

Chapter 21

Yield Potential



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Abstract This chapter provides an analysis of the processes determining the yield potential of wheat crops. The structure and function of the wheat crop will be presented and the influence of the environment and genetics on crop growth and development will be examined. Plant breeding strategies for raising yield potential will be described, with particular emphasis on factors controlling photosynthetic capacity and grain sink strength.

Keywords Yield potential · Grain sink strength · Radiation-use efficiency · Trait-based breeding

21.1 Learning Objectives

- Identify the developmental stages and underlying processes that limit yield potential in modern wheats

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- Understand the reasons for yield variation between modern wheat genotypes according to the expression of traits determining source and sink strength
- Suggest pre-breeding crossing strategies to optimise the source-sink dynamic and increase yield potential

21.2 Rationale for Raising Yield Potential

Wheat (*Triticum aestivum* L.) is globally grown on more than 220 million hectares of land with a global average yield of 3.43 t ha⁻¹ determining a current global annual production of c. 750 Mt. ([1]; Fig. 21.1). Wheat is the most widely grown crop and contributes c. 20% of calories and proteins to human beings [2]. The current level of production was achieved over a period with a stable global area over the last 25 years, and therefore the critical increase in production was due to the yield per unit area (Fig. 21.1). At least 30–50% of the critical increase in yield observed was due to the improved yield potential through breeding; and, due to environmental and economic reasons, future growth in production will depend more on improving yield potential through breeding than in the past [2].

Crop yield potential (YP) is defined as the maximum attainable yield per unit land area that can be achieved by a particular crop cultivar in an environment to which it is adapted when pests and diseases are effectively controlled and nutrients and water are non-limiting. Attainable yield (AY) may be defined as the yield a skilful farmer should reach when taking judicious account of economics and risk, i.e. it would be close to YP under irrigated conditions and to water-limited YP in rainfed conditions. The exploitable yield gap (i.e. gap between farm yield and attainable yield) has been estimated at 30% for winter wheat in the UK and 50% for spring wheat in Mexico [2]. Given these yield gaps, at first sight it may not appear cost effective to invest in increasing genetic yield potential. However, the

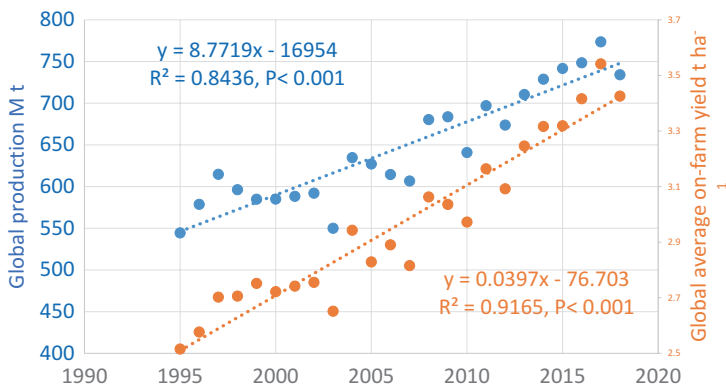


Fig. 21.1 Global production and average yield for bread wheat from 1995 to 2018. (Prepared with data from [1])

implementation of improved agronomic practices is much less straightforward – both practically and economically – for farmers than changing cultivars. Furthermore, increasing yield potential is the only avenue to improve productivity where growers have fully closed the exploitable gap. Strong precedents for yield improvement through wheat breeding started with and have extend well beyond the Green Revolution (e.g. [3]). The fast-growing fields of both genetics with the availability of the wheat genome sequence and high-throughput field phenotyping platforms (Chap. 27) offer considerable promise for more efficient screening of genetic resources, parental characterization and progeny selection to accelerate breeding progress. The existence of well-established national and international crop improvement networks, such as those coordinated by CIMMYT, will enable new genotypes to be rapidly and extensively tested in and delivered to representative target regions.

In addition, an important outcome of breeding for yield potential is higher attainable yields under moderate abiotic stresses. Selection for greater yield potential has frequently resulted in higher production in environments subject to abiotic stress (usually water and heat) in wheat.

In the following sections of the present chapter the physiological traits associated with current rates of yield gains are examined and then the major breeding challenges for raising future yield potential are considered. For concision in these following sections we will show and discuss the most common descriptions of physiological traits summarizing where necessary conflicting results that naturally can be always found in the literature.

