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Wheat yield is not causally related to the duration of the growing season

Gustavo A. Slafer[a,b,*], Roxana Savin[b], Víctor O. Sadras[c]

[a] ICREA (Catalonian Institution for Research and Advanced Studies), Spain
[b] Department of Agricultural and Forest Sciences and Engineering, University of Lleida – AGROTECNIO-CERCA Center, Av. R. Roure 191, 25198 Lleida, Spain
[c] South Australian Research and Development Institute, and School of Agriculture, Food and Wine, The University of Adelaide, Australia

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ABSTRACT

A common conceptual model for crop growth analysis assumes biomass is proportional to the accumulation of radiation intercepted by the canopy during the growing season, and yield is the product of biomass and harvest index. This model assumes that biomass and harvest index are independent, and that biomass has the same value for yield across developmental stages; here we focus on the latter assumption. A corollary of this model is that yield and duration of the growing season are causally related. In this article, we analyse the evidence for and against this causal relationship. We use both a physiological perspective and agronomic evidence to challenge this causality. An alternative, phenology-focused model is outlined that is based on the following principles: crops accommodate environmental variation through grain number, grain number is defined in a species-specific critical developmental period, and grain number is a function of three traits in the critical period: duration, growth rate, and partitioning to reproduction. Against this framework, we analyse dual purpose wheat, where a substantial part of the biomass is removed, effectively shortening the growing season, with little or no effect on yield; timing of nitrogen fertilisation, where delayed application reduces the growth rate early in the season, with little or no effect on yield; and the correlation between season length and yield of winter wheat and spring wheat - wheat yield in Southern Chile, with a sowing-to-maturity season of ~ 5 months, could be as high as that of winter wheat in the UK, with a sowing-to-maturity season of ~ 10 months. Physiological principles and agronomic evidence support the conclusion that the duration of, and growth rate and partitioning during the critical period, rather than the duration of the growing season, are the drivers of wheat yield.

1. Introduction: rationale for a link between yield and the duration of the growing season

Wheat is one of the most widely grown crops (Slafer et al., 2021). Owing to its production level and its contribution to human diet (Braun et al., 2010; Shewry and Hey, 2015), wheat is already critical for food security (Reynolds et al., 2012), and will become more critical as both global population and the average individual demands increase simultaneously (Godfray et al., 2010; Tilman and Clark, 2014). As a significant increase in growing area is unlikely (Cassman et al., 2003; Foley et al., 2011; Albajes et al., 2013), higher yield per unit area and time must match the expected increase in wheat demand (Neumann et al., 2010; Slafer et al., 2022).

Yield is the agronomically most relevant aspect of the crop phenotype that results from the three-way interaction between genotype, environment, and management. Complementary perspectives and tools converge to improve varieties and practices, with a strong emphasis on data-driven technologies (Mahmood et al., 2022; Wang and Su, 2022). In common with others concerned with the understanding and manipulation of the phenotype (Nurse, 2021; Noble, 2014), we have argued that conceptual models of the phenotype are a bottleneck in agriculture (Slafer, 2003; Sadras, 2019; Sadras, 2021; Slafer et al., 2022). In this context, this paper focuses on the conceptual model that links crop yield and duration of the growing season.

Until the first half of the 20th century, plant growth analysis accounted for growth rate as a function of net assimilation rate and leaf area ratio (Blackman et al., 1953; Radford, 1967). At the core of this model is Blackman (1919) analogy of compound interest in the economy and plant growth, whereby plant biomass at time t (W_t) is a function of initial biomass (W_0), growth rate (r) and time:

$$W_t = W_0\, e^{rt} \tag{1}$$

The intuitive link between growth and time was thus formalised. Owing to ontogenetic drift and other limitations, the inadequacy of this

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* Corresponding author at: ICREA (Catalonian Institution for Research and Advanced Studies), Spain.
E-mail address: slafer@pvcf.udl.cat (G.A. Slafer).

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model was apparent (Evans, 1972). A model based on capture and efficiency in the use of resources was advanced in the 1970 s (Monteith, 1977; Monteith et al., 1994) that remains the centre of contemporary crop growth analysis and modelling. In this conceptual model, yield is a fraction of total biomass commonly quantified as harvest index; therefore, improving biomass would improve yield proportionally assuming both traits are independent (Fig. 1a; Slafer and Savin, 2006). Genetic and agronomic interventions to increase photosynthesis and biomass are expected to increase yield (Reynolds et al., 2009; Wu et al., 2019). A recent "wiring diagram" identifies opportunities to increase photosynthesis, biomass, and yield of wheat (Murchie et al., 2023). The effects of availability of other resources (water, nutrients) and non-resource factors such as daylength and temperature, can be incorporated in this model as modulators of development, growth, and partitioning.

