A wiring-diagram to integrate physiological traits of wheat yield potential

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ABSTRACT

As crop yields are pushed closer to biophysical limits, achieving yield gains becomes increasingly challenging and will require more insight into deterministic pathways to yield. Here, we propose a wiring-diagram (WD) as a platform to illustrate the interrelationships of the physiological traits that impact wheat yield potential and to serve as a decision support tool for crop scientists. The WD is based on the premise that crop yield is a function of photosynthesis (source), the investment of assimilates into reproductive organs (sinks), and the underlying processes that enable expression of both. By illustrating these linkages as coded wires, the WD can show connections among traits that may not have been previously apparent, and can inform new research hypotheses and guide crosses designed to accumulate beneficial traits and alleles in breeding. The WD can also serve to create an ever richer common point of reference for refining crop models in the future.

Main

Wheat is increasingly in demand from farmers, consumers and the food industry due to its high grain-protein content, wide growing range and adaptability to most environmental stresses. However, investments in wheat improvement have fallen behind other staple crops [1]. Published developments in plant science and genetics can be harnessed to wheat breeding through translational research, capitalizing on powerful new tools in genomics, phenomics and informatics, among others [2,3]. Such approaches are justified by the high return on investment in agricultural research[4] -in wheat in particular [5]- while meta-analysis of thousands of published simulations indicate that genetic improvement is the most effective technology for achieving crop adaptation[6].

To date, wheat breeding programs have been addressing the demands of a growing global population through both incremental genetic gains in yield potential [7] and introducing broad-spectrum resistance to pests and diseases [8]. Although rarely grown under optimal conditions, multiple crop species show that improvements in yield potential bring about increases in actual yields under a broad range of mild and moderately stressful conditions[9]. Therefore, increasing yield potential is essential to raise farm yields, especially where crop management is close to its economic optimum. Modern technologies that leverage plant traits impacting photosynthesis and the partitioning of photo-assimilates to grain yield can accelerate genetic gains through breeding, as well as being powerful research tools. However, many promising plant discoveries are not translated into breeding technologies, while key bottlenecks in understanding of root physiology, hormone cross-talk, source-sink balance and respiration, for example, limit the level of integration of knowledge [10]. To maximize the impact of the research portfolio, a framework is needed to identify relevant traits and leverage interactions among them.

Source and sinks in yield determination

Crop physiology can be viewed as a set of engineering challenges whose interactions ultimately determine the performance of a crop. The plant's energy source -photosynthesis- drives growth and reproduction via the physical structures of the plant (photosynthetic canopy, stems, roots, floral structures and seeds), assisted by the necessary transport and communications infrastructure (vascular system, hormones and other signals) to coordinate activities [11,12]. Coordination includes partitioning of resources among growing structures, the most important of which -in the commercial context- are the reproductive sinks determining grain yield. A myriad of activities at the cellular, subcellular, biochemical, biophysical and genomic levels underpin these high level processes. Therefore, to help frame hypotheses, a simplified source-sink model has often been used that considers the photosynthesis of leaves or canopy as the 'source', and the growth and fecundity of reproductive organs and related processes as the 'sinks', as well as interactions between them. The model is reasonably easy to understand and has been used as a basis for physiological breeding [13] and dissection of genetic gains [14]. However, the challenge of raising crop yields to full biological potential, often under extreme growing conditions, will require a more detailed model.

While the original source-sink model remains valid, it must embrace complexity more explicitly. For example, wheat, like other small-grain cereals produces many tillers which as they grow behave first as sinks, then as sources via their leaves and green stem, and ultimately, when the spike emerges performing both roles, acting as a 'nursery' for developing seeds while simultaneously photosynthesizing. Photosynthesis by the wheat spike itself significantly contributes to grain-filling and shows genetic variation that is independent of leaf photosynthesis [15]. To add further complexity, the stems of tillers which are green and capable of photosynthesis also amass fructans and nitrogen as reserves which may later be transported to grains or other sinks. There are other traits and processes that cannot neatly be characterized as source or sink. Crop phenology affects the photosynthetic canopy in a dynamic fashion over development while at the same time having a profound effect on the formation of sinks (**Fig. 1**). Lodging resistance comprises a set of physical traits that when expressed sub-optimally, result in structural failure that compromises the photosynthetic canopy as well as spikes and seeds. Communications and transport related functions -for which genetic diversity in wheat has been documented, e.g. signaling[11,16], vascular anatomy [17] phloem loading [18]- also impact the expression of source and sink traits. For example, transgenic approaches that boost phloem loading show significant and positive effects on source : sink in wheat [19]. Clearly, the designation of source and sink is quite fluid in time, and spatial dimensions and a more comprehensive model is needed to guide research, crop modelling and breeding decisions. With this in mind, a WD was conceived to show explicitly connections between and among yield-related traits over crop development, along with an estimate of their potential impact and the likelihood that adequate genetic variation exists to exploit in breeding for improved yield potential.