21.3 Current Rates of Progress in Yield Potential and Associated Traits

The current annual rate of genetic gain in wheat yield potential from datasets reported globally averages 0.6% (0.3%–1.1%) [2]. Annual genetic gains for grain yield of wheat in CIMMYT international Elite Spring Wheat Yield Trials were 0.5% in optimally irrigated environments [4]. However, in different regions with relevance for global wheat production there seems to have been no genetic gains in yield over the last few decades (e.g. [5]). Moreover, the rate of yield gains required to meet predicted global demand for wheat in 2050 at *ca.* 1.3% per annum is higher than the present rates of genetic gains [6], even those in the regions where gains are still apparent. The levelling off of yield in some countries and regions may occur because: (i) farmers cannot achieve the crop and soil management required to reach attainable yield and/or (ii) crop response to additional inputs exhibits a diminishing marginal yield benefit as yield approaches the ceiling; and/or (iii) genetic progress has been counteracted by climate change (particularly by heat stress).

During the Green Revolution in the 1960s and 1970s, yield progress was associated with gains in harvest index (grain dry matter as a proportion of the above-ground dry matter; HI) due to the introduction of semi-dwarf (*Rht*: Reduced Height)

genes. Field studies on sets of historic cultivars show grain yield progress in recent decades has been associated with greater above-ground biomass in the UK [7], Australia [8], China [9] and NW Mexico [3]. Yield progress was also associated with continued progress in HI in China [9] and Argentina [10]. Overall, this evidence indicates that a simultaneous increase of photosynthetic capacity and grain partitioning in modern wheat cultivars is a crucial task for wheat breeders for future gains in yield potential.

21.4 Opportunities for Future Gains in Yield Potential

Wheat crops harvest light – they convert solar energy, carbon dioxide and water into biomass. Water is required in proportion to the energy captured. Under light-limited conditions wheat yield potential depends on the following (Eq. 21.1):

$$Yield (g\ m^{-2}) = Incident\ radiation (MJ\ m^{-2}) \times Radiation\ capture (\% / 100) \times Radiation\ -\ use\ efficiency (g\ MJ^{-1}) \times Harvest\ Index \tag{21.1}$$

The physiological processes determining radiation capture and conversion and grain dry matter partitioning, as well as water and nutrient capture, are summarized in Fig. 21.2. These processes are discussed further below.

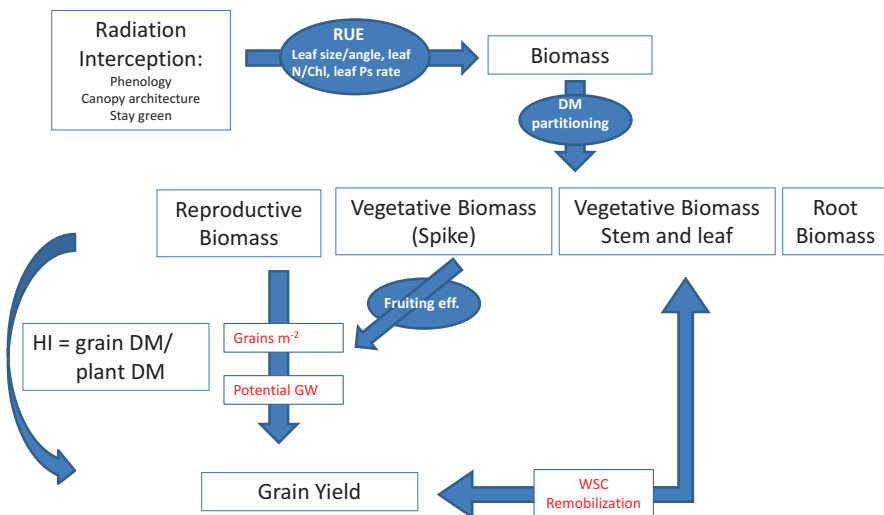


Fig. 21.2 Schematic diagram of physiological processes determining yield potential in wheat (under light limited conditions)

