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REVIEW

# Genetic and molecular bases of yield-associated traits: a translational biology approach between rice and wheat

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**Abstract** Transferring the knowledge bases between related species may assist in enlarging the yield potential of crop plants. Being cereals, rice and wheat share a high level of gene conservation; however, they differ at metabolic levels as a part of the environmental adaptation resulting in different yield capacities. This review focuses on the current understanding of genetic and molecular regulation of yield-associated traits in both crop species, highlights the similarities and differences and presents the putative knowledge gaps. We focus on the traits associated with phenology, photosynthesis, and assimilate partitioning and lodging resistance; the most important drivers of yield potential. Currently, there are large knowledge gaps in the genetic and molecular control of such major biological processes that can be filled in a translational biology approach in transferring genomics and genetics informations between rice and wheat.

## Introduction

Cereals represent the most important group of cultivated crop plants. Rice and wheat are the two important food crops, accounting for more than 40 % of global food production. Globally, the genetic gain of both crops is less than 1 % p.a. (Hawkesford et al. 2013) although the predicted demand is higher (1.7 % p.a. for wheat, Rosegrant and Agcaoili 2010; and 1 % p.a. for rice, Kruse 2010) until 2050. It is estimated that decreasing yield gaps between potential and farmers yields worldwide could increase yield of wheat and rice by 71 and 47 %, respectively (Mueller et al. 2012). The existence of large yield gaps highlights the crucial roles of crop management, environmental trade-offs (e.g. $CO_2$, Slattery et al. 2013) and socio-economic constraints towards sustainable cropland intensification. However, monitoring the genetic architecture of crop plants remains a major force driving yield potential and productivity (Yu et al. 2012), and several yield traits potentially influencing grain yields have been proposed (Murchie et al. 2009; Foulkes et al. 2011; Parry et al. 2011; Reynolds et al. 2012).

Rice and wheat differ in plant architecture, zones of adaptation, physiology, number of chromosomes and genome size (Salse et al. 2008; Nagai and Makino 2009; Shingaki-Wells et al. 2011). Despite the apparent differences, they hold similar set of genes and share relative conservation of gene order along the chromosomes (Sorrells et al. 2003; Salse et al. 2008; Crismani et al. 2011). Due to the small genome size, availability of a genetic map as well as close representatives of the grass ancestor (structures in 12 chr. covered by ~10,000 founder genes), rice has been marked as a model species for cereal genomic understanding and therefore can greatly benefit other cereals, for example wheat (Bennetzen and Ma 2003; Salse 2012a). In contrast, biological entities unique to wheat such as earliness per se genes, but absent in rice, could pave a way for improving genetic understanding of flowering pathways in rice (Faricelli et al. 2009). Owing to many shared genetic duplications and close colinearity in many aspects of

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physiology and metabolism, knowledge from both species could mutually benefit each other (Salse 2012a).

In this review, we summarize the current understanding of several aspects of plant biology and mark the similarities and differences between rice and wheat. To this end, we follow a conceptual model for yield (Reynolds et al. 2009, 2010, 2012) and yield-associated traits (Murchie et al. 2009; Foulkes et al. 2011; Parry et al. 2011; Reynolds et al. 2012) for the physiological, genetic and molecular understanding in both species. This allowed us to identify several research gaps in both species. We believe that mutual sharing of knowledge hotspots is important to increase yield gains in both species and to strengthen food security in the future.

## Comparative genomics between wheat and rice for translational-based dissection

Comparative genomics, i.e. the studies of the relationships between genomes of phylogenetically related species, aims at identifying the portion of genomes that are conserved and those that are species specific allowing changes in genome structure and content to be related to differences in phenology. Comparative genomics in families that have a relatively recent history such as grasses are especially interesting because they allow understanding of the basis of diversity, adaptation and domestication that can help a better exploitation of genetic resources for crop improvement. Comparative analyses between Triticeae (wheat) and other cereals (rice) have been the focus of intense research in the past decades. Comparative genomics, performed at the marker-based level (comparing wheat genetic maps to the rice genome) as well as sequence-based level (comparing wheat sequenced loci to rice genome fragment sequences), have indicated good conservation of the markers' order at the genetic map level as well as gene order at the genome level promoting rice as a reference genome for the Triticeae and more particularly for wheat (Salse 2012b).

Sequence comparisons between the genes annotated in rice (42654 gene sequences) and the mapped wheat genes (6426 mapped ESTs) revealed 13 blocks of colinearity covering 83 and 90 % of the rice and wheat genomes, respectively (Salse et al. 2008). They correspond to the following chromosome pairs: w1-r5, w1-r10, w2-r4, w2-r7, w3-r1, w4-r3, w4-r11, w5-r3, w5-r9, w5-r12, w6-r2, w7-r6 and w7-r8. A comparison of the linear order of the rice and wheat genes indicated that for 27 % of them, the identified wheat ortholog is not located in the orthologous wheat region indicating additional rearrangements (such as wheat specific local duplications, translocations and transpositions) within orthologous regions between rice and wheat. Despite the gene conservation between rice and wheat, 10 major large duplicated blocks covering 67.5 % of the wheat genome have been identified in Triticeae genomes (Salse et al. 2008). Further comparisons with duplicated regions in rice and wheat revealed that seven of the intraspecific duplications are conserved at orthologous positions between rice and wheat. These ancestral shared duplications were found in the following chromosome pair combinations: w1-w2/r5-r4, w1-w3/r5-r1, w1-w4/r10-r3, w2-w4/r7-r3, w2-w7/r4-r8, w5-w7/r9-r8 and w6-w7/r2-r6. Altogether, they represent 68 % of the rice genome and 66 % of the wheat genome, an evidence for the occurrence of an ancestral polyploidization event (Salse et al. 2008) dating back to 90 million years ago (MYA).

Further analyses of the origin and evolution of the shared duplications in maize, sorghum and *Brachypodium*, led to the proposed model for grass genome evolution from an ancestor with 7 chromosomes structured with protogenes and with a physical coding space size of <50 Mb that underwent a whole genome duplication (WGD), 50–70 MYA followed by two interchromosomal translocations and fusions that resulted in a $n = 12$ intermediate ancestor (Murat et al. 2010; Murat et al. 2014). In this model, rice has retained the original chromosome number (12), whereas chromosome number has reduced in the other cereal genomes. In wheat, 5 chromosomal fusions resulted in an ancestral wheat genome with $n = 7$ chromosomes. Thus, the 10 duplicated regions observed in the wheat genome reflect the ancestral WGD and 3 additional segmental duplications (SD) that have occurred after the rice/wheat speciation (Salse 2012a, b). In the recent history, wheat ancestors ($n = 7$) went through two neopolyploidization events leading to *Triticum aestivum*, which originated from two hybridizations between *T. urartu* (A genome) and an *Ae. speltoides*-related species (B genome) 1.5 MYA, forming *T. turgidum* ssp. *diccocoides;* and between *T. turgidum* ssp. *durum* (genomes AB) and *Ae. tauschii* (D genome) 10,000 years ago (Fig. 1).