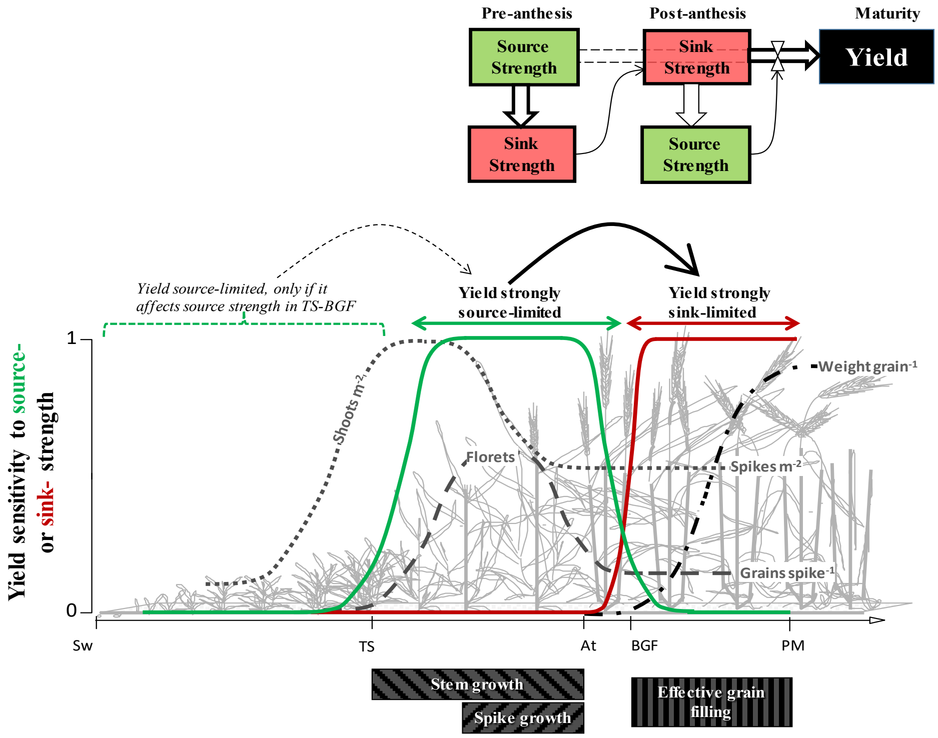


Figure 1. Graphical representation of how source- and sink-strengths may interact with crop developmental stage to determine yield. In the period immediately before to shortly after anthesis, source strength determines both the number of grains set and also the potential size of those grains, which together constitute the sink strength which then limits yield during the effective grain filling period (and consequently may down-regulate post-anthesis photosynthesis). Sw, TS, At, BGF and PM represent sowing, terminal spikelet, anthesis, beginning of grain filling, and physiological maturity, respectively. Adapted from Slafer and Savin[20]. Examples of how genetic variation expressed early in source development affects sink development and yield are given in Box 1.

Designing the wiring diagram

The common analytical frameworks to examine traits that control wheat yield [20,21] consider yield either as a fraction of biomass produced by the crop (**Fig. 2**, left) or as the product of a few numerical components (**Fig. 2**, right). These can be thought of as simple wiring diagrams or flow charts, with a syntax developed from deWit in the 1960s [22].