21.4.1 Optimize Root Traits

Breeding for enhanced biomass may be partly dependent on breeding for deeper or denser root systems to increase soil water and nutrient uptake in the absence of improvements in above-ground water and nutrient-utilization efficiencies, particularly in rainfed environments. Nevertheless, breeding for root characteristics has been seldom implemented to date, principally because of the difficulties of screening root phenotypes directly. Lower canopy temperatures might be taken as an indirect indication of a greater root water uptake capacity. Genetic variation in root system size has been widely reported in wheat. There is some evidence that root size of wheat landraces is larger compared with that of modern cultivars [11]. There is also evidence that derivatives of primary synthetic spring wheats (resynthesized hexaploid wheat lines by crossing modern durum wheat (*Triticum turgidum* L.), donor of the AB genome, with the wild progenitor goat grass (*Aegilops triuncialis* L.), donor of the D genome), have greater root biomass compared to bread wheat recurrent parents [12]. Future genetic progress could potentially be accelerated by the development of markers for marker-assisted selection. To develop such markers there is a need for a high precision root phenotyping because the genetic differences may be small, and detailed root physiological measurements are difficult when large numbers of genotypes are involved. A detailed summary of how today's non-invasive phenotyping technologies that measure roots can be strategically combined to speed up germplasm enhancement of roots is beyond the scope of this chapter; however, fortunately comprehensive recent reviews are available, e.g. Watt et al. [13].

21.4.2 Optimize Phenology

Crop phenology must be conducive firstly to avoid catastrophic climatic effects on productivity (frost immediately before anthesis, severe heat during grain filling). This is known as “adaptation” through modifying the duration to anthesis to avoid such extreme events. Secondly, improvements in crop phenology could also contribute to spike fertility as well as being tailored to different photoperiod and temperature regimes. Physiologically, the following stages are usually distinguished: plant emergence, tillering, terminal spikelet (mostly coinciding with onset of stem elongation in field conditions), initiation of booting, spike emergence, anthesis and maturity. These stages may be grouped into: emergence to onset of stem extension (1); onset of stem extension to initiation of booting (2); initiation of booting to anthesis (3); and anthesis to maturity (4). The time-span of each development phase essentially depends on temperature, day-length and genotype (as affected by sowing date) and genetic sensitivity to these two environmental factors.

Once the terminal spikelet is formed, stem elongation starts and slightly later the spike begins to grow. Floret initiation occurs during this phase from the onset of stem elongation to booting and determines maximum number of floret primordia.

This process is not responsive to spike growth (as the metabolic cost of initiating floret primordia is extremely low, the process may be largely independent of availability of resources); and the maximum number of floret primordia does not correlate with the final numbers of fertile florets and grains. Spike growth, slow in its early stages, increases greatly about the time of booting. Floret abortion starts in the booting stage due to competition for carbohydrates during this phase and finishes at anthesis. It has been shown that lengthening the duration of the stem-elongation phase improves grain number through allowing a larger biomass accumulation during this critical phase and consequently increasing assimilate supply to the juvenile spike determining the proportion of floret primordia as competent florets at anthesis [14].

The dynamics of tillering and tiller mortality in wheat are also strongly linked to the timing of developmental stages. The timing of tiller emergence is linked to leaf appearance. When plants experience an increase in shading of lower tiller buds in the canopy changing the red – far red ratio of light coinciding with onset of stem extension, tillering ceases. Under field conditions tiller mortality starts coinciding with the onset of stem elongation; as stems start to be dominant sinks reducing the availability of assimilates to late-formed tillers. Mortality of tillers stops at anthesis, stabilising the number of tillers that will reach maturity. Large genetic variation has been identified in the potential amount of dry matter wasted by non-surviving shoots that could potentially be exploited to minimise their detrimental effects on spike DM partitioning and increase grain number [15].

21.4.3 Increase Radiation-Use Efficiency

Radiation-use efficiency (RUE), defined as the solar energy conversion into above-ground biomass, is a major bottleneck to improve grain yield potential in breeding. It is expected that future genetic gains in wheat yield will rely on improved biomass production [2] whilst achieving a stable expression of HI at values of 0.50 and above; and modest increases in biomass have been reported in recent years [3, 7, 9]. Photosynthesis is the primary determinant of plant biomass with more than 90% of biomass derived directly from photosynthetic products. Compelling evidence that increasing photosynthesis does increase yield, considering that other constraints do not become limiting, comes from the 30 years of free-air carbon dioxide enrichment (FACE) experiments.

RUE together with light interception, both components that determine biomass, are the most integrative estimates of photosynthesis and can be used directly to boost yield through their combination with positive expression of sink traits such as harvest index. Molero et al. [16] proposed the use of exotic material (land-race and synthetic derivative lines) as a valuable resource to increase RUE among other traits.