The rationale of this model is unquestionable: as solar radiation is the source of energy for photosynthesis and crop growth, biomass depends on the amount of accumulated intercepted radiation. In this formulation, the model makes two assumptions. First, that the value of biomass is the same across developmental stages; this is the focus of this paper. The second assumption, that biomass and harvest index are independent, is important but is beyond our scope; emerging evidence supports the lack of independence between biomass and harvest index (Molero et al., 2019).

A corollary of the model is that yield is causally linked with the duration of growth; i.e. lengthening the growing season would increase yield (Fig. 1b). The main reason for this link is that a longer growing season increases capture of resources, chiefly radiation that cannot be stored for later use, hence reducing the "seasonal loss" *sensu* (Reynolds et al., 2012; their Fig. 3). Indeed, an analysis of opportunities to increase wheat yield in Southern Australia and the Pacific Northwest of the United States concluded that '*lengthening crop life cycle is one of the simplest ways to improve crop yield potential through increased biomass and grain number*' (Cann et al., 2020).

The aim of this article is to sample the evidence supporting or challenging a *causal* link between yield and duration of the growing season, all other things being equal. The implicit assumption that the value of growth for yield is the same across phenological stages is revised against both our current understanding of crop physiology, and agronomic evidence.

2. Supporting a link between yield and duration of the growing season

There are myriad examples in the literature supporting, more or less directly and more or less explicitly, the link between yield and duration of the growing season. Some examples:

(i) yield can be increased by increasing the cumulative intercepted solar radiation from sowing to maturity (Guarin et al., 2022). This aligns with the view that '… *yield is a consequence of resource accumulation and use by a crop*' (Sinclair and Jamieson, 2006).
(ii) yield reduction with warming, in the context of climate change, associates with a shorter growing season (Wang et al., 2009; Mäkinen et al., 2018).
(iii) the effects of stresses on yield reflect the effects on growth regardless of the timing of occurrence of the stress (e.g., Sinclair et al., 1990). This is also implicit in production functions that relate relative yield and relative evapotranspiration in the context of irrigation management (Steduto et al., 2012).
(iv) in particular regions of the world, locations with longer season often return higher yield, even in well-irrigated and fertilised crops; for instance

(a) in Europe, both the duration of the growing season and yield increase northwards (e.g., Semenov and Shewry, 2011; Senapati et al., 2019).
(b) in Argentina, both the duration of the growing season and yield increase southward (Magrin et al., 1993).
(c) in Oceania, the growing season is longer, and yield is higher in New Zealand than in Australia.

(a) in the same locations of the Northern hemisphere, the growing season is longer and yield is higher for winter wheat than for spring wheat (Cann et al., 2020).

Indeed, it is our experience from scientific meetings that the community of agronomists, geneticists, breeders, plant- and crop-physiologists, and modellers assumes a *causal* link between duration of the growing season and yield. Perhaps this is rooted in the tradition of considering time, or resources that become available to the crop through time, a major determinant of crop growth and yield (Eq. 1, Fig. 1a).

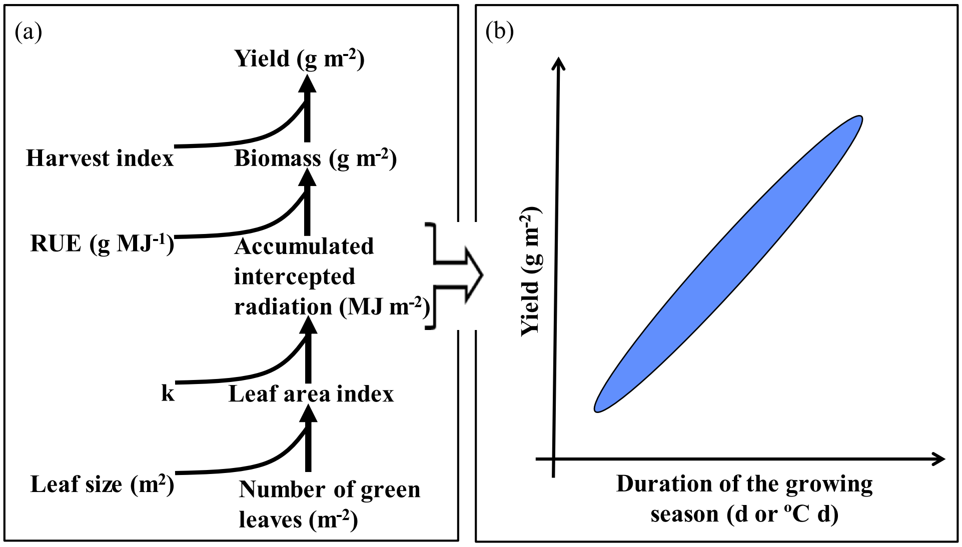

Fig. 1. (a) Conceptual model of yield based on resource-driven crop growth (and partitioning). k is the light coefficient extinction; RUE is radiation use efficiency. Arrows indicate putative causal associations. (b) Corollary: yield would be causally linked with duration of the growing season because longer season ensures higher interception of radiation and biomass production.