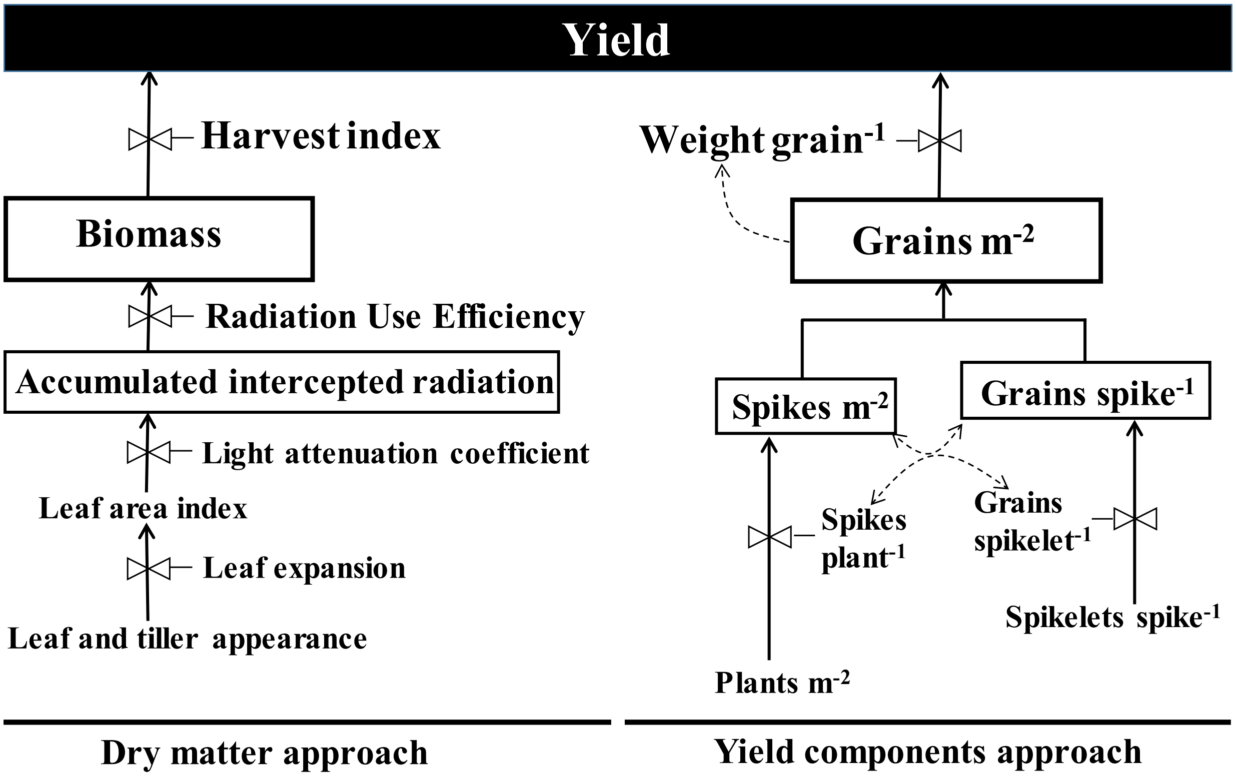


Figure 2. Schematic representation of two analytical frameworks for dissecting wheat yield. The dry matter approach considering yield as simply a fraction of the total growth produced by the crop (left) and the yield components approach considering yield simply a function of the multiplication of its numerical components (right). Time advances from bottom to top of the scheme, although it is naturally represented here only qualitatively. The dashed lines on the right represent expected negative interactions (for more details, see Slafer *et al.*[21]). (Adapted from Slafer and Savin[20]).

The two approaches have different biases in inferring how the final yield is determined. The dry matter approach infers that yield is predominantly limited by photosynthesis, and there is no explicit indication of the relevance of sink-strength in yield determination (it is implicit in harvest index), giving an unbalanced view that yield can be increased simply by increasing growth. For example, this framework is the basis of a spring wheat simulation model by Amir and Sinclair[2323], and is still applied in a number of wheat models [24]. However, when the physiological basis for genetic yield gains achieved over the last century is analyzed, the vast majority of studies conclude that wheat yields have dramatically increased without simultaneous gains in biomass (e.g., Mondal *et al*.[25]). Nonetheless, some exceptions can be also found (e.g. Ferrante et al.[26]). Furthermore, there is evidence of a likely trade-off between biomass and harvest index when the former is genetically improved (e.g. Aisawi et al.[27]), emphasizing that genetic improvement in biomass might not result in yield improvements if there are no tandem gains in sink strength.

In contrast, the yield components approach used across other wheat crop models [24] is a simple description of the average distributions of seeds, tillers and plants and often does not capture some of the dynamic and possibly regulatory feedback mechanisms among these components (dashed lines **Fig. 2**, right). This can be problematic as it suggests that yield is only sink-limited with no explicit indication of the relevance of source in yield determination as suggested by other studies. For example, Fischer[28] and subsequent studies [29,30] have demonstrated that grain yield depends directly on crop growth and biomass partitioning in the period immediately before anthesis. In addition, pre-anthesis growth affects grain development and size [31].