Wheat genomics resources have been recently published with the release of the wheat genome shotgun hexaploid (Brenchley et al. 2012) and diploid (D genome) ancestor sequences in Jia et al. (2013) and Luo et al. (2013), as well as the A genome progenitor sequence in Ling et al. (2013), sequences as well as genome-wide diversity maps in hexaploid (Allen et al. 2011, 2013; Chao et al. 2009; Winfield et al. 2012; Lai et al. 2012; Cavanagh et al. 2013), tetraploid (Saintenac et al. 2011a, b; Trebbi et al. 2011; Ren et al. 2013) or diploid progenitors (Wang et al. 2013; You et al. 2011). The integrations of both genomic and genetic resources, described in the previous section, offered recently the opportunity to provide the most accurate wheat syntenic (or also referenced as computed, Pont et al. 2011) gene order (i.e. syntenome) and to test its accuracy as this will probably represent in the medium term the wheat genome reference, until complete pseudomolecules

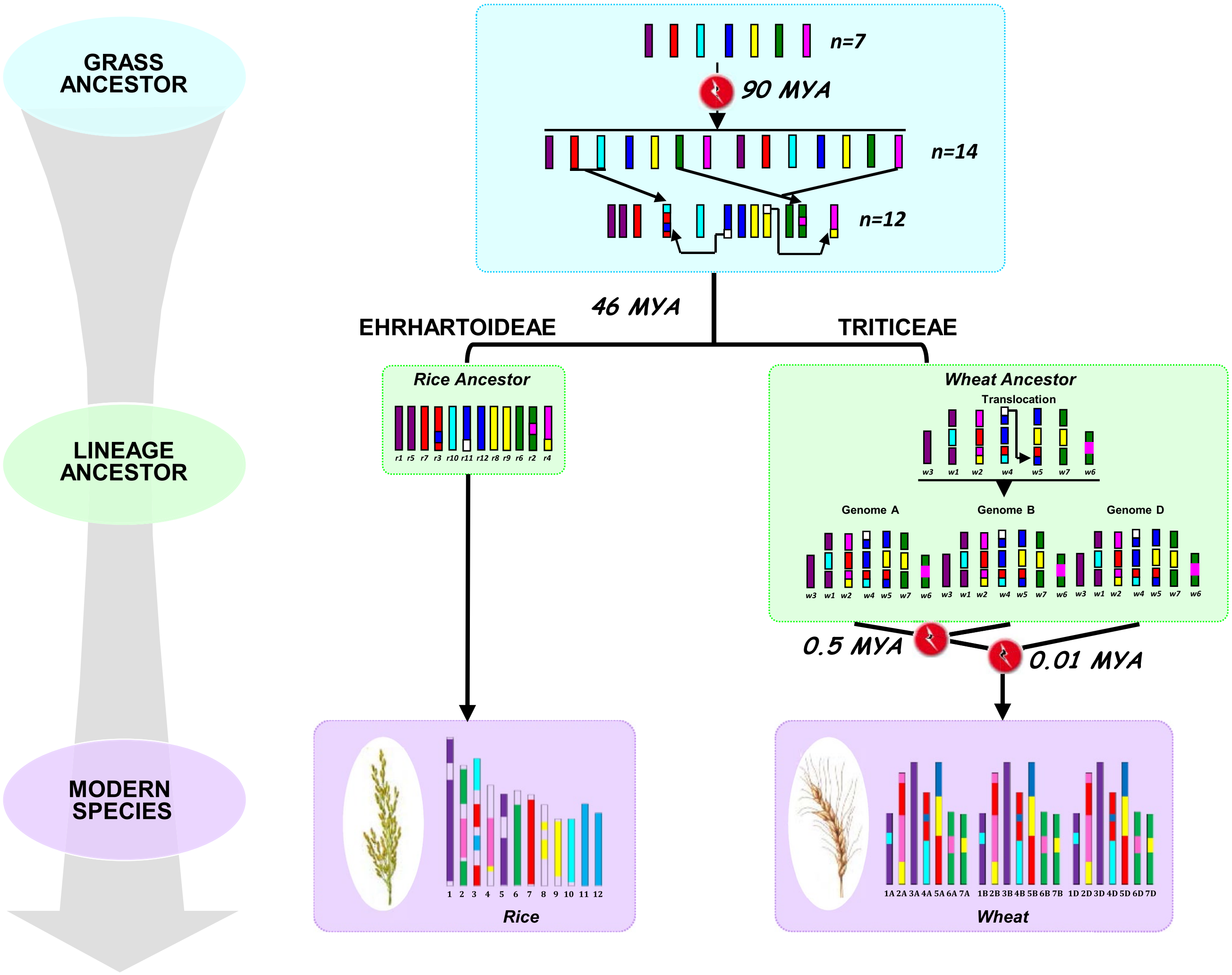

**Fig. 1** Rice and wheat genomes evolutionary history from the grass ancestor. The modern rice (*left*, Chr 1 to 12) and wheat (*right* Chr 1A to 7D) chromosomes (*bottom*) are represented with colour codes to illustrate the evolution of segments from a common grass ancestor with seven protochromosomes (*top*). Whole genome duplications (WGD or polyploidy) are illustrated with *red dots*. The origin of the 21 bread wheat chromosomes is shown with two-hybridization event between A, B and D progenitors (adapted from Murat et al. 2014 and Pont et al. 2013)

are publicly released for the 21 chromosomes. Such validated wheat syntenome offered the opportunity to perform a comprehensive analysis of wheat gene space evolutionary plasticity during the last 100 million years, suggesting a contrasted mode of evolution between A, B and D subgenomes (Pont et al. 2013). Contrasted plasticity was observed where the B subgenome appears sensitive (i.e. plastic) in contrast to A as dominant (i.e. stable) in response to the neotetraploidization event 1.5 MYA and D subgenome as supradominant (i.e. pivotal) in response to the neohexaploidization event 10,000 years (Pont et al. 2013).