21.4.3.1 Case-Study 1: Genetic Variation in RUE Was Characterized in a Modern Panel of Spring Wheat. Results Indicated Significant Underutilized Photosynthetic Capacity in Existing Wheat Germplasm

Unpublished data on RUE evaluated at different growth stages in CIMMYT spring wheat cultivars released from 1966 until 2014 shows genetic gains in RUE during grain filling while a negative trend was observed for RUE evaluated pre-grain filling during the critical phase when grain number is determined (Fig. 21.3). These findings, together with the genetic variation observed for RUE expressed at different growth stages [16], strongly support the case for significantly underutilized photosynthetic capacity in existing wheat germplasm and that gains in grain yield may come from increasing RUE particularly in the pre-anthesis period to increase grain number.

However, as part of a translational research approach, stacking of different traits that significantly boost genetic gains needs to be combined in a common platform. For example, as alternative strategies to increase RUE, recent studies propose to exploit natural existing variation in elite material for spike [17], leaf lamina [18] and leaf sheath [19] photosynthesis, pigment composition [20] and carboxylation capacity of Rubisco [21], among others. Prins et al. [22] recently demonstrated the potential benefit of replacing Rubisco of *T. aestivum* with Rubisco from *Hordeum vulgare* or the wild *Aegilops cylindrica*, in terms of achieving higher assimilation rates. McAusland et al. [18] identified a wide variation for flag-leaf photosynthesis rate that was accession and not species dependent.

In parallel with these “steady-state” approaches, recent interest in evaluating dynamic responses of photosynthesis in a fluctuating light environment identified photosynthesis induction as a critical trait for improving productivity in rice [23]. Taylor and Long [24] proposed that slow photosynthesis induction rates in wheat

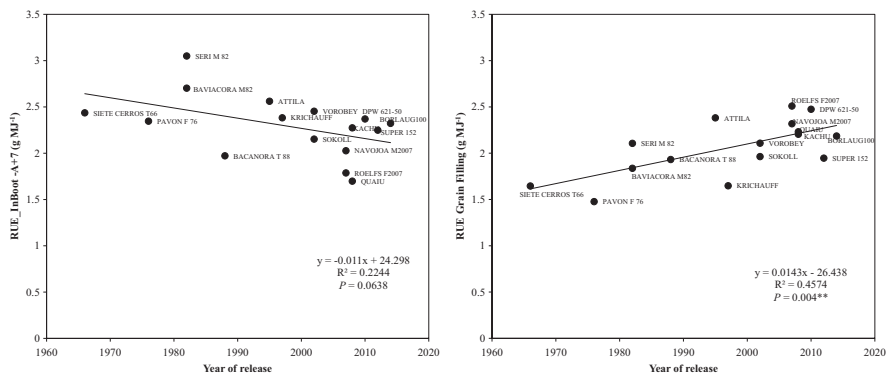


Fig. 21.3 Radiation-use Efficiency (RUE) measured from initiation of booting until 7 days after anthesis (RUE_InBoot-A+7) and from 7 days after anthesis until physiological maturity (RUE_GF) versus year of release from 16 varieties evaluated during 2015–2016 and 2016–2017 under yield potential conditions in NW Mexico. (Unpublished data from G. Molero)

could reduce daily carbon accumulation by up to 20% for a single leaf. In addition, genetic variation for photosynthetic induction has been recently identified in wheat [25]. However, the link between rapid induction and increased RUE or yield is yet to be demonstrated. Field phenotyping methods for RUE and related traits in wheat have been recently reviewed by Reynolds et al. [26]. The development of new methodologies based on remote sensing techniques will be crucial in selecting lines with high RUE together with other photosynthetic-related traits to accelerate genetic gains (Chap. 27).

21.4.4 Increase Spike Partitioning and Fruiting Efficiency

Grain yield improvement is highly associated with grain number per unit area in wheat [7, 27]. Current evidence suggests grain sink strength remains a critical yield-limiting factor and that improving the balance between source and sink is critical for further raising yield potential [2]. Grain growth of modern wheat cultivars is in general little limited by the source during grain filling [27], although co-limitation by source may occur in some cases [3, 7].

The period of stem elongation is critical for yield determination when grains per unit area is determined. Grain number is far more responsive to crop growth during this phase than the preceding phase from emergence to onset of stem extension [2]. During the stem-elongation phase, stem and spike growth overlaps affecting assimilate supply to the spike hence floret survival and grain number (e.g. Rivera-Amado et al. [28]). Since stem and spike growth mainly overlaps during the rapid spike growth phase from booting to anthesis, the extent of competition between the spike and stem differs between stem internodes. A recent investigation on CIMMYT spring wheat elite lines showed decreased DM partitioning to stem internodes 2 (top down, peduncle –1) and 3 was most effective in enhancing spike dry matter partitioning, spike growth and grain number per unit area [28].