Although the above-mentioned evidence supports the link between yield and duration of the growing season, the *causality* of this link is precarious, unless we frame the model phenologically.

3. Challenging the causal link between yield and duration of the growing season: from the perspective of crop physiology

The main challenge to the causality of the relationship between yield and duration of the growing season is the implicit assumption that growth has the same value for yield irrespective of crop developmental stage. Our current understanding of the physiology of crop yield does not support this assumption.

First, we know that crops accommodate environmental variation through grain number; grain weight is conserved, with a heritability typically above 0.70 (Sadras, 2007; Sadras, 2021). Grain number is thus a "coarse" regulator of yield, whereas grain weight is a "fine" regulator; e.g., a 5–10% variation in yield can be related to either grain number or grain weight, but a two-fold variation *must* be related to grain number (Slafer et al., 2014). Second, grain number is defined in a species-specific critical developmental period. The notion of a critical developmental period for reproduction is well established; Darwin (1859) noted '*…very trifling changes, such as a little more or less water at some particular period of growth, will determine whether or not the plant sets a grain*'. Using sequential shading, Fischer (1985) formalised the critical developmental period for grain set and yield in wheat, that spans from approximately the onset of stem elongation to 7–10 days after anthesis. Alternative experimental approaches demonstrated the robustness of this developmental period, which is largely independent of genotype, environment, and management (Slafer et al., 2021). Third, grain number is a function of three traits: the duration of the critical period, the growth rate during the critical period, and the partitioning of growth to spike (Slafer et al., 2021; Sadras et al., 2022). A corollary of this phenology-focused model is that crop growth influences yield primarily in the critical period (Fig. 2). Higher growth rate (Savin and Slafer, 1991; Abbate et al., 1997; Dreccer et al., 2000; Demontes-Meynard and Jeuffroy, 2004; Ferrante et al., 2010; Sadras et al., 2012; Ferrante et al., 2013), longer critical period (González et al., 2003, 2005; Miralles and Slafer, 2007; Ferrante et al., 2020; Sadras et al., 2022), or higher partitioning to reproduction (Miralles et al., 1998) favour grain set and yield.

The conceptual model of yield based on resource-driven crop growth (Fig. 1a) can thus be refined to account for the variation in the value of growth with phenological stage (Fig. 2). The thick line representing the dynamics of yield-response-to-growth (Fig. 2) mirrors the curve of yield vs timing of shading (Fischer, 1985). The model emphasises the causal relations between yield and grain number, and grain number and the duration of the critical period. Thus, increasing the duration of the growing season by lengthening earlier phases would not necessarily translate into yield, unless early growth (Fig. 2, light green box) influences growth in the critical period (Fig. 2, dark green box); for instance, a combination of late sowing and low plant population density can lead to low growth rate early in the season that compromises growth rate during the critical period. The relevance of this proposition is two-fold. Physiologically, variation in duration of the growing season is most frequently associated with variation in the duration of the vegetative phases (Slafer and Rawson, 1994). Agronomically, interventions such as early weed control or increasing sowing rate in late-sown crops could have an impact on yield that is mediated by the connection between early growth and growth in the critical period. Increasing the duration of the growing season by increasing the duration of grain fill could increase grain weight and yield (Senapati and Semenov, 2019), but this effect is small compared to the yield variation associated with grain number (Slafer et al., 2014).

This phenology-focused model has a parallelism in a long-held discussion in the literature regarding whether source or sink limits wheat yield, with implications for trait-based breeding. As sources and sinks vary dynamically with crop development, here we use the simplified definitions of source and sink advanced by Murchie et al. (2023) and Slafer et al. (2023) in the context of wheat yield determination. Briefly, source strength is taken as the capacity of the crop canopy to provide resources for reproductive organs (the juvenile spikes before anthesis and grains after anthesis) and sinks are exclusively these reproductive organs. Source-strength includes canopy photosynthesis and crop growth, and partitioning and remobilisation to the reproductive organs; sink-strength is the number of grains and their potential size. Thus, source strength in the critical period is crucial for survival of both tillers, which determines spikes m^{-2}, and floret primordia, which determines grain per spike (Fig. 2, top); hence, source strength in the critical period drives the sink strength that limits yield during grain filling (Fig. 2, bottom). Wheat yield therefore shifts from source-limited in the critical period to sink-limited during grain filling, highlighting the insights from