Finally, accurate comparative genomic relationships led to an improved representation of cereal genomes in concentric circles providing a new reference tool for improved gene annotation and cross-genome markers development (Bolot et al. 2009). Comparative genomics data provide information about the 16 K non-redundant ancestral plant gene set that can be used as a platform for the development of conserved orthologous set (COS) markers for SNP discovery (Quraishi Masood et al. 2009; Pont et al. 2011), to support cross-genome (also referenced as translational) map-based cloning strategies. COS-based translational genomic approaches have been widely used in plants to identify trait expression associated with non-sequenced genomes such as wheat on the orthologous regions identified in the rice reference sequenced genome. This translational genomics strategy has been successfully applied in wheat to identify genes associated with nitrogen use efficiency (Quraishi et al. 2011a), grain fibre content (Quraishi et al. 2011b) and carotenoid content (Dibari et al. 2012)

**Table 1** Genes driving yield-associated traits in wheat and rice

| Trait | Wheat genes | References | Rice genes | References |
|---|---|---|---|---|
| Vernalization | *VRN* | Cockram et al. (2007), Colasanti and Coneva (2009) | *Hd1, Ehd1, DTH2*[a] | Izawa et al. (2007), Wu et al. (2013) |
| Photoperiod response | *PPD* | Cockram et al. (2007) | *Hd1, Ehd1, Hd3a, OsGI, SPIN1, OsPRR37* | Izawa (2007), Wu et al. (2013), Koo et al. (2013) |
| Earliness per se | *Eps* | Lewis et al. (2008), Faricelli et al. (2009) | *Hd1* and *2*[b] | Faricelli et al. (2009) |
| Floral transition | *WAP1* (*TaMADS11*), *WAP2* (*Q gene*) | Murai et al. (2002), Ning et al. (2009) | *RAP1B, RFT1, EF7, SE5* | Kyozuka et al. (2000), Saito et al. (2012), Takahashi et al. (2009) |
| Tillering | *tin* | Kebrom et al. (2012) | *Moc1, OsTB1* | Xing and Zhang (2010) |
| Leaf architecture | *Pa2, His2, Hl1* and *2* | Wu-yun et al. (1999), Dobrovolskaya et al. (2007) | *RTFL, OsDWARF4, OsAGO7, NAL2/3, OsBAK1, Roc5* | Tsukaya (2006), Sakamoto et al. (2006), Shi et al. (2007), Ishiwata et al. (2013), Li et al. (2009), Zou et al. (2011) |
| Leaf photosynthesis and Rubisco | *RCA* | Ristic et al. (2009) | *Chl1* and *9, PHD1* | Zhang et al. (2006), Li et al. (2011) |
| Leaf senescence | *Gpc* | Olmos et al. (2003) | *SUB1, SAGs* | Fukao et al. (2012), Lee et al. (2001) |
| Panicle development | | | *LAX1, Moc1, FZP* | Xing and Zhang, (2010) |
| Spikelet development | *Bh, Eps* | Faricelli et al. (2009), Peng et al. (2000) | *APO1, SP1, DEP1* | Xing and Zhang, (2010) |
| Grain characteristics | *TaGW2, TaCKX2* | Bednarek et al. (2012), Zhang et al. (2010b) | *Gn1a (OsCKX2), GS3, GW2* and *5* | Ashikari et al. (2005), Fan et al. (2006), Takano-kai et al. (2009), Song et al. (2007) |
| Grain-fill | *TaISA3* | Kang et al. (2013) | *GIF1, GW2, rg5* | Song et al. (2007), Wang et al. (2008a, b), Ishimaru et al. (2005a, b) |

[a] The variation in the expression of these proteins is reported to be associated with the rice adaptation to different latitudes

[b] These genes are reported to be associated with earliness in rice

using rice as a pivotal model genome. This strategy has opened new perspectives in enlarging the yield potential of both crops based on comparative biology of phenology, photosynthesis, assimilates partitioning and lodging resistance traits.

## Crop phenology adaptation to environments

Wheat adaptation to a wide range of environments is largely governed by allelic diversity in vernalization (*VRN* genes, 1, 2, 3 on chr. 5, spring vs. winter), photoperiod genes (*PPD* genes, A1, B1, D1 on chr. 2, photoperiod-sensitive and -insensitive) and genes controlling earliness per se (Tables 1, 2; Lewis et al. 2008; Zhang et al. 2008; Faricelli et al. 2009; Distelfeld et al. 2009; Dhillon et al. 2010; Mayfield et al. 2011). Earliness per se locus, *Eps-A*$^{m}$1, affects the duration of early developmental phases in wheat (Lewis et al. 2008; Faricelli et al. 2009), and 33 chromosomal regions were identified for earliness in hexaploid wheat (Gouis et al. 2011). Many of them colocalize with vernalization and photoperiod genes (Chen et al. 2010), indicating that an appropriate combination of these alleles would modify developmental phases in wheat. A recent study reported that *VRN-A1*, *PPD-D1* and *VRN-D3* show greatest impact on the development at stem elongation period, heading time and physiological maturity, respectively (Chen et al. 2010). In addition, several QTLs on chr. 1, 2, 5 and 7 were linked to different developmental phases;

**Table 2** Major QTLs regulating yield-associated traits in wheat and rice

| Trait | Wheat chromosomes | References | Rice chromosomes | References |
|---|---|---|---|---|
| Vernalization | 5 | Cockram et al. (2007), Colasanti and Coneva (2009) | – | – |
| Photoperiod response | 2 | Cockram et al. (2007) | 3 and 6 | Yano et al. (1997), Yin et al. (1997), Yamamoto et al. (2000), Lin et al. (2006) |
| Earliness per se | 1 and 2 | Lewis et al. (2008), Faricelli et al. (2009) | 6 and 7 | Nakagawa et al. (2005) |
| Grain yield | 2, 4, 5, 6, and 7 | Peleg et al. (2011), Maccaferri et al. (2008), Huang et al. (2006), Quarrie et al. (2006) | 1, 3, 5, 6, and 7 | Ishimaru et al. (2001a, b), Zhang et al. (2004), Xing and Zhang (2010) |
| Grain-filling | 1, 2, 3, 4, 5, 6, and 7 | Wang et al. (2008a, b), Salem et al. (2007), Kajimura et al. (2011) | 2, 4, 5, 8, and 12 | Song et al. (2007), Wang et al. (2008a, b), Ishimaru et al. (2005a, b) |
| Kernels per spike/panicle, thousand kernel weight, spike number | 1, 2, 3, 4, 5, and 6 | Peleg et al. (2011), Narasimhamoorthy et al. (2006) | 1, 2, 3, and 7 | Zhang et al. (2009), Liu et al. (2010) |
| Grain length, size, weight | 1, 4, 5, and 7 | Gegas et al. (2010), Mir et al. (2012) | 2, 3, 5, 6, 7, and 8 | Song et al. (2007), Fan et al. (2006), Weng et al. (2008), Shomura et al. (2008), Qiu et al. (2012), Bai et al. (2010) |
| Lodging resistance/stem strength/stem diameter | 4, 5, and 6 | Lanning et al. (2006), Hai et al. (2005), Ma (2009), Verma et al. (2008), Huang et al. (2006) | 1, 5, 6, 7, 8, and 12 | Kashiwagi and Ishimaru (2004), Ookawa et al. (2010), Kashiwagi et al. (2008), Kashiwagi et al. (2010) |
| Flag-leaf characters | 1, 2, 5, and 6 | Coleman et al. (2001), Wang (2009), ter Steege et al. (2005), Kulwal et al. (2003) | 1, 2, 3, 4, 6, 8, and 9 | Hu et al. (2012), Chen et al. (2011), Farooq et al. (2010), Zeng et al. (2009), Dong et al. (2004), Yue et al. (2006) |
| Chlorophyll content | 1, 2, 4, 5, and 7 | Quarrie et al. (2006), Yang et al. (2007), Zhang et al. (2009), Yan et al. (2010a, b) | 1, 3, 4, and 8 | Abdelkhalik et al. (2005), Zhang et al. (2006), Jiang et al. (2012), Dong et al. (2007) |
| Rubisco content (Barley and rice) | 4 | Becker and Heun (1995), Forster et al. (2000), This et al. (2000) | 8, 9, and 10 | Ishimaru et al. (2001a, b), Kanbe et al. (2009) |
| Net photosynthesis | – | – | 4 | Teng et al. (2004), Adachi et al. (2011), Gu et al. (2012) |
| Leaf senescence | 1, 2, 3, 5, 6, and 7 | Bogard et al. (2011), Li et al. (2012a, b) | 6 and 9 | Abdelkhalik et al. (2005), Fu et al. (2011), Lin et al. (2010) |
| Nitrogen uptake, use efficiency | 3, 4, 5, and 7 | Quraishi et al. (2011a, b), Habash et al. (2006), Fontaine et al. (2009) | 2, 8, and 9 | Obara et al. (2004), Piao et al. (2009), Wang et al. (2010) |

