinall D. (1982) Abnormal sporogenesis in wheat (*Triticum aestivum* L.) induced by short periods of high temperature. *Annals of Botany*, **49**, 835–846.
- Sanna G., Giunta F., Motzo R., Mastrangelo A.M., De Vita P. (2014) Genetic variation for the duration of pre-anthesis development in durum wheat and its interaction with vernalization treatment and photoperiod. *Journal of Experimental Botany*, **65**, 3177–3188.
- Semenov M.A., Stratonovitch P., Alghabari F., Gooding M.J. (2014) Adapting wheat in Europe for climate change. *Journal of Cereal Science*, **59**, 245–256.
- Simmonds J., Leverington-Waite M., Wang Y., Greenland A., Snape J.W. (2006) Discovering QTL controlling yield and yield components in wheat. In *Proceedings of the 13th International EWAC Conference. European Cereals Genetics Cooperative*, pp. 122–123. Norwich, UK: John Innes Centre.
- Slafer G.A., Rawson H.M. (1994) Sensitivity of wheat phasic development to major environmental factors: a reexamination of some assumptions made by physiologists and modelers. *Australian Journal of Plant Physiology*, **21**, 393–426.
- Slafer G.A., Kantolic A.G., Appendino M.L., Miralles D.J., Savin R. (2009) Crop development: genetic control, environmental modulation and relevance for genetic improvement of crop yield. In *Crop Physiology: Applications for Genetic*

- Improvement and Agronomy*, pp. 277–308. Eds V.O. Sadras and D.F. Calderini. Burlington, MA, USA: Academic Press.
- Snape J.W., Butterworth K., Whitechurch E., Worland A.J. (2001) Waiting for fine times: genetics of flowering time in wheat. *Euphytica*, **119**, 185–190.
- Steinmeyer F.T., Lukac M., Reynolds M.P., Jones H.E. (2013) Quantifying the relationship between temperature regulation in the ear and floret development stage in wheat (*Triticum aestivum* L.) under heat and drought stress. *Functional Plant Biology*, **40**, 700–707.
- Stickel E., Maidl F.X., Retzer F., Fischbeck G. (1999) Nitrogen uptake and utilization in winter wheat under different fertilization regimes, with particular reference to main stems and tillers. *Journal of Agronomy and Crop Science: Zeitschrift für Acker und Pflanzenbau*, **183**, 47–52.
- Stickel E., Maidl F.X., Retzer F., Dennert J., Fischbeck G. (2000) Efficiency of grain production of winter wheat as affected by N fertilisation under particular consideration of single culm sink size. *European Journal of Agronomy*, **13**, 287–294.
- Stone P.J., Nicolas M.E. (1995a) Effect of timing of heat stress during grain-filling on two wheat varieties differing in heat tolerance. I. Grain growth. *Australian Journal of Plant Physiology*, **22**, 927–934.
- Stone P.J., Nicolas M.E. (1995b) Comparison of sudden heat stress with gradual exposure to high temperature during grain filling on two wheat varieties differing in heat tolerance. I. Grain growth. *Australian Journal of Plant Physiology*, **22**, 935–944.
- Stone P.J., Nicolas M.E. (1995c) A survey of the effects of high temperature during grain filling on yield and quality of 75 wheat cultivars. *Australian Journal of Agricultural Research*, **46**, 475–492.
- Subedi K.D., Gregory P.J., Summerfield R.J., Gooding M.J. (1998) Cold temperatures and boron deficiency caused grain set failure in spring wheat (*Triticum aestivum* L.). *Field Crops Research*, **57**, 277–288.
- Sylvester-Bradley R., Scott R.K., Stokes D.T., Clare R.W. (1997) The significance of crop canopies for N nutrition. Optimising Cereal Inputs: Its Scientific Basis. *Aspects of Applied Biology*, **50**, 103–116.
- Sylvester-Bradley R., Foulkes J., Reynolds M.P. (2005) Future wheat yields: evidence, theory and conjecture. In *Yields of Farmed Species: Constraints and Opportunities in the 21st Century*, pp. 233–260. Eds R. Sylvester-Bradley and J. Wiseman. Nottingham, UK: Nottingham University Press.
- Sylvester-Bradley R., Berry P., Blake J., Kindred D., Spink J., Bingham I., McVittie J., Foulkes J. (2008) *The Wheat Growth Guide*. 2nd edn. Stoneleigh, UK: Home Grown Cereals Authority.
- Tang Z.H., Zhang L.P., Yang D., Zhao C.P., Zheng Y.L. (2011) Cold stress contributes to aberrant cytokinesis during male meiosis I in a wheat thermosensitive genic male sterile line. *Plant, Cell and Environment*, **34**, 389–405.