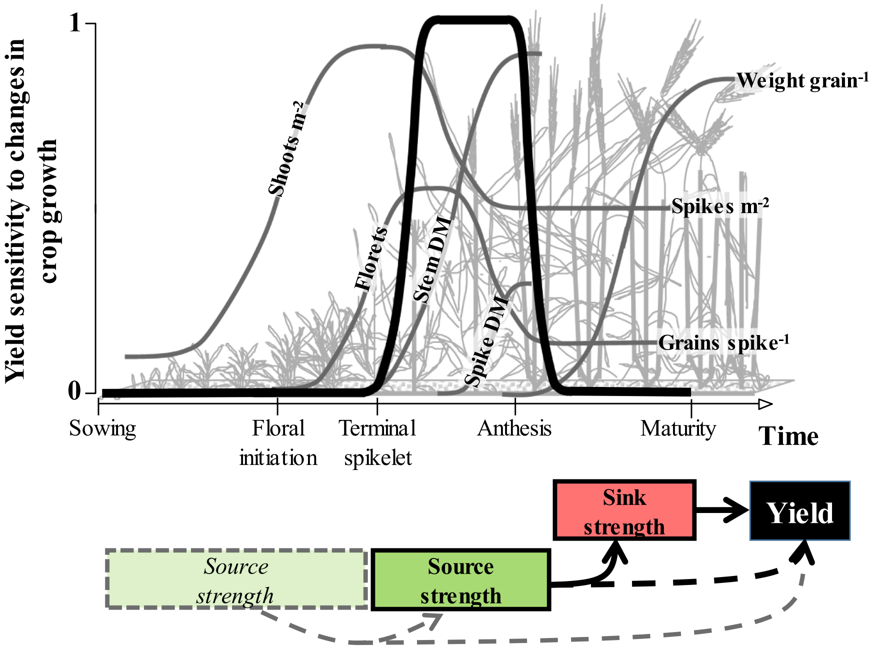

Fig. 2. Changes in the sensitivity of yield to crop growth from sowing to maturity (thick black line). The thinner grey lines show (not to scale) the dynamics of (i) tillering and tiller survival (Shoots m^{-2}) resulting in the final number of spikes m^{-2}; (ii) floret initiation and mortality (Florets) determining firstly the number of fertile florets and later the number of grains per spike; (iii) growth of stems (Stem DM) and spikes (Spike DM) before anthesis; and (iv) grain growth (weight grain^{-1}). Crop growth before the critical period (light green box) would affect yield only to the extent that it affects growth during the critical period (dashed grey arrow). (a) Coloured boxes highlight the minor role of source-strength before the critical period (light green), the major role of source strength in the critical period driving grain number (dark green), and the sink-limitation during grain fill (red box). (b) Plain arrows refer to the fact that yield is mostly sink-limited by the number of grains set (and their potential weight; Slafer et al., 2023) during the effective period of grain filling, and that the level of sink-strength at that stage is determined by the source-strength (linearly related to crop growth) during the critical period (when source-strength does determine yield; black dashed line).
(c) Adapted from Slafer and Savin (2006); Slafer et al. (2021); and Reynolds et al. (2022).

a developmental perspective to identify relevant traits for improving yield (Fig. 2).

Then the conceptual model described in Fig. 1a can be improved considering phenological stage; the model in Fig. 3 emphasises the causal relations between yield and grain number, and grain number and three traits in the critical period: duration, growth rate, and partitioning to spike.

4. Challenging the causal link between yield and duration of the growing season: agronomic evidence and implications

In this section, we sample few of the many agronomic examples supporting the framework in Fig. 3, and challenge the causality of the link between yield and the duration of the growing season.

4.1. Grazing or defoliation before the critical period reduces biomass but rarely affects yield

Dual purpose wheat seeks to capture the benefit of plant biomass for animal production with small or no trade-off for grain production (Bartmeyer et al., 2011; Harrison et al., 2011; Seymour et al., 2015; Hu et al., 2019). Farmers exploiting this practice are aware that the timing of grazing is important, and experiments with actual grazing or mechanical defoliation show yield is unresponsive to biomass removal before the onset of the critical period (Fig. 4a), provided heads are not removed and early removal of biomass does not compromise growth during the critical period (Seymour, 2015; Sprague et al., 2021; Bell et al., 2020). Defoliation alters the patterns of water use, allocation of both structural and labile carbohydrates in plant, and responses to nitrogen (Harrison et al., 2011; Hu et al., 2019). However, the key for the lack of yield response to defoliation is that the duration of the critical period and the growth rate during the critical period are maintained. This is illustrated in Fig. 4b showing Merino hoggets grazing during 30 d at 1965 dry sheep equivalents (DSE)/ha shifted the growth curve of rainfed wheat crops, with no effect on the duration of the sowing-to-harvest period, no effect on the duration of the critical period, a slight increase in the growth rate during the critical period, and no effect on grain yield despite a significant, 17% reduction in shoot biomass at maturity reflecting the biomass lost in early phases of development. Grazing effectively "shortened" the growing season by four months, with no consequence for yield.