however, they have not been explored yet (Kato et al. 2002; Borràs-Gelonch et al. 2010, 2011, 2012).

In contrast, three major photoperiod genes explain the adaptation of rice cultivars to local environments: *Heading date 1* (*Hd1*), *Early heading date 1* (*Ehd1*) and *Hd3a* (Yano et al. 2001; Nakagawa et al. 2005; Izawa 2007; Cockram et al. 2007). At least 14 QTLs controlling photoperiodic response in rice were mapped on distinct chromosomes (Yano et al. 1997; Yamamoto et al. 2000; Lin et al. 2006; Yin et al. 1997), and five QTLs, *Hd1, 2, 3, 6* and *9* were mapped precisely on the genetic linkage groups of chr. 3 and 6 as a single Mendelian factors (Yano et al. 1997; Yamamoto et al. 2000; Lin et al. 2006; Yin et al. 1997). The adaptation of rice cultivars to the northern latitudes/cooler climates (for example wild rice, *Oryzae rufipogon,* is limited to 31°N, while the cultivated rice, *Oryzae sativa*, is adapted to until 45°N, Izawa 2007) is believed to be due to the balance of *Hd1* repression and *Ehd1* promotion (Izawa 2007; Doi et al. 2004; Ebitani et al. 2005; Takeuchi et al. 2006). The absence of these two alleles may probably increase yields in the tropics because plants may have extended vegetative development in warm climates regardless of the natural photoperiod (Doi et al. 2004; Izawa 2007). Recently, a nucleotide polymorphism in DTH2 (days to heading; Wu et al. 2013) and natural variation in OsPRR37 (Koo et al. 2013) were shown to influence rice cultivation at a wide range of latitudes. Although *Hd1* and *2* alleles on chr. 6

and 7, respectively, of rice are proposed to be associated with earliness (Nakagawa et al. 2005), since earliness per se loci are absent (Faricelli et al. 2009) further, translation of understanding of adaptive mechanisms in wheat could help extend rice cultivation to cooler environments. Additionally, circadian-associated genes should be explored for their effects on developmental phases in both crops.

Despite the progress of molecular understanding of flowering time, it has been of limited use in crop improvement. A wheat MADS (MCM1, AGAMOUS, DEFICIENS, SRF) box gene responsible for the transition from vegetative to reproductive phases in wheat was identified as wheat *AP1* (*Apetala1*) gene, *WAP1* (formerly *TaMADS11*, Murai et al. 2002). Several lines of evidences strongly support that *WAP1* acts as an activator in the vernalization pathway in wheat. First, *WAP1* transcripts are expressed at double-ridge stage, the stage at which growth phase changes from vegetative to reproductive growth, and also coincide with the expression of *TaVRT-1* (Danyluk et al. 2003). Second, *WAP1* is an ortholog of *VRN1* (only 5 amino acids changes), and the three homoeologous genes of *WAP1* correspond to three homoeologous genes of *VRN* genes (Yan et al. 2003). Third, *WAP1* transcripts are up-regulated by cold (Murai et al. 2003). Fourth, *WAP1* is up-regulated by long photoperiods and acts on different pathways as compared to *Ppd* genes in promoting the floral transition (Murai et al. 2003). Finally, *WAP1* acts at the downstream of *WFT* (wheat *FT*, Ogihara et al. 2003). Since *AP1* is involved in the short-day regulation of flowering time (Ruttink et al. 2007), it is reasonable to propose that *WAP1* might be involved in the short-day regulation of flowering network in wheat; yet definitive studies are lacking. As *WAP1* shares high sequence similarity with *TaVRT-1* of wheat (differs for three amino acids, Danyluk et al. 2003), *VRN1* of *T. monococcum* (Yan et al. 2003), *BM5* of barley (Schmitz et al. 2000) and *RAP1B* of rice (Kyozuka et al. 2000), this gene might be conserved among species playing key roles in plant adaptation to environments.

The *Q* gene has been validated as an *AP2*-like gene (*Apetala2*), *WAP2* in wheat (Simons et al. 2006; Ning et al. 2009). An *AP2*-like gene was identified from barley (*HvAP2*), which is homoeologous to Q gene of wheat, and shown to regulate spike morphology in barley and wheat (Gil-Humanes et al. 2009; Nair et al. 2010). Wheat harbours nine *AP2*-like genes (*AP2-1* to *2-9*; Zhuang et al. 2010); however, their exact functional roles are largely unknown although they can be suspected to play roles in phenological phase transitions associated with vernalization (Mutasa-Gottgens et al. 2012) and in the parental control of grain development (Ohto et al. 2005). Recently, a gene *OsAP2-39* was shown to control key interactions between abscisic acid and gibberellin in rice (Yaish et al. 2010), suggesting that *AP2*-like genes, in general, appear to have multifunctional roles in plants.

In rice, several regulatory genes for the photoperiodic control of flowering time were reported: *heading date1* (*Hd1*, Hayama et al. 2003; Takahashi et al. 2009), *heading date3a* (*Hd3a*, Ishikawa et al. 2005), rice ortholog of *Gigantia* (*OsGI*, Hayama et al. 2003), *Early heading date1* (*Ehd1*), Spotted leaf11-interacting protein1 (*SPIN1*), *rice flowering locus T1* (*RFT1*), Early flowering 7 (*Ef7*) and Photoperiod sensitivity5 (*SE5*) (Vega-Sánchez et al. 2008; Andrés et al. 2009; Komiya et al. 2009; Takahashi et al. 2009; Saito et al. 2012). The variations in Hd1 proteins, Hd3a promoters and Ehd1 expression level have been shown to contribute to the flowering time diversity in cultivated rice (Takahashi et al. 2009). However, the genetic and molecular regulation of different phenological phases is largely unknown. Mutations in, polymorphisms of, these genes might be linked to phenological phase modifications as was shown for barley in which mutations in early maturity 8 (*EAM8*) adapt domesticated barley to short growing seasons (Faure et al. 2012).