The apparent limitations of both approaches (**Fig. 2**) could be minimized by combining them in a more comprehensive scheme of yield determination where yield potential is a function of the dynamic balance between sources and sinks over time[32]. While crop simulation models incorporate aspects of both, some of the potential dynamic interactions are not captured [10,24]. The WD concept provides a comprehensive platform to present all documented and conceptually probable trait interactions without making assumptions about which traits are key drivers. The fact that simulation model ensembles typically achieve better predictions than any single model [24] is indicative of how the WD could help establish an inclusive baseline that would facilitate the discovery of yield boosting or yield-limiting traits more holistically, while explicitly highlighting knowledge gaps.

For the most part, realized genetic gains in wheat have been achieved by increasing sink strength, as indicated by the relatively stable expression of biomass over time. Nonetheless, source strength is generally the limiting factor determining grain set (sink strength)(**Fig. 1)** [33]. The WD therefore focuses on traits most commonly associated with source and sink strength.

Many processes determine how source and sink traits interact with each other and with the developmental stage to determine final grain yield (Fig 1 and Box 1). Some of these are accepted to be critical, e.g. the impact of leaf area growth on light interception (source) and the impact of the survival of developing florets and seed set on harvest index (sink). Other trait interactions are based on empirical data collected in a limited range of genetic backgrounds and environments, such as the boost to post-anthesis radiation use efficiency (RUE) by increasing sink strength[34], the down regulation of photosynthesis during grain filling, reflecting a lack of sink strength (e.g. Serrago *et al*.[35]), or the trade-off between partitioning of assimilates to spikes versus stem internode growth [36]. Other hypotheses remain to be tested, such as the potential to boost RUE through further optimization of canopy architecture or upregulation of key Calvin cycle enzymes[37], or the potential role of spike hormones in determining floret death and/or grain abortion [34]. The complexities of interacting processes that determine yield potential can be bewildering, so the WD introduced here attempts to illustrate the many relevant relationships graphically and will be developed to explicitly consider their interaction with growth stages. To present the rationale for a WD, we focus on its framework, including the major source and sink traits and traits and processes that underpin the expression and coordination of source and sink (**Fig. 3**). Genes of major effect that impact such traits and processes (**Box 1)** are examples of specific genes influencing traits during early source growth that later affect source-sink balance and yield. As illustrated in **Fig. 1**, sink-strength (grain number and potential size) is determined in an approximately 20-30 day window spanning anthesis and is strongly influenced by current carbon assimilation rates[28]. After this, the realization of photosynthetic capacity is driven largely by the potential of grains to grow and remobilization of reserves, with attendant respiratory costs (**Fig. 3**).