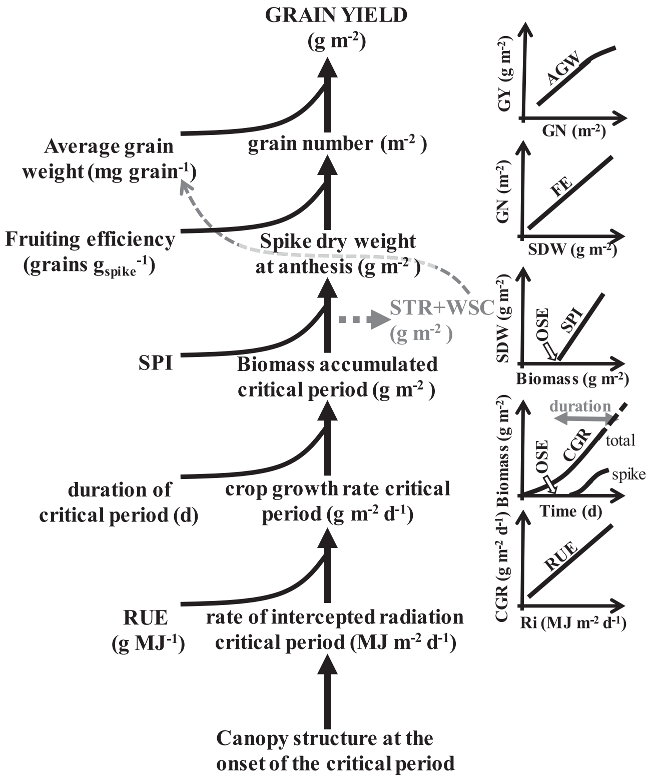

Fig. 3. Conceptual model of grain yield based on four physiological principles: (i) crops accommodate environmental variation through grain number; (ii) grain number is defined in a species-specific critical period and is proportional to (iii) the rate of growth in the critical period, (iii) the duration of critical period, and (iv) reproductive allocation. Solid arrows indicate putative causal associations. RUE is radiation use efficiency; SPI is the spike partitioning index; and OSE is the onset of stem elongation. The dotted arrow pointing to STR (structural) and WSC (water-soluble carbohydrates) in non-reproductive tissues highlights the trade-off between allocation to reproduction and other functions; e.g. negative correlations between grain set and WSC in some settings. The dashed grey arrow highlights the role of reserves buffering grain fill. Based on the early work of Fischer (1985) and updated physiological frameworks including Slafer (2003); Slafer and Savin (2006); Sadras and Slafer (2012); Sadras (2021); Sadras et al. (2022).

4.2. Fertilising with nitrogen before the critical period increases early growth but not necessarily yield

The framework of capture and efficiency in the use of radiation (Fig. 1a) has been used in early studies of yield response to nitrogen (N) fertilisation (e.g., Gallagher and Biscoe, 1978) and remains relevant for modelling. The rationale is that increasing N availability favours crop growth, leading to higher yield. Timing of N application is important to manage both environmental risk, i.e., to reduce nitrogen losses, and financial risk, as fertiliser rates can be adjusted according to seasonal conditions, primarily rainfall in dryland systems (Fischer et al., 1993; Monjardino et al., 2015). In a study with irrigated wheat grown in a low fertility soil, where the unfertilised crop yielded just below 2 t ha^{-1}, crops fertilised at the onset of stem elongation returned the same yield as their counterparts fertilised at sowing (Fig. 5a). This supports the proposition that crop growth before the critical period is of a lesser importance to yield, provided the duration of the critical period, and the rate of growth and partitioning during the critical period are not affected (Fig. 3). This was elegantly illustrated by Fischer (1993) who showed crops fertilised with 180 kg N ha^{-1} at DC30 produced 17,190 grains m^{-2} and yielded 6.7 t ha^{-1} (with 10% moisture content, as shown in Fischer et al., 1993) in comparison to crops fertilised with the same rate at sowing that produced 18,330 grains m^{-2} and yielded 7.1 t ha^{-1}, despite a large reduction in biomass at anthesis and maturity (Fig. 5b). Delayed N fertilisation effectively "shortened" the growing season (i.e. shortened the period of active growth, phenology was similar across N treatments) by c. 3 months, with a clear reduction in total biomass (c. 3 t ha^{-1}, from 18 to 15 t ha^{-1}), but minor consequences for yield (c. 0.4 t ha^{-1}) as expected from the model in Fig. 3. Consistent with this case study, a global meta-analysis including 542 pairwise comparisons of fertiliser timing across 127 environments showed wheat yield did not vary with timing of fertilisation, provided crops have sufficient nitrogen in the critical period (Giordano et al., 2023), supporting the conclusion of the detailed case study in Fig. 5. This is also consistent with a previous meta-analysis showing that split N fertilisation does not produce a yield penalty, and frequently increases yield, compared with fertilisation at sowing (Hu et al., 2021). Studies on timing of irrigation return similar results, emphasising that the value of growth depends on growth stage (Steduto et al., 2012).