## Photosynthesis and associated traits

Photosynthesis ultimately limits crop productivity and hence constitutes a highly desirable trait to modify genetically (Evans 2013). Both rice and wheat show the highest rates of photosynthesis per unit of leaf N as compared to the other C3 cereals due to greater N allocation to Rubisco (Makino et al. 1992), and higher mesophyll conductance (Caemmerer and Evans 1991). Being an allopolyploidy species, wheat has undergone many genomic modifications (Saintenac et al. 2011a, b) and at a physiological level, an allopolyploid genome is often associated with high plant vigor and increased fertility (Akhunova et al. 2010). Recently, an affymetrix wheat genome array revealed evidence of homoeolog-specific coordinated up- and down-regulation of several gene categories, including those involved in photosynthesis processes, suggesting the coevolution of *cis*- and *trans*-regulators, which may lead to divergence and incompatibility of regulatory networks in allopolyploid species (Akhunova et al. 2010). The up-regulation of photosynthetic pathways only in A and B subgenomes of wheat provides good targets for studying the molecular basis of photosynthesis. On the other hand, the small genome of rice has permitted genetic and molecular exploration of several processes influencing crop photosynthesis including the control of tillering (*moc1*, Li et al. 2003), leaf development (*RTFL* gene, Tsukaya 2005), leaf architecture and erectness (*OsDWARF4* gene, Sakamoto et al.

2006), and rolled or V-shaped leaf (*OsAGO7* gene, Shi et al. 2007). Although the current understanding of plant architecture is still incomplete, a significant molecular basis has been accumulated mainly through the characterization of rice mutants.

Rice and wheat differ for photosynthetic capacity as they exhibit different trait expressions associated with photosynthesis. Two large consortiums involving multidisciplinary approaches such as C4 rice (C4R; Sheehy et al. 2007) and wheat yield consortium (WYC; Reynolds et al. 2010) were initiated to improve the photosynthetic capacity and efficiency in rice and wheat, respectively. Both consortiums partly differ in their working objectives: C4R mainly focuses on phenotype and mutant screens to explore natural diversity and to establish a known pool of genes that confer 'C4-ness'. Genomic approaches are designed to compare the gene expression between (1) C3 and C4 leaves, (2) mesophyll and bundle sheath cells, (3) developmentally distinct regions of a leaf and (4) different growth stages within a leaf. Using molecular engineering approaches, these genes are transformed into cultivated rice for C4 traits such as leaf anatomy, core C4 genes (PEPC, PPDK, NADP-ME and MDH) and regulatory elements (e.g. transporters) associated with C4 metabolic dynamics (Rizal et al. 2012; Covshoff and Hibberd 2012). In WYC, the phenotypic selection for photosynthetic capacity and efficiency of leaf and spike together with optimizing canopy photosynthesis and its duration are considered. At the molecular level, introducing $CO_2$ concentrating pumps, increasing RuBP regeneration capacity, improving thermal stability of Rubisco activase and modifying Rubisco protein structure (large subunits) are under progress (Parry et al. 2011).

### *Leaf traits, light interception and conversion efficiency*

Light interception and conversion efficiency are determined by the speed of canopy development and closure, leaf absorbance, canopy longevity, size, architecture and antenna size (Zhu et al. 2010). Leaf anatomy plays a major role in the light use efficiency and thus in the genetic diversity for maximum net $CO_2$ exchange rate ($A_{max}$). For example, a large genetic diversity for $A_{max}$ was reported for *T. urartu* (about 35 % higher $A_{max}$, Austin 1982) and emmer wheat (Carver et al. 1989). The potential of manipulating leaf anatomy to gain increased photosynthetic properties in both crops has been neglected partly due to the genes controlling $C_4$ leaf anatomy, largely unknown (Tholen et al. 2012). Therefore, exploring the variation for better leaf anatomy, higher vein density and lower number of mesophyll cells through phenotypic and mutant screens would, therefore, be crucial (Smillie et al. 2012). A higher interveinal distance between minor and major veins was recently highlighted to improve light absorption using rice deletion mutant population (Smillie et al. 2012) suggesting that modifying interveinal spaces would improve light absorption. Alternatively, lowering chlorophyll content of photosynthetic tissue has been proposed as a potentially robust strategy to improve light conversion efficiency (Zhu et al. 2010; Ort et al. 2011). A rice mutant with a low content of chl *b* and a high chl *a*/*b* ratio of 4.7 (Chen et al. 2007) was reported to have improved canopy light penetration. This is also beneficial for altering canopy temperature, maintaining cooler canopies (Ort et al. 2011), and therefore down-regulation of chlorophyll synthesis early in the pathway might improve light conversion efficiency (Zhu et al. 2010).

Light use efficiency by the photosynthetic apparatus is a conserved trait among plants (Skillman et al. 2011); thus, identifying QTLs/genes controlling plant architecture would be an important step in improving photosynthesis. Several loci for flag-leaf characteristics were mapped on several chromosomes in both crops. In wheat, chr. 1, 2, 5 and 6 (Table 2, Wang 2009; Coleman et al. 2001; ter Steege et al. 2005) while in rice, chr. 2, 4 and 6 have been shown to control flag-leaf characteristics such as length, width, angle, size and the ratio of length to width (Dong et al. 2004; Yue et al. 2006; Fan et al. 2007; Zeng et al. 2009; Farooq et al. 2010; Chen et al. 2011; Hu et al. 2012). Many of these QTLs were co-localized with QTLs for leaf elongation rate and days to flag-leaf emergence in both crops (ter Steege et al. 2005; Dong et al. 2004). As chr. 2 and 6 were commonly reported in both crops, they might be important regions for improving flag-leaf characteristics in both crops. These QTLs would be useful for improving flag-leaf characteristics, leaf development and thus the selection of fast growing genotypes before heading. However, due to multiple loci controlling leaf traits, the genetic architecture of leaf traits would be small with little epistasis, environmental interaction or pleiotropy as was reported for maize (Tian et al. 2011).

A gene, *chlorina-1* encoding chlorophyll *D* (ChlD) subunit of Mg-chelatase identified (on chr. 3) in rice (Zhang et al. 2006) would represent a key initiative for increasing light use and conversion efficiency in both crops as ChlD has a high light-absorption spectrum of 700–750 nm (Chen and Blankenship 2011). Moreover, identifying tissue-specific gene regulation would be important, for example a gene, *OsPNH1*, was shown to play significant role only in leaf, but not in stem and root, vascular development in rice (Nishimura et al. 2002). In rice, genes, *narrow leaf 2 & 3* controlling leaf width (Ishiwata et al. 2013); *OsBAK1* controlling leaf erectness (Li et al. 2009) and *Roc5* controlling leaf rolling (Zou et al. 2011) while in wheat, Pa2 and His2 (leaf sheath hairiness, Wu-yun et al. 1999) and Hl1&2 (leaf pubescence, Dobrovolskaya et al. 2007), have been reported. These genes are yet to be explored for the effects on leaf architecture and their utility in crop improvement.