The fruiting efficiency (FE; number of grains set per unit of spike dry weight at anthesis) is a key trait which reflects the efficiency with which resources allocated to the growing juvenile spike are used to set grains. The fruiting efficiency subsumes the dynamics of floret production, floret survival and grain abortion which determines the grain number. There is clear genetic variability in FE among modern wheat cultivars which is well correlated with grains per unit area with genetic loci identified (e.g. Gerard et al. [29]). Improvements in FE could be associated with better intra-spike partitioning, for example, by reduced partitioning to the rachis or awns [28]. Alternatively genetic variation in FE may be influenced by levels of spike cytokinins, which play a key role in the stimulation of cell division, from booting to anthesis (see Sect. 21.5).

It is important that higher FE should not be achieved at the expense of having smaller florets with smaller potential grain weight (see Sect. 21.4.5). However, evidence suggests FE can be improved independently of effects on ovary size [30] likely through an improved partitioning of DM within the spike. In addition, it has

been suggested that anatomical structure of the vascular system within the spikelet could be modified to increase FE by favouring translocation of assimilate to the distal floral primordia within a spikelet [31]. The florets closer to the rachis node are directly supplied by the principal vascular bundles of the rachilla, while the distal florets lack a direct connection to the vascular bundle and therefore might not have an equal chance of accessing assimilates from the source [31]. Fruiting efficiency should be amenable for breeding as it is heritable and responds to selection. Another avenue for increasing FE may be improving the loading of sucrose in the phloem in the vascular system for more efficient moving of photo-assimilates from source to sink tissues to enhance grain number [27].

21.4.4.1 Case-Study 2: Genetic Variation in Spike Partitioning Index (SPI) and FE and Related Traits in a Modern Spring Wheat Panel Was Characterized by Rivera-Amado et al. [28]. Variation Was Highly Correlated with HI

The genetic variation in novel grain partitioning traits was characterized in a panel of 26 CIMMYT spring wheat cultivars: stem internode 2 and 3 dry matter partitioning at anthesis was correlated with spike dry matter partitioning index (SPI) and rachis specific weight was correlated with FE [28] (Table 21.1). These results indicated that there is sufficient variation within modern CIMMYT spring wheat cultivars for these traits alone to achieve a step-change in HI in CIMMYT spring wheat to 0.60 by combining within a novel plant ideotype the largest expression of target traits for grain partitioning.

Table 21.1 Grain partitioning traits (mean of 26 genotypes of CIMMYT CIMCOG spring wheat panel and value for best genotype) and relevant correlations with spike partitioning index, FE and HI. Values represent means 2011–2012 and 2012–2013

Trait	Spike partitioning index	Fruiting efficiency	Stem internode 2 + 3 partitioning index	Rachis specific weight	Florets per spikelet
Units	Unitless	grains g ⁻¹	Unitless	g cm ⁻¹	Florets spklt ⁻¹
<i>Mean expression</i>	0.236	85.51	0.165	13.6	2.40
<i>Best expression</i>	0.266	123.81	0.133	11.0	2.75
<i>Relevant corr: (r)</i>	0.37 *** (with HI)	0.36 *** (with HI)	0.61 *** (with SPI)	0.46 *** (with FE)	0.81 *** (with HI)

***P < 0.001

21.4.5 *Increase Potential Grain Weight*

Although average grain weight is frequently negatively related to grains per m², evidence indicates that in the vast majority of conditions wheat grains do not experience a shortage of assimilates to be filled. These assimilates include not only: (i) actual crop photosynthesis, which over the first half of grain filling is predominantly in excess of demands (as grains start growing slowly and the canopy photosynthetic capacity is at its maximum and exposed to increasing radiation levels), but also (ii) water soluble carbohydrates accumulated in stems and leaf sheaths before the onset of grain filling that can be remobilised to complement current photosynthesis. This lack of source limitation for grain growth is supported by evidence that: (i) grain weight does not respond (or responds only slightly) to severe manipulations of source strength (e.g. to defoliations) during the effective period of grain filling and (ii) sizeable amounts of water soluble carbohydrates often remain in the stem when measured at physiological maturity [19]. Thus, in most circumstances, grain filling is sink-limited; i.e. the capacity of the grains to grow largely determines their final weight. This explains why grain weight is much less plastic (and has higher heritability) than grain number.