4.3. Winter wheat outyields spring wheat but not because it has a longer growing season

Winter wheat has a longer season and usually outyields spring wheat; for example, by 28% in trials in Canada (Stoskopf et al., 1974), by 39% in Norway (Koppel et al., 2020), and by 1.8–3.2-fold in Germany (Krato and Petersen, 2012). And it is not unusual that both attributes are seen

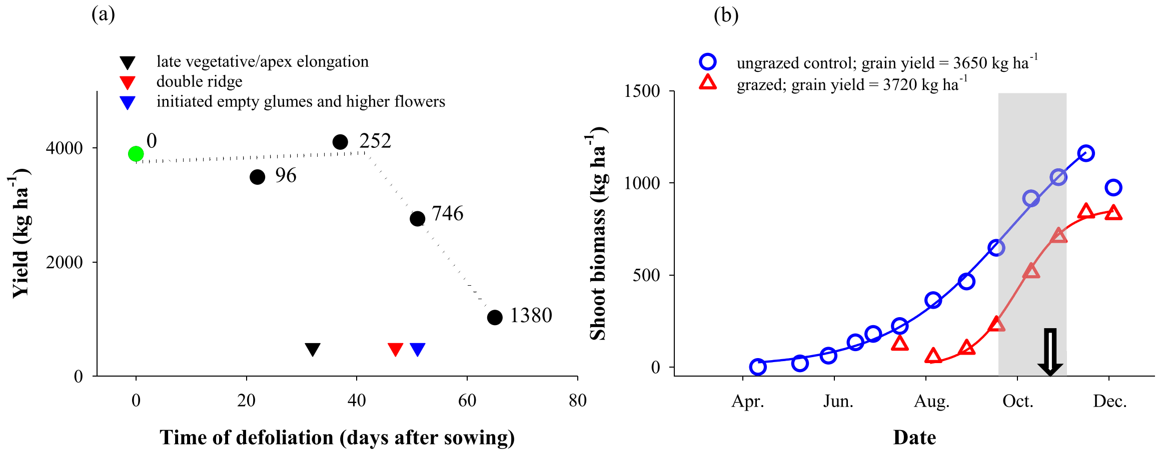

Fig. 4. The value of crop growth depends on ontogeny – evidence from mechanical defoliation and grazing in rainfed wheat crops. (a) Yield of wheat in response to timing of defoliation. Green circle is undefoliated control, and arrowheads show spike and spikelet development. (b) Dynamics of growth of grazed wheat and ungrazed controls. Curves are 3-parameter sigmoidals. The arrow shows anthesis, and the grey area is the critical period from 30 d before to 10 d after anthesis. Sources: (a) experiments in central Queensland, Australia, Zhu et al. (2004); (b) experiments near Canberra, Australia, Harrison et al. (2011).

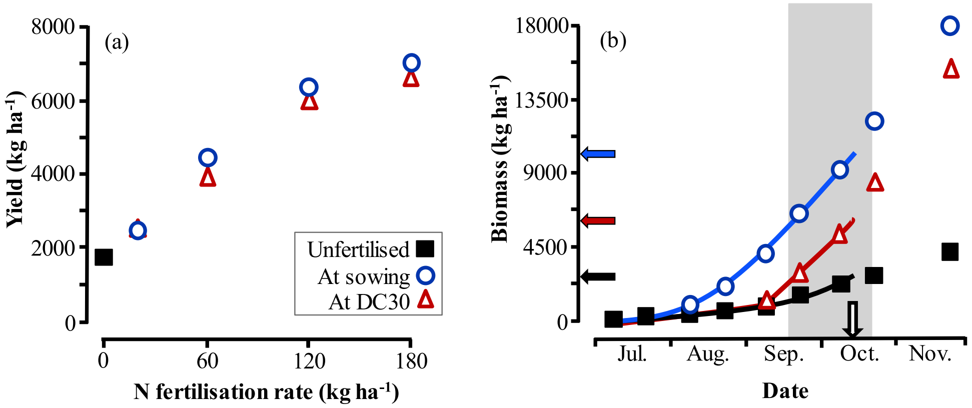

Fig. 5. The value of crop growth depends on ontogeny – evidence from timing and doses of fertilisation in irrigated wheat crops. (a) Yield response to N fertilisation (20, 60, 120 or 180 kg N ha^{-1}) at sowing (4 June) or just before the onset of stem elongation on 26 August (stage DC30 in the scale of Zadoks et al., 1974). (b) Seasonal dynamics of biomass accumulation in unfertilised control and crops fertilised with 180 kg N ha^{-1} at either sowing or DC30. The vertical arrow indicates the time of anthesis, and the shaded area represents the period from 30 d before to 10 d after anthesis. The horizontal arrows indicate the biomass of the crop at anthesis.