### *Leaf and canopy photosynthesis*

C3 species show considerable variation in their maximum $CO_2$ fixation capacity (Flood et al. 2011), varying from 29 $\mu$mol $m^{-2}$ $s^{-1}$ in wheat to as low as 6 $\mu$mol $m^{-2}$ $s^{-1}$ in *Picea* (Wullschleger 1993) due to differences in carboxylation capacity (6–194 $\mu$mol $m^{-2}$ $s^{-1}$) and electron transport rate (17–372 $\mu$mol $m^{-2}$ $s^{-1}$) (Lawson et al. 2012). High photosynthetic capacity per unit leaf area needs lower mesophyll resistance and mesophyll thickness as mesophyll cell walls could account for >50 % of the total resistance (Evans et al. 2009). However, altering mesophyll cell wall thickness alone to increase mesophyll conductance is not sufficient due to smaller chloroplast surface area in wheat (76 % of the cell periphery is covered by chloroplasts, Sage and Sage 2009), and chloroplasts are pressed against the cell periphery by large vacuoles. Therefore, the surface area of chloroplast exposed to intercellular airspace per unit leaf area needs to be increased, in addition to reducing mesophyll cell wall thickness to increase the photosynthetic capacity in wheat (Evans et al. 2009; Giuliani et al. 2013). In contrast, rice has chloroplasts that dominate the overall volume of the cytoplasm of mature chlorenchyma cells covering >95 % of the cell (von caemmerer and Evans 1991; Sage and Sage 2009). The dense and chloroplast-rich cytosol offset the lower mesophyll thickness, and thus rice has a photosynthetic capacity that is nearly 80 % of the wheat (Sage and Sage 2009). Recently, mesophyll cell expansion was shown to be closely associated with vein density changes in rice mutants (Smillie et al. 2012) emphasizing the importance of genes associated with vein density changes in exploiting leaf anatomy variation in both species, wheat and rice.

Increasing photosynthesis during grain-filling period is necessary, and several QTLs (chr. 1, 4, 5 and 7) were mapped for several photosynthetic traits during grain-filling period in wheat (Quarrie et al. 2006; Yang et al. 2007; Zhang et al. 2009; Yan et al. 2010a, b). Interestingly, the QTL on chromosome 5B was mapped for intercellular $CO_2$ concentration ($C_i$), which explained a large phenotypic variation for $C_i$ in wheat seedlings (Yan et al. 2010a, b). Consistently, QTLs on chr. 5 were represented in all these studies suggesting that chr. 5 could be an important in explaining the variation in chlorophyll content and $C_i$. In rice, several QTLs were identified (chr. 1, 3, 4 and 8) and, however, only one positive allele was observed on chr. 4, which were the net effects during the period from tillering to heading (Jiang et al. 2012), and this has been consistently showed to influence several photosynthetic traits such as net photosynthesis, stomatal conductance, transpiration efficiency, quantum yield of PSII and chlorophyll fluorescence parameters (Adachi et al. 2011). QTLs on chr. 4 have pleiotropic effects on leaf nitrogen content and hydraulic conductance by increasing the root surface area and hydraulic conductivity (Adachi et al. 2011). These QTLs/genes need to be explored to improve not only photosynthetic traits but also for their pleiotropic effects on other traits related to yield potential.

Molecular engineering approaches to transfer photosynthesis-associated genes in cereals have been achieved; however, manipulating cell biochemistry has yielded partial results in transgenic rice (Taniguchi et al. 2008). Limited number of genes such as genes encoding for photosystem II subunits (PsbS; Hubbart 2012), sedoheptulose-1,7-bisphosphate (SBPase) and fructose-1,6-bisphosphate (FBPase) have shown to increase net photosynthesis (6–12 %, Tamoi et al. 2006; Feng et al. 2007, 2009), suggesting that improving photosynthesis might be limited to specific set of biochemical changes. This might be partly due to the fact that many of the genes encoding the core photosynthesis processes are known to be highly conserved and therefore subject to limited levels of variation (Shi et al. 2005). Nevertheless, many essential photosynthesis genes in chloroplasts exhibit natural variation (El-Lithy et al. 2005), and a whole chloroplast genome comparison of rice and wheat revealed that rice chloroplast genes tend to have evolved more slowly than wheat at loci where rate heterogeneity exists (Matsuoka et al. 2002). Only one photosynthetic gene, *psbC*, has shown fourfold heterogeneity for nucleotide substitution rate between rice and wheat (Matsuoka et al. 2002). Plastid-encoded *psbC* gene encodes CP43 subunit, a chlorophyll-binding antenna protein of photosystem II, and forms an operon together with other photosynthetic-related genes in higher plants. These genes might be interesting targets for plant breeding because they might exhibit genetic variation among crop species reflecting local climatic adaptation, as was reported for proline biosynthesis enzyme, *Pyrroline-5-carboxylate synthetase1* (*P5CS1*, Kesari et al. 2012). Exploring natural variation in photosynthesis through phenotyping would narrow down the key photosynthetic genes or traits. For example, a comparative transcriptional profiling has established the ‘awn’ as the major photosynthetic organ of barley spike during the grain-filling period (Abebe et al. 2009).

### *Rubisco and its regulation*

C3 species overexpress Rubisco due to its low catalytic efficiency and altering Rubisco kinetic properties has been proposed to increase photosynthesis (Parry et al. 2012). Mutations in Rubisco protein at several amino acid sites, 101, 258, 270, 281 and 309, have resulted in different catalytic properties in C4 lineages (Christin et al. 2008) and have been proposed for genetic engineering of Rubisco. Consistently, isoleucine 309 was identified as a catalytic switch for faster carboxylation rates in C4 species (Flaveria). Whether such catalytic sites would increase carboxylation rates in C3 species such as wheat and rice are yet to be examined (Whitney et al. 2011). Identifying such catalytic switches in both crops would be a key step to increase Rubisco capacity. Overall, these studies suggest that Rubisco nucleotide diversity and its polymorphism (Kapralov et al. 2012) could be a potential source for manipulating Rubisco dynamics in both crops. In rice, altering the $CO_2$ and $O_2$ specificity of Rubisco has been attempted by transforming Rubisco small subunits (*RbcS*, Suzuki et al. 2009; Ishikawa et al. 2011), which increased Rubisco content by 30 % and *RbcS* levels 1.5–2.0-fold on a leaf area basis (Suzuki et al. 2007, 2009; Ishikawa et al. 2011). Nevertheless, photosynthesis was not enhanced due to lower electron transport, which is insufficient to support the increased Rubisco capacity. At high light conditions, the maximum electron transport rate correlates with cytochrome $b_6/f$ and ATPase contents, suggesting that greater amounts of these two would be linked to higher electron transport rate (Yamori et al. 2011). Alternatively, introducing a parallel electron carrier between cytochrome *f* and PSI, as was shown in Arabidopsis (Peterhansel et al. 2008) and a selection for *p*FNRII proteins (*p*FNRII bind strongly with ferredoxin due to the mutations to double lysine residue of N-terminal region of *p*FNRII proteins as was shown in wheat, Bowsher et al. 2012) may increase electron transport rate.