Therefore, yield potential can be genetically increased by increasing post-anthesis sink-strength given by the number of grains set by the crop and their potential weight. Thus, genetic gains in yield potential would be also achieved through improving potential grain weight (i.e. the capacity of the grains to accumulate resources). As grain growth is largely sink-limited, the potential size of the grains would have been established before the actual growth: the storage capacity is firstly set and then that capacity is filled with dry matter. Indeed, the timing of determination of potential grain weight seems to comprise pre- and post-anthesis processes. As elegantly described recently by Calderini et al. [32], the capacity of the grains to grow is chiefly defined by the size of the carpels of the florets and by the number of endosperm cells.

The floret carpel will become the pericarp after grain set, thus likely setting an upper limit for grain weight realisation during the effective grain filling. Carpels grow for a short period (c. 7–15 days, depending on temperature) immediately before anthesis [32]. The relationship between the size of the carpels at anthesis and the final weight of the grains developed in them after pollination has been shown for a wide range of different genotypes and background environmental conditions (e.g. Reale et al. [33]). This is commensurate with the fact that grain weight has been related to the amount of pericarp dry matter [34].

Endosperm cells are the actual units where starch will be stored, thus their number may also limit the capacity of the grain to store dry matter. The association of grain weight with the number of endosperm cells, developed over the first c. 7–15 days (depending on temperature) immediately after anthesis, is well established. Indeed, reductions in grain weight potential due to the effect of heat were related to reductions in endosperm cell number (e.g. Kaur et al. [35]).

Thus, breeding for improved potential grain weight is a real alternative to grain number that can be exploited, if the increased potential grain weight is not linked to a reduced number of grains [14]. Indeed, genetic factors controlling potential grain weight, without representing a compensation due to reductions in grain number, have been identified; and transgenic lines over-expressing expansins (proteins relaxing cell walls) produced significant increases in yield of field-grown wheat through increasing potential grain size [32].

21.5 Plant Signalling Approaches to Increase Yield Potential

There is increasing evidence that variation in grain number is regulated by plant growth regulators during the rapid spike growth phase from booting to anthesis in wheat. Cytokinins play a key role in the stimulation of cell division and nucleic acid metabolism. Altering spike cytokinin concentration through expression level of two cytokinin oxidase genes has been shown to increase grain number in wheat [36]. Cytokinin levels are regulated by a balance between biosynthesis enzymes (e.g. isopentenyl pyrophosphate transferase) and degradation enzymes (e.g. cytokinin oxidase/dehydrogenase). The grain sink strength of the spike meristem could therefore be enhanced by altering cytokinin homeostasis through the upregulation or the downregulation of these enzymes, respectively, to coordinate growth and floret fertility.

In addition, it has been observed that excessive ethylene production results in wheat grain abortion under high temperature stress, suggesting that reduced grain accumulation of ethylene in wheat may be a desirable trait. A negative association was observed between spike dry weight at anthesis and ethylene production in a GWAS population at high temperatures in the field and genetic bases were indicated [37]. Stress ethylene production, for example under soil compaction or drought, can also induce grain abortion. High ethylene levels also inhibit grain-filling rates by restricting assimilate partitioning to developing grains resulting in low starch biosynthesis and high accumulation of soluble carbohydrates, ultimately decreasing grain yield. In addition, there is evidence that the ABA/ethylene ratio is positively related to grain filling rate by regulating starch synthesis [27]. Pinpointing the plant hormone signals underlying grain set/abortion and their genetic basis in wheat should therefore permit the development of genotypes with less conservative strategies for determination of grain number.

An alternative plant signalling avenue to increase grain sink strength may be to increase the concentration of trehalose-6-phosphate (T6P), a sugar signal that regulates growth and development, and increases starch synthesis in spikes. Genetic modification of trehalose-6-phosphate phosphatase and chemical intervention approaches have been used to modify the T6P pathway and improve crop performance under favourable conditions in the wheat [27].

21.6 Trait-Based Breeding for Yield Potential

Increased genetic yield potential is a key driver of both productivity and variety replacement. Some of the key traits have already been discussed in this chapter and it is important that crossing strategies achieve an effective balance among them. For example, increasing RUE alone does not guarantee increased yield unless additional assimilates result in more and/or larger grains. The fact that increased photosynthetic potential does not necessarily optimize yield is supported by the negative association observed between harvest index and biomass [3]. Therefore, to achieve full expression of yield potential, it is necessary to optimize the source:sink dynamic by ensuring that expression of grain set matches the photosynthetic potential of current and future genotypes (Fig. 21.3).