Sources: Fischer et al. (1993) and Fischer (1993).

as cause and consequence (e.g., Stoskopf et al., 1974; Entz and Fowler, 1991; Cann et al., 2020). For instance, an USDA guide reads: '*winter wheat has a higher yield potential than spring [wheat] because of its longer growing season*' (Vocke and Mir, 2013). This rationale aligns with the model of yield related to total biomass (Fig. 1a) and the corollary that yield can be improved through increasing the duration of the growing season (Cann et al., 2020).

However, the difference in yield between winter and spring wheat can be more adequately explained with the model accounting for phenology with emphasis on the critical period (Fig. 3). Winter wheat is sown in early autumn (or even late summer), have vernalisation requirements to advance into reproductive development after the crop is exposed to winter temperatures, and flowers in spring. Vernalisation sensitivity in winter wheat drives a longer vegetative phase (Slafer, 2012), which is critical for adaptation to autumn sowing, avoiding frosts impairing reproduction, but is not relevant for yield determination (see Fig. 2 and associated text). Spring wheat is sown in spring after soil temperature allows crop establishment, and flowers in summer (Slafer et al., 2021). Therefore, the critical period occurs in early- to mid-spring in winter wheat, and in late-spring to early/mid-summer in spring wheat (Fig. 6).

As the season advances from spring to summer, the photothermal conditions worsen for development, grain number and grain size, hence yield. Radiation tends to increase, which favours carbon assimilation, crop growth, grain number, and yield. Temperature rises relatively faster than radiation, particularly the developmentally perceived temperature; i.e., actual minus base temperature 4.5 °C (Fischer, 1985). Importantly, all three traits in our model - duration of critical period, growth rate, and partitioning in the critical period - are non-linear functions of temperature (Sadras et al., 2022). Increasing temperature

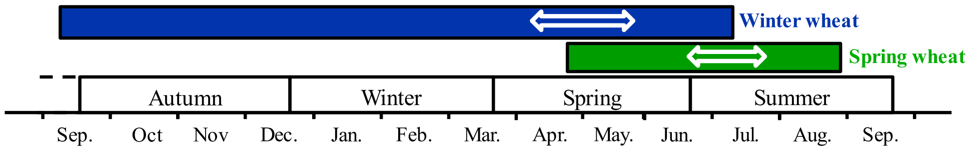

Fig. 6. Crop cycles from sowing (start of the rectangle) to maturity (end of the rectangle) for typical winter and spring wheats grown in the Northern hemisphere. The double arrows show the critical period. The critical period is shortened in spring wheat compared to winter wheat due to higher temperature that accelerate development. The timings of sowing, critical period and maturity are broad averages to illustrate the contrasting environmental conditions between wheat types at critical stages. The grain filling is also under worse conditions in spring than in winter wheat also affecting the average size of the grains, but most of the differences in yield are associated to differences in grain number.

in the range from ~10–30°C increases wheat developmental rate 3-fold with a smaller effect on carbon assimilation, hence the sharp decline in assimilation per unit developmental time (see Fig. 1d in Lohraseb et al., 2017). Thus, the developmental response to temperature in this range trumps the response of assimilation to temperature and radiation. High temperature could also reduce allocation to reproduction (Sadras et al., 2022), partially because high temperature (> 31°C) can disrupt the development of floret primordia (Vara Prasad and Djanaguiraman, 2014; Slafer and Savin, 2018). Consistently with this model, yield of late-spring flowering wheat in Australia declined linearly with increasing mean temperature in the critical period, in the range from 9 to 17°C, at a rate of 0.5 t ha^{-1} °C^{-1} (Sadras et al., 2022). Our framework may also contribute insights in the context of climate change, where reduced yield with higher temperature can be mistakenly attributed to shorter growing season (Wang et al., 2009; Mäkinen et al., 2018).

More definitive evidence against the causal link between yield and duration of the growing season arises from the comparison of winter wheat in the Northern hemisphere (e.g., in the UK where yield records are frequently claimed) and "spring" wheat in Southern Chile. Wheat in Southern Chile is actually sown in late winter, and achieves extremely high yields (e.g., up to 15 t ha^{-1} of dry grains; Bustos et al., 2013; García et al., 2013; Guarin et al., 2022). This very high yield is related to the high radiation and relatively low temperatures during the critical period in spring (e.g., Mera et al., 2015). Yield in Southern Chile with a sowing-to-maturity season of ~ 5 months, could be as high as that of winter wheat in the UK with a sowing-to-maturity season of ~ 10 months (Fig. 7). Thus, the timing of the critical period in relation to the photothermal environment provided the canopy structure allows exploiting that environment, rather than season length, drives high yield.