At the genetic level, despite the identification of QTLs regulating chlorophyll content, the QTLs regulating Rubisco content have not yet been identified in wheat but were identified in barley on chr. 4. This QTL also colocalizes with the QTLs for Rubisco activase gene (Becker and Heun 1995), stomatal conductance and chlorophyll content in barley (Forster et al. 2000), indicating the importance of this QTL for improving photosynthetic traits (This et al. 2000; Poorter et al. 2005). In contrast, in rice, QTLs controlling Rubisco content were mapped on chr. 8, 9 and 10 (Ishimaru et al. 2001b; Kanbe et al. 2009). None of these QTLs were co-localized with the QTLs for total leaf N content, suggesting that different genetics would control both Rubisco contents and total leaf N (Ishimaru et al. 2001b). Consistently, QTLs controlling the ratio of Rubisco to total leaf N were detected on chr. 1, 5 and 12 (Ishimaru et al. 2001b), suggesting that genetic regulation of Rubisco content may vary with the development stage of the considered plant (Ishimaru et al. 2001a; Kanbe et al. 2009). No clear varietal differences in Rubisco content at any identical leaf nitrogen content were observed in rice (Hirasawa et al. 2010), indicating that the genetic regulation of other traits (e.g. stomatal conductance) should be considered for improving photosynthetic rate.

At the molecular level, small (*rbcS*) and large (*rbcL*) subunits of Rubisco could be candidate targets for increasing Rubisco levels in the plants. However, *rbcL* is largely conserved among plant species and is up-regulated by nuclear-localized *rbcS* (Suzuki and Makino 2013). Since the *rbcS* expression declines faster than *rbcL* expression with age (Suzuki and Makino 2013), the genetic variation in *rbcS* may be closely associated with the variation in Rubisco contents and thus photosynthetic rates. However, an overexpression of *rbcS* gene did not increase photosynthetic rate in transgenic rice due to lower N investment in other components (Suzuki et al. 2007). Since rice has higher contents and lower specific activity of Rubisco as compared to other plants (e.g. wheat), introduction of a more efficient Rubisco may be a strategy to improve photosynthesis and N-use efficiency in rice. In contrast, wheat has higher specific activity of Rubisco (Makino 2011); whether an overproduction of *rbcS* (higher Rubisco contents) could improve photosynthetic rate in wheat remains to be tested.

### *Leaf senescence*

The remobilization of carbon (C) and N compounds to grains during the grain-filling phase is largely governed by leaf senescence, and several QTLs have been identified in wheat (Bogard et al. 2011; Li et al. 2012a). A genomic region of *T. turgidum* spp. *dicoccoides* carrying the high grain protein content (GPC) gene was mapped as a QTL on chr. 6BS (Joppa et al. 1997), which increased GPC in both tetraploid and hexaploid wheat (Olmos et al. 2003). Later, this allele has been shown to encode a NAC transcription factor, *NAM-B1* (Uauy et al. 2006; Distelfeld et al. 2006, 2007; Bogard et al. 2011; Carter et al. 2012). The allele is functional in ancestral wild wheat, whereas modern wheat (both tetraploid and hexaploid) carries a non-functional *NAM-B1* allele (because the allele has a 1-bp frameshift mutation in the 5′ end; Gregersen et al. 2008). It is, thus, conceivable that early domestication of wheat involved a selection for delayed senescence originating from a non-functional *Gpc-B1* gene, possibly due to the selection for higher yield cultivars (Gregersen et al. 2008).

In rice, both *indica* and *japonica* exhibit different leaf senescence patterns being early for the former and the latter exhibiting late senescence (Yoshida 1981; Abdelkhalik et al. 2005). Several QTLs were mapped, and QTLs on chr. 6 and 9 were consistently reported in all these studies (Cha et al. 2002; Toojinda et al. 2003; Abdelkhalik et al. 2005; Lin et al. 2010; Fu et al. 2011). They also show high synteny (see first section) with stay-green QTLs in sorghum (Xu et al. 2000). Such positional correspondence may imply the conserved organization of the genes in the genome and also the functions of the genes underlying the stay-green traits that need to be explored. In addition, several genes have been reported to be associated with the senescence in rice such as senescence-associated genes (SAGs, Lee et al. 2001; Liu et al. 2008, 2010). Rice plants overexpressing these genes showed an altered source/sink relation, with nitrogen content decreasing more slowly, and sugars were removed more rapidly than the wild-type plants. A submergence tolerance gene, SUB1A, was shown to delay dark-induced flag-leaf senescence through hormonal regulation (limits ethylene production) in rice (Fukao et al. 2012). Such genes could be interesting as they exhibit dual functions, altering ethylene production, which is a major hormone associated with the apical dominance constraints in rice spikelets (Mohapatra et al. 2011) and spikelet fertility in wheat (Hays et al. 2007). In this regard, identifying genes not only in leaves but also in awns and spike green structures could be interesting to delay spike senescence and to improve assimilate filling in the grains.

## Assimilate partitioning and lodging resistance

### *Assimilate partitioning and yield traits*

Dynamic processes such as the rate and duration of grain filling determine the individual grain size and grain weight. Several QTLs were identified in bread wheat (Wang et al. 2008b; Salem et al. 2007), and most grain yield QTLs were derived from the domesticated allele (LDN) from a strong selection for grain yield per se (Ladizinsky 1998; Li et al. 2002; Kumar et al. 2006; Kuchel et al. 2007; Cuthbert et al. 2008; Maccaferri et al. 2008; Ali et al. 2011; Peleg et al. 2011). While the loci located on chr. 1–5 are overrepresented, QTLs on the chr. 3 were constantly reported indicating that these QTLs might be associated with the rate of grain filling in wheat (Table 1, Wang et al. 2008b). In rice, several QTLs for grain yield were mapped explaining 10–20 % variation (Ishimaru et al. 2001a; Zhang et al. 2004; Xing and Zhang 2010). Many of these QTLs were colocated with QTLs for biomass (chr. 1 and 3) and harvest index (chr. 1) suggesting that grain yield increase could be genetically explained by the improvement of either biomass or harvest index (Zhang et al. 2004). Interestingly, QTLs for biomass and harvest index did not overlap; suggesting a genotype with higher biomass and harvest index could be achievable by the combination of the positive alleles of both traits (Zhang et al. 2004; Xing and Zhang 2010).