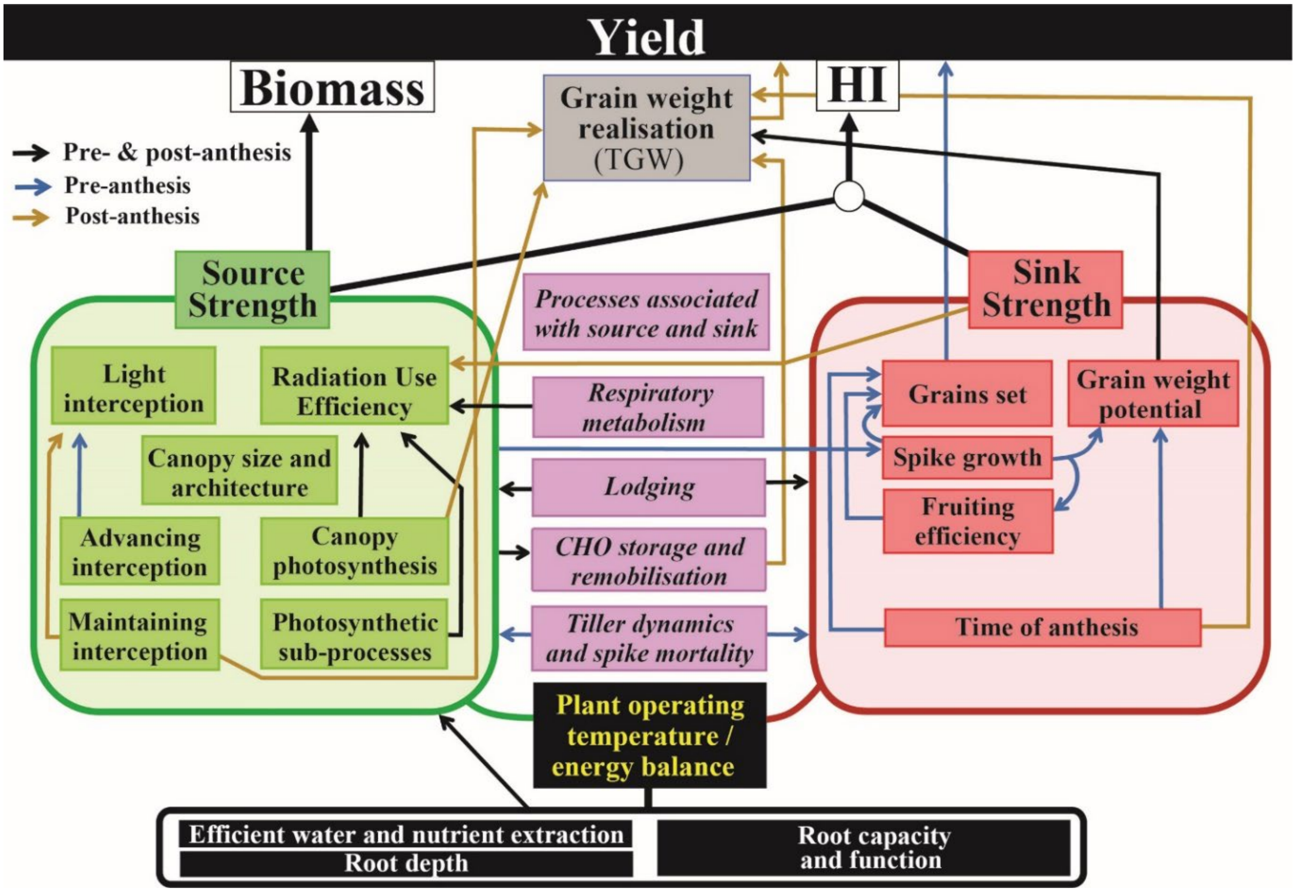


Figure 3. A generalized wiring diagram (WD) for wheat. The diagram depicts the traits most commonly associated with source (left) and sink (right) strength and others (middle) that impact sink and source, largely dependent on growth stage.

At this relatively high level of integration, achieving a step-change in yield potential could, in summary, be achieved by increasing RUE between onset of stem elongation until the end of grain-set shortly after anthesis, and responding to the increased RUE by increasing spike growth, grain set and grain weight potential. The resulting increased sink strength would enable photosynthetic potential to be more fully utilized. It is fully recognized that achieving such goals is dependent on a large number of underlying variables and genetic systems, some of which are known (Box 1) and are used to generate the connections in the WD and others yet to be elucidated. The genetic bases for these connections include, for example, gene-based mapping of biochemical pathways (e.g. trehalose biosynthetic pathway genes that reveals association with source- and sink-related yield traits[38]), genetic manipulation of developmental pathways such as those of spike growth by increasing specific transcription factor activity[39] and transport pathways that move carbohydrate between source and sink[23]. A recent transgenic study overexpressed expansin in wheat, thereby increasing grain weight potential (and yield) without any reduction in grain number[31], calling into question the widely accepted trade-off between these traits.