- Thomas W.T.B. (2014) The value of decimal cereal growth stages. *Annals of Applied Biology*, **165**, 303–304.
- Tottman D.R. (1977) Identification of growth stages in winter wheat with reference to application of growth-regulator herbicides. *Annals of Applied Biology*, **87**, 213–224.
- Tottman D.R. (1982) The effects of broad-leaved weed herbicides applied to cereal crops at different growth stages. Broad-leaved weeds and their control in cereals. *Aspects of Applied Biology*, **1**, 201–210.
- Tottman D.R. (1987) The decimal code for the growth stages of cereals, with illustrations. *Annals of Applied Biology*, **110**, 441–454.
- Tottman D.R., Makepeace R.J., Broad H. (1979) An explanation of the decimal code for the growth stages of cereals, with illustrations. *Annals of Applied Biology*, **93**, 221–234.
- Vahamidis P., Karamanos A., Economou G., Fasseas C. (2014) A new scale for the assessment of wheat spike morphogenesis. *Annals of Applied Biology*, **164**, 220–231.
- Waldren R.P., Flowerday A.D. (1979) Growth stages and distribution of dry matter, N, P, and K in winter wheat. *Agronomy Journal*, **71**, 391–397.
- Wegulo S.N., Zwingman M.V., Breathnach J.A., Baenziger P.S. (2011) Economic returns from fungicide application to control foliar fungal diseases in winter wheat. *Crop Protection*, **30**, 685–692.
- Weightman R.M., Kirby E.J.M., Sylvester-Bradley R., Scott R.K., Clare R.W., Gillett A. (1997) Prediction of leaf and internode development in wheat. *Journal of Agricultural Science*, **129**, 385–396.
- Weisz R., Crozier C.R., Heiniger R.W. (2001) Optimizing nitrogen application timing in no-till soft red winter wheat. *Agronomy Journal*, **93**, 435–442.
- Westgate M.E., Passioura J.B., Munns R. (1996) Water status and ABA content of floral organs in drought-stressed wheat. *Australian Journal of Plant Physiology*, **23**, 763–772.
- Whaley J.M., Sparkes D.L., Foulkes M.J., Spink J.H., Semere T., Scott R.K. (2000) The physiological response of winter wheat to reductions in plant density. *Annals of Applied Biology*, **137**, 165–177.
- Wheeler T.R., Hong T.D., Ellis R.H., Batts G.R., Morison J.I.L., Hadley P. (1996) The duration and rate of grain growth, and harvest index, of wheat (*Triticum aestivum* L.) in response to temperature and CO₂. *Journal of Experimental Botany*, **47**, 623–630.
- Wibberley E.J. (1989) *Cereal Husbandry*. Ipswich, UK: Farming Press.
- Wiersma J.J., Motteberg C.D. (2005) Evaluation of five fungicide application timings for control of leaf-spot diseases and fusarium head blight in hard red spring wheat. *Canadian Journal of Plant Pathology-Revues Canadienne de Phytopathologie*, **27**, 25–37.
- Wiersma J.J., Dai J., Durgan B.R. (2011) Optimum timing and rate of trinexapac-ethyl to reduce lodging in Spring wheat. *Agronomy Journal*, **103**, 864–870.

- Wilson B.J., Cussans G.W. (1978) Effects of herbicides, applied alone and in sequence, on control of wild-oats (*Avena fatua*) and broad-leaved weeds, and on yield of winter wheat. *Annals of Applied Biology*, **89**, 459–466.
- Woodford E.K., Evans S.A. (1965) *Weed Control Handbook*. 4th edn. Oxford, UK: Blackwell Scientific Publications.
- Worland A.J., Korzun V., Roder M.S., Ganai M.W., Law C.N. (1998) Genetic analysis of the dwarfing gene *Rht8* in wheat. Part II. The distribution and adaptive significance of allelic variants at the *Rht8* locus of wheat as revealed by microsatellite screening. *Theoretical and Applied Genetics*, **96**, 1110–1120.
- Zadoks J.C. (1985) This week's citation classic. *Current Contents*, **41**, 14 October, p. 14.
- Zadoks J.C., Chang T.T., Konzak C.F.A. (1974a) A decimal code for the growth stages of cereals. *Eucarpia Bulletin*, **7**, 42–52.
- Zadoks J.C., Chang T.T., Konzak C.F. (1974b) A decimal code for the growth stages of cereals. *Weed Research*, **14**, 415–421.
- Zadoks J.C., Chang T.T., Konzak C.F.A. (1975a) A decimal code for the growth stages of cereals. *Annual Wheat Newsletter*, **21**, 9–16.
- Zadoks J.C., Chang T.T., Konzak C.F.A. (1975b) A decimal code for the growth stages of cereals. *Cereal Rusts Bulletin*, **3**, 14–23.