4.4. *Other agronomic evidence*

We briefly describe two other agronomic cases further supporting the model presented in Fig. 3, that challenges the causal relationship between yield and the duration of the growing season.

4.4.1. *Plant population density maximising yield does not maximise growth in early phenological phases*

Wheat yield responds to plant population density hyperbolically, reaching a maximum at a certain density that depends on environment, management, genotype, and their interaction (Bastos et al., 2020). However, in general the plant population density maximising wheat yield is relatively modest in timely-sown crops (e.g., Spink et al., 2000; Bustos et al., 2013; Fischer et al., 2019), and is much lower than the density that maximises crop growth during vegetative growth (Harper, 1977). This is because the plant population density maximising yield is the one that maximises growth rate during the critical period, but not earlier (Fischer et al., 2019).

4.4.2. *Extending the duration of the season with winter-type wheat sown in early-autumn produces more biomass but not always higher yield*

Wheat farmers in Australia have traditionally paired fast-developing spring cultivars and late-autumn sowing to time the critical developmental stages minimising frost risk, and terminal drought and heat in the critical period. Changes in rainfall seasonality and the logistics of timely sowing farms that have been becoming larger (Fletcher et al., 2016), in addition to the belief that the longer the growing season the higher the yield, have stimulated the investigation of pairing slow-developing "winter" types and early-autumn sowing, that effectively extend the growing season by ~20–30% or 1.5–2 months (Flohr et al., 2018; Hunt et al., 2019; Cann et al., 2020; Porker et al., 2020; Shackley et al., 2022). Yield benefits of this strategy were strongly dependent on environmental conditions and might be particularly relevant under terminal drought where deeper roots of longer cycle phenotypes allow to capture soil water stored in the sub-soil (Flohr et al., 2020). In some cases, the benefits might have been overestimated for not adjusting plant population density to late sowing. In any case, the lack of consistency in yield gains expected from an extended growing season challenges the causal link between yield and duration of the growing season. Our 3-trait model, that requires phenotyping for duration of the critical period, and growth rate and partitioning in the critical period, could be useful to further support this technology. Partitioning during the critical period needs particular attention as low harvest index partially cancels the biomass advantage of the slow-developing phenotype (Porker et al., 2020), as it had been shown in earlier studies with isogenic lines for developmental rates in which yield in response to the longer season was inconsistent (Gomez-Macpherson and Richards, 1995). The study of Fischer (2016) is also consistent with the idea that lengthening the cycle would increase biomass but not yield, even comparing lines differing in the length of the growing cycle but with the same anthesis date. The pairing of slow-developing "winter" types and early-autumn sowing can be agronomically justified, despite the counter evidence for a causal link between yield and duration of the growing season.

5. Concluding remarks

The widespread model based on capture and use of resources, implicitly assuming that growth has the same value for yield irrespective of growth stage, leads to the conclusion that yield is causally related to the duration of growing season. Based on this model, it is commonly assumed that differences in yield between locations, particularly across latitudes, are related to the duration of the growing seasons, and consequently that an avenue to improve yield would be lengthening the growing season. This misconstructed concept can compromise breeding and agronomic efforts for yield improvement. We highlighted the weakness of this model overlooking the developmental dimension of the crop phenotype, and illustrated with agronomic examples the lack of causal relation between yield and duration of the growing season. A more robust perspective is based on the principles that crops accommodate environmental variation mainly through grain number, which in turn is defined in a critical developmental period, and hence grain number and yield are a function of the duration of the critical period, and the crop growth rate and partitioning during the critical period. This perspective provides a solid basis for practices including pairing of cultivar and sowing date, fertilisation, and grazing, and trait-based breeding.

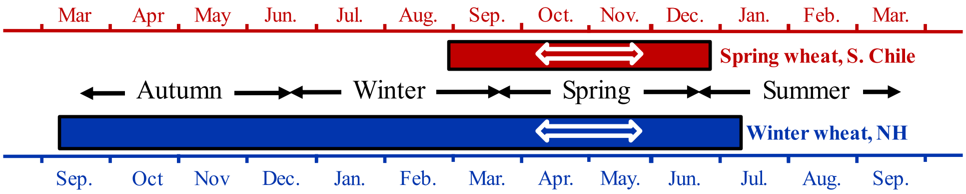

Fig. 7. Crop cycles from sowing (start of the rectangle) to maturity (end of the rectangle) for typical winter wheat grown in the Northern hemisphere (NH) and so called "spring" wheat (actually sown in late winter) in Southern Chile. The double arrows show the critical period.

CRediT authorship contribution statement

G.A. Slafer: Conceptualization, Methodology, Formal analysis, Visualization, Writing - original draft, Writing - review & editing, **R. Savin**: Conceptualization, Formal analysis, Writing - review & editing, **V.O. Sadras**: Conceptualization, Methodology, Formal analysis, Visualization, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

We have used data from the literature and the references are properly given.

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