Potential of wiring diagrams in wheat research

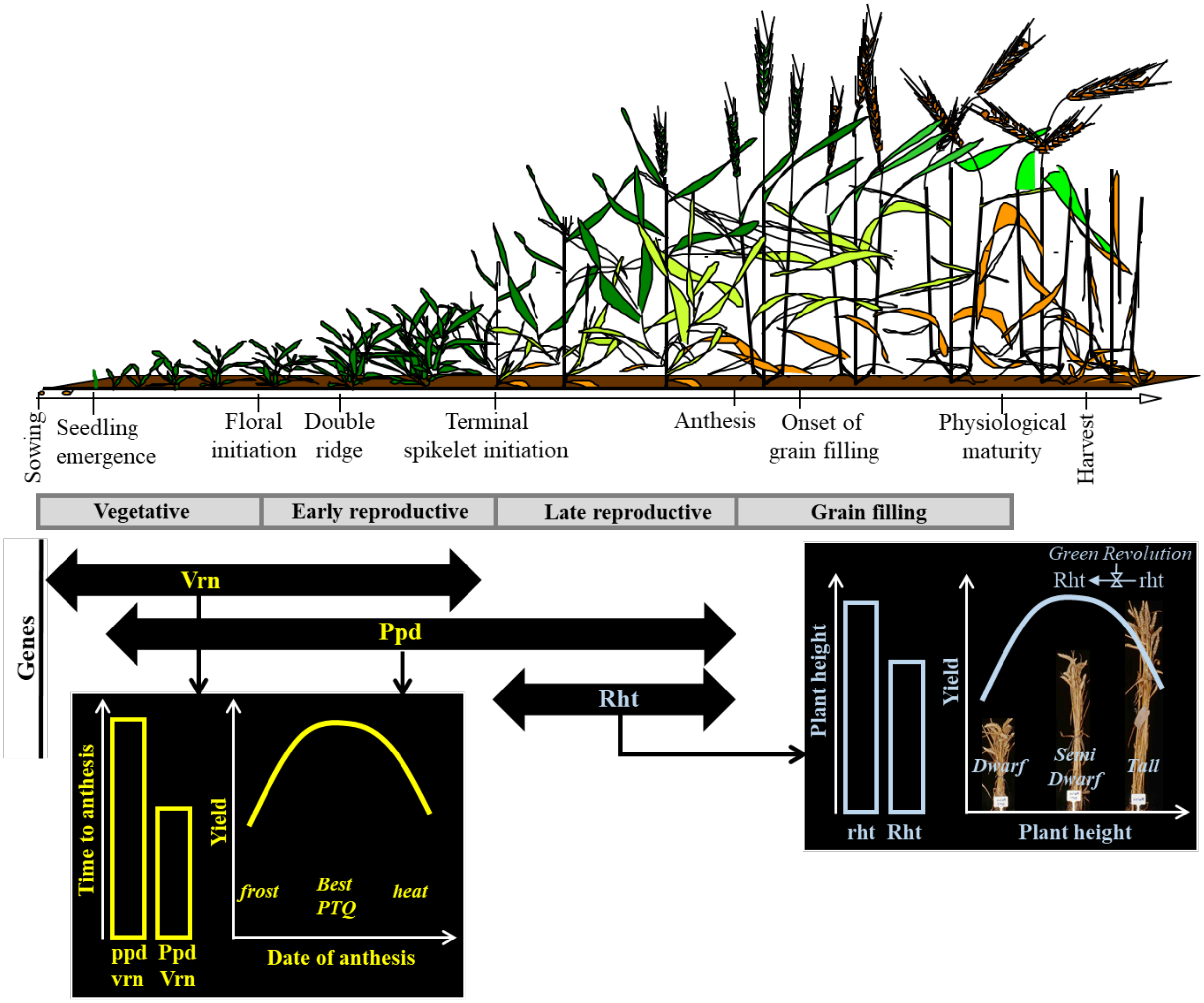
The WD (**Fig. 3**) has been principally developed at the whole crop and plant organ scale and includes plant signaling and metabolic traits that influence yield. The WD intends to capture traits expressed and able to be measured in field-grown plant organs or canopies, rather than data from controlled conditions or *in vitro* research looking at cellular and subcellular processes. Nonetheless, the current integrative-trait level WD can provide a platform for framing research at many different levels of integration.

The trait interactions addressed have an explicit focus on yield potential under relatively favorable environments. However, most of the traits and interactions among them are relevant across a wide range of environmental conditions. When comparing optimal trait interactions among environments, the main differences will be more quantitative than qualitative.

The WD (**Fig. 3**) is not intended to be a static figure, but rather a framework that can be actualized as the science base grows, providing a range of different functions. For example, a graphically-assisted guide integrating current knowledge of physiological traits that determine yield potential in wheat. The WD can also be used as an interactive forum to map new knowledge along with credible hypothesis around current knowledge gaps, within a comprehensive and rigorous scientific framework. One of the main reasons for designing the WD is to provide a qualitative tool for breeders when designing crosses among physiologically and genetically well-characterized parents. The WD can also provide a new context to refine or redesign crop simulation models, by illustrating the relative importance of the different connections among traits in their appropriate phenological context, while highlighting where major ‘black boxes’ still exist. In the longer term, the WD could become a universal decision support tool which if adopted by the wheat improvement community at large, could be customized to discrete target environments to sharpen research focus and highlight context-specific knowledge gaps. The WD can also provide a roadmap to help frame and prioritize research at other levels of integration such as for metabolomic or gene expression studies. The WD concept could also be adapted to other species, as many of the same traits and processes are relevant across crops. Finally, the WD can be adapted as a novel, interactive training tool and as a prioritization framework for strategists and science funding agencies.