The higher harvest index could be achievable by increasing assimilate partitioning to grains. Harvest index is negatively correlated with plant height, heading date, panicle length and width while positively correlated with seed set, grain/panicle weight (Sabouri et al. 2009; Li et al. 2012b). In wheat, QTLs for stem-reserve mobilization were mapped on different chr. 2D, 5D and 7D (Salem et al. 2007; Kajimura et al. 2011) while in rice, QTLs on chr. 4 (GIF1, Wang et al. 2008a) and chr. 5 (rg5) were mapped (Ishimaru et al. 2005a). The near-isogenic rice line carrying *rg5* showed high sink activity and increased assimilate partitioning to particularly inferior caryopses in the late stage, and improved the total ratio of filled grains (Ishimaru et al. 2005b). A strong correlation between the number of stem vascular bundles and yield traits was reported in rice (Peterson et al. 1982; Cui et al. 2003), suggesting that a high number of large vascular bundles per spikelet may contribute to the rapid accumulation of assimilates in grains (Xing and Zhang 2010). Exploring the genetic variation for vascular tissues and its capacity to accommodate more carbohydrates and other nutrients would be interesting.

Many of the QTLs detected for grain yield were co-localized with QTLs for yield-associated traits in both crops. Until now, none of the major QTLs for grain number representing grains per spike and per square metre were cloned in Triticeae (McIntyre et al. 2010; Sreenivasulu and Schnurbusch, 2012). Recent studies revealed that grain size and shape are largely independent traits, controlled by different QTLs located on different chromosomes in wheat (Gegas et al. 2010). Further, the proximity of grain size QTLs to *Rht-B1* and *Rht-D1* indicates pleiotropic effects of dwarfing loci on grain architecture parameters. However, modern hexaploid wheat has significantly reduced grain shape variation compared to ancestral wheat species while retained a relatively large percentage of the nucleotide diversity of A and B genomes of tetraploid ancestors (Gegas et al. 2010). Thus, grain size/weight appears to exhibit less variation and improving grain weight, for example overexpression of GIF1 gene in the ovular vascular tissues might improve grain weight (Xing and Zhang 2010). Grain width and weight were shown to be regulated by genes such as *GW2* (Song et al. 2007), *GW5* (Weng et al. 2008), *qSW5* (Shomura et al. 2008) in rice and *TaGW2* in wheat (Bednarek et al. 2012), while an increased rice grain length is controlled by qSS7 (Qiu et al. 2012; Bai et al. 2010). These genes are not yet widely used in crop improvement programmes. A gene (*GS3*) regulating grain length and weight was cloned, and it was mapped on chr. 3 and 6 (Fan et al. 2006; Yu et al. 1997; Tan et al. 2000; Xing et al. 2002; Thomson et al. 2003; Aluko et al. 2004; Li et al. 2004; Xing and Zhang 2010). The increase in grain size was largely due to longitudinal increase in cell number and has been detected in a diverse range of rice germplasm in the cultivated rice species, *O. sativa* (Fan et al. 2008; Takano-Kai et al. 2009; Xing and Zhang 2010), highlighting the importance of cell size variation, particularly aleurone organization, to increase grain weight in both crops.

### *Metabolic and enzymatic regulation of grain development*

Metabolic processes associated with sucrose and starch synthesis in the endosperm would influence grain development. The lower activity of carbon metabolic enzymes in the endosperm occurs due to their interaction with inhibitory proteins, thermo-sensitivity and structural limitations. Enzymes such as sucrose phosphate synthase (SPS) and starch synthase III (SSIII) exhibit low activity due to the presence of certain phosphorylation sites, which interact with inhibitory proteins, 14-3-3 (Castleden et al. 2004; Song et al. 2009). This suggests that eliminating SPS and SSIII interaction with 14-3-3 proteins would increase their activity and grain carbon accumulation. Alternatively, lowering the activity of 14-3-3 proteins (e.g. the removal of ε subunit of 14-3-3 proteins resulted in decreased activity of these proteins) could reduce their interaction with carbon metabolic enzymes, which may increase leaf starch accumulation (2- to 4-fold increase in Arabidopsis, Sehnke et al. 2001a).

Many of the carbon metabolic enzymes are temperature sensitive in both crops (Farooq et al. 2011), and this has been shown to be controlled by a single-nucleotide polymorphism in rice (granule-bound starch synthase, GBSS, Larkin and Park 1999); thus, it could be a target for genetic improvement. Structural modifications to AGPase (Meyer et al. 2007) or mutagenesis of cysteine 81 with serine in APS1 subunit of AGPase (Hädrich et al. 2012) showed yield advantage in wheat and improved leaf starch accumulation in Arabidopsis, respectively. Further, a rice mutant lacking a large subunit of AGPase has drastically reduced starch content in the culm but increased starch in leaves and showed normal plant productivity, revealing plasticity in the photosynthates distribution among different temporary carbohydrate storage pools within the plant (Cook et al. 2012). These studies suggest that AGPase activity could be increased by improving its structural arrangement (Meyer et al. 2007; Cook et al. 2012) and its substrate availability (trehalose 6-phosphate, Martínez et al. 2011) during grain-filling period.

Sucrose accumulation in the endosperm shows spatial variation in order to maintain metabolic homeostasis and energy (ATP) balance (Rolletschek et al. 2011). Several other genes associated with maternal tissues influence sucrose and nutrient transfer to endosperm cells. For example, *maternally expressed gene1* (*Meg1*) in maize was shown to control the establishment and differentiation of endosperm nutrient transfer cells and promote nutrient allocation to the seed offspring (Costa et al. 2012). While it is unknown if there is any maternal tissue regulation of sucrose import into the wheat endosperm (e.g. endosperm-mediated *AP2* gene, whose influence was described as being of maternal origin; Ohto et al. 2005), it is conceivable that optimal spatial metabolic variation of endosperm contributes to high carbon conversion efficiency, as was shown for maize starchy endosperm (Alonso et al. 2011). However, the possibilities of metabolites such as sucrose and starch being as markers to increase grain yields are largely unexplored (see section on metabolomics-assisted plant breeding).

### *Hormonal regulation of grain development*

In addition to their remarkable roles in growth and development, hormonal concentration and their balance play major roles in grain development (Brenner and Cheikh 1995). Hormones exert several effects on grain development during grain filling. Cytokinin (CK) oxidases genes (TaCKX2.1 and 2.2) were shown to be linked to grain yield in both crops (Ashikari et al. 2005; Zhang et al. 2010b). Reduced expressions of *HvCKX1* and *OsCKX2* resulted in higher grain yield in barley (Zalewski et al. 2010) and rice (Ashikari et al. 2005). High CK levels increased seed yield (~55 %) without increasing the $