Evidence for genetic variation in source:sink balance (SSB) and its importance in boosting yield and radiation-use efficiency in field-grown plots has come from various sources. Experiments in wheat have shown that a high demand for assimilates—determined by sink strength of the grains—can stimulate the supply of photo-assimilates based on light treatments, as well as studies with cytogenetic stocks [38]. More recently, a cross designed to combine high sink strength in high RUE backgrounds resulted in doubled-haploid lines expressing exceptional yield and biomass in a high yielding environment in Southern Chile [30].

However, for novel approaches to be adopted, proofs-of-concept must be demonstrated in a breeding context. This necessarily involves translational research via pre-breeding that demonstrates genetic gains from new innovations across an appropriate range of target environments, and in lines that also contain the component agronomic traits essential to make new cultivars marketable. The pre-breeding steps include: (i) designing crosses to combine promising yield-boosting traits; (ii) identifying the best sources of those traits among diverse genetic resources using phenotypic and where available genomic data; (iii) validating new trait combinations through crossing and trialing the best new progeny; and (iv) sharing the new germplasm and breeding technologies with breeding programs for validation globally. Results of the CIMMYT Wheat Yield Collaboration Yield Trial (WYCYT) have shown significant increases in yield potential across international wheat targets in the selected progeny of crosses designed to combine favourable sources of source and sink traits. In summary, stacking “source” and “sink” related traits (Fig. 21.4) via strategic crossing seems to be a viable way to boost genetic yield gains while at the same time involving intuitively valuable traits for increasing for potential yield.

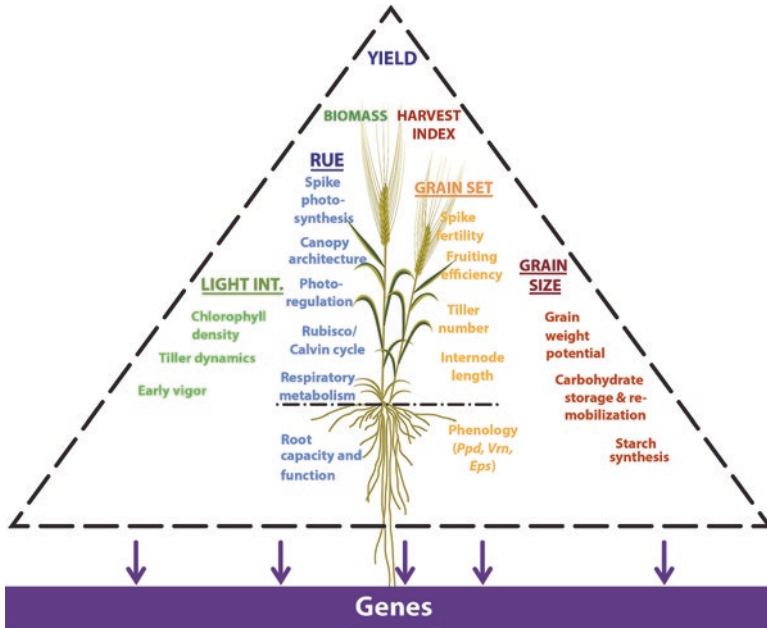


Fig. 21.4 Trait hierarchy in relation to approximate degree of integration, depicting some of the established drivers of biomass (source) on the left of the plant, and harvest index (sink) on the right side. Abbreviations: *Int* interception. (Reprinted with permission from [26])

21.7 Genetic Regulation of Grain Number and Yield Potential

The genetics of phenology in wheat are relatively well understood. The genes controlling winter/spring growth habit (*Vrn-1*) and photoperiod response (*Ppd-1*), which are responsible for coarse-tuning time to anthesis, are often completely fixed in breeders' gene pools targeting a specific environment. QTL with smaller effects on phenology are collectively recognized as earliness *per se* genes and also are critical for fine-tuning time to anthesis as well as for the duration of particular sub-phases composing time to anthesis. There is an increasing body of evidence for the role of these phenology genes in increasing grain number and yield. With regard to plant height, beyond GA-insensitive *Rht-B1b* and *Rht-D1b* genes that have been extensively deployed to increase yield potential, other dwarfing genes such as *Rht13* or *Rht18* have also been shown to increase grain yield, and others such as *Rht8* may also increase yield but just under particular environmental conditions. As plant height has been already optimized in most growing regions, further increases in the availability of assimilates for spike growth may require reductions limited to small specific stem internodes to favour spike growth as proposed by Rivera-Amado et al. [28]. Several studies have identified QTL which control height by disproportionate

reduction in the length of specific internodes, e.g., Cui et al. [39]. However, these studies did not include the measurement of SPI or grain yield.

Grain yield improvement is highly associated with grain number per unit area in wheat as described in Sects. 21.4.4 and 21.4.5. Outside the major adaptive genes for phenology and plant height, the QTLs and trait marker associations described for grain number are generally of small effect and subject to strong environmental interactions. This results in the low heritability of this trait. Nevertheless, a few genes have been found to be robust and validated. For example, GNI-1A on chromosome 2AL encodes a homeodomain leucine zipper class I (HD-Zip I) transcription factor, the expression of which was highest in the distal floret primordia of the spikelet and in parts of the rachilla [40]. In tetraploid wheat, reduced function mutations resulted in increased grain set per spikelet, grain number, and yield. Another example is TaAPO-A1 which is the wheat orthologue of Aberrant Panicle Organization in rice [41] on chromosome 7A in wheat. A mutation in the F-box domain defines two common alleles in modern global bread wheat which are strongly associated with spikelet number. Further study and manipulation of these pathways provides targets for the deployment of induced and natural variation for increased grain number.

21.8 Key Concepts

Under light limited conditions wheat yield potential depends on the following:

$$\begin{aligned} \text{Yield}(\text{g m}^{-2}) &= \text{Incident radiation}(\text{MJ m}^{-2}) \times \text{Radiation capture}(\% / 100) \\ &\times \text{Radiation-use efficiency}(\text{g MJ}^{-1}) \times \text{Harvest Index} \end{aligned} \quad (21.2)$$

Current evidence suggests grain sink strength remains the critical yield-limiting fact and that improving the balance between source and sink is critical for further raising yield potential. Thus, in most circumstances, grain filling is sink-limited; i.e. the capacity of the grains to grow largely determines their final weight. Therefore, yield potential can be genetically increased by increasing post-anthesis sink-strength given by the number of grains set by the crop and their potential weight. There is significantly underutilized photosynthetic capacity in existing wheat germplasm and gains in grain number could come from increasing pre-anthesis RUE. Alternatively, grain number can be increased through enhancing partitioning to spikes at anthesis through optimized phenology and/or favouring partitioning of assimilates to spikes at the expense of specific stem internodes. In addition, grain sink strength may be raised by increasing potential grain weight via increasing carpel weight at anthesis or endosperm cell number and/or size. Simultaneous increases in these source and sink traits are required to accelerate rates of genetic gain. Stacking “source” and “sink” related traits via strategic crossing in trait-based breeding is a crucial task to boost genetic yield gains while at the same time involving intuitively valuable traits for increasing for potential yield.

21.9 Summary

Crop yield potential is defined as the maximum attainable yield per unit land area that can be achieved by a particular crop cultivar in an environment to which it is adapted when pests and diseases are effectively controlled and nutrients and water are non-limiting. Under light limited conditions wheat yield potential depends on: Incident radiation (MJ m^{-2}) \times Radiation Capture ($\%/100$) \times Radiation-use efficiency (g MJ^{-1}) \times Harvest Index. Yield potential can be genetically increased by increasing post-anthesis sink-strength given by the number of grains set and their potential weight, and grain sink strength remains a critical yield-limiting factor. The period of stem elongation is critical for yield determination when grains per unit area is determined. There is scope to exploit natural existing variation in elite material for spike, leaf lamina and leaf sheath photosynthesis, pigment composition and carboxylation capacity of Rubisco to increase RUE during stem elongation and hence grain number. Furthermore, grain number may be increased by fine-tuning of the phenological phases using phenology genes to favour spike growth during stem elongation, or optimizing the trade-off between partitioning of assimilates to spikes versus stem internode growth. Complementary to these avenues for increasing grain number, fruiting efficiency can be increased through modifying spike hormone regulation or intra-spike partitioning to maximize grains set per unit spike weight. Finally, potential grain weight is an alternative trait to increase grain sink strength that can be exploited through increasing the carpel weight at anthesis or endosperm cell number and/or size. Achieving a simultaneous increase of photosynthetic capacity and grain partitioning in modern wheat cultivars is a crucial task for breeders. Stacking these “source” and “sink” related traits via strategic crossing in trait-based breeding is a viable way to boost genetic yield gains while at the same time involving intuitively valuable traits for increasing for potential yield.

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