Application of wiring diagram in stacking complex traits in breeding

Deterministic progress in crop breeding has relied mainly on deploying genes of major effect, such as those described in **Box 1**. Acceleration of genetic yield gains will require new favorable combinations of genes of minor effect, including from sources outside the elite gene-pools used to train genomic selection models. Trait stacking through hybridization is a way to achieve this, recognizing that incomplete understanding of physiological and genetic interactions will result in unexpected and sometimes disappointing outcomes, as with any semi-empirical process. Thus detailed considerations of the relationships among traits and their contributions to yield, as defined in WDs, aids formulation of trait stacking and hybridization strategies without full knowledge of the underlying genetics that underpin crop improvement.



Box 1. Impact of major genes in wheat (*Ppd, Vrn* and *Rht*) -at different development stages (indicated by horizontal arrows)- that have been widely deployed in breeding[36] and are responsible for several traits considered in the WD. The Vrn and Ppd genes responsible for conditioning to vernalization and photoperiod, respectively (left side of box), have been critical to adjust time to anthesis. This helps the crop to experience a favorable photo-thermal quotient (PTQ) during spike growth, a major driver for sink-strength. Allelic variation at the MADS box gene *Vrn-1*[40], differentiates spring and winter wheat with spring habit alleles being dominant. *Ppd-1* expressed during vegetative growth modulates the strength of the floral promoting signal (FT) that moves from leaves to spike meristems during early reproductive development and influences the conversion of axillary meristems to spikelet meristems[41]. Through modifying the duration of growth phases, *Vrn* and *Ppd* genes also affect the architecture of the

canopy and therefore source potential. *Rht* genes (right side of box) are associated with reduced height. Semi dwarf alleles of *Rht-1* especially, drove a step change in yield potential (i.e. the Green Revolution) by decreasing partitioning of photo-assimilates to stems in favor of juvenile-spike growth, thereby increasing sink-strength and ultimately harvest index[42]. Deployments of these genes have been largely optimized through conventional breeding of winter and spring wheats because of their sizeable and largely heritable phenotypic effects. However, since phenotypes associated with major genes show interaction with genetic background and environment (albeit less than that seen for the combined effect of many minor genes), their deployment in breeding can require 'retuning' to optimize expression of phenology and harvest index [43]. These genes can be mapped to the WD based on previous studies with isogenic lines[42,44]. However, timing of expression of particular alleles, their dominance and epistatic relationships implies influence on several 'wires' of the WD depending on growth stage.

Trait interactions derive from genetic interactions as well as a variable environment within and across seasons (Box 1). The identification of all the causal genes determining a trait under realistic growing conditions is, therefore, a painstaking and resource-demanding process, especially when taking into account climate variability within a target environment. When working with complex traits having a relatively low heritability, they become major challenges for genetics research and breeding, despite progress[45]. An alternative rationale for more deterministic hybridization approaches is to stack traits to enrich the frequency of potentially yield-boosting alleles in breeding gene pools. This is not different in a genetic sense from using GS models to stack favourable small-effect alleles for yield [46], except that it also embraces the potential of additional genetic variation for key traits identified from outside current gene-pools.

The trait-stacking approach, informed by the WDs, increases the probability of accumulating novel, potentially favorable allelic combinations. Clearly, linkage drag of unfavorable alleles from novel sources can also occur. However, pilot studies have shown that this can be overcome if the relatively exotic sources are selected for important agronomic traits [13,47],(which has not generally been the case when exotic germplasm was a source of urgently needed disease resistance genes, for example).

In other words, the deterministic approach hybridizes complementary sources of relatively heritable, beneficial complex traits, and uses phenomic and genomic selection models to identify progeny with a winning combination of traits and alleles. A mundane analogy is playing cards, which like crop breeding requires a mixture of strategy and luck to be successful. By holding specific or higher value cards (the equivalent of potentially beneficial traits expressed in parents) the probability of achieving a final winning combination (equivalent of higher yield in progeny) is increased, in spite of not knowing the winning combinations in advance. Outcomes from such trait combinations can then be used to update the WDs.

This approach can be extended by analyzing results from multi-location trials of such progeny to identify marker-trait associations at the genome level [48]. Modelling outcomes of interactions among candidate traits and genes will also lead to better focused screening of crop genetic resources. Since many factors are involved in yield determination, overcoming one set of genetic bottlenecks will likely highlight others, leading to additional breeding cycles, with each iteration generating refined trait targets, and new information to populate the WD.

Where a trait, or more likely a constellation of traits, is particularly rewarding in terms of productivity gains, the outcome will enable a more focused application of wheat sequencing and gene expression technologies, potentially leading to genetic manipulation using cis or transgenic approaches, targeted mutagenesis, gene editing, etc. [49]. The WD will enable wires representing multi-genic effects to be dissected systematically because the WD not only indicates empirically documented physiological links but also hierarchies in terms of cause and effect, models testable through genomic and metabolic research. As Box 1 indicates, crop phenology which is integral to understanding crop genetics and physiology, invokes more wires and genetic interactions as the crop develops.

The wiring program as a resource to improve crop simulation models

Crop simulation models are implicitly based on a similar concept as the WD. However, the WD is quite different in that it makes no assumptions as simulations must but rather offers a comprehensive springboard based largely on empirical evidence. The WD can be seen as a trait and process-based roadmap to help refine crop simulation models of yield, by illustrating the relative importance of the different connections among traits in their appropriate phenological context, while highlighting where major knowledge gaps still exist. It also provides a framework to analyze outputs of simulation exercises with respect to the assumptions used therein. For example, Messina and colleagues[50] employed the concepts of a WD approach in developing a dynamical model of cohorting of reproductive structures along the maize ear, using empirical data and detailed phenological and carbon/water supply and demand balances to predict emergent phenotypic responses to drought.

Implementing the crop physiological knowledge of the WD is likely to improve the performance of NWheat and other crop models. The validation of NWheat model [55] with de-graining experiments showed that NWheat simulated most yields well, but it did not consider calculating a potential grain weight determined before and around anthesis as outlined in the WD, because it had a maximum grain size of 55 mg as a constant parameter [56]. The exposure to de-graining and shading experiments also indicated that the NWheat model failed sometimes to simulate grain numbers correctly during severe source limitations around anthesis [51]. Implementing the crop physiological knowledge of the WD is likely to improve the performance of NWheat, but also other crop models. For example, the Agricultural Model Intercomparison and Improvement Project AgMIP (https://agmip.org/) [52] has compared 27 of the estimated 35 wheat crop models existing world-wide, showing that a third of the models employ yield components, another third just harvest index, while the remainder uses intermediate or other approaches to simulate grain yield [24]. All these crop models are mostly source-limited in calculating grain yield, despite some of them setting a sink-strength via grain number, but without considering that potential grain size -another component of the sink- is set during a similar period, well before the linear phase of grain filling starts. As a result, most models are likely to perform well when the source tends to limit yield, but will fail when the sink is limiting. The model comparison in AgMIP also identified large crop model uncertainties [24], some of which have been reduced through targeted model improvements, based on crop physiology and experimental data [53,54]. In summary, the combination of WD with crop simulation may be used iteratively to refine each other, incorporating new knowledge as it comes to light.

Conclusions

The WD suggests ways to improve elite breeding material and to explore untapped genetic resources for unique traits and alleles. These approaches along with rapid generation cycling, production of doubled haploids, marker-based chromosome engineering etc., now enable proofs of concept to be established relatively fast. Furthermore, knowledge from other -and especially related- crops via comparative phenomics, genetics and genomics adds a further dimension to translational research and deterministic-orientated breeding.

In addition, the WD can serve as a platform onto which new empirical data are routinely mapped and new concepts added, thereby creating an ever richer common point of reference for refining models in the future, as well as an up-to-date decision support tool for research, breeding and investment strategies.

Acknowledgements. We are indebted to Richard Richards, Yann Manes and Jaques LeGouis for reviewing a first draft of the WD. The authors acknowledge the role IWYP played in identifying the need for a tool to drive crop research and physiological breeding and financial support to develop the WD.

Author contributions: RF proposed the creation of a wiring diagram for wheat traits; MR and GS led the writing of the paper; all authors contributed suggestions and reviewed and refined text.

Ethics declarations: A**uthors declare no ethical conflicts**

Competing interests: A**uthors declare no competing interests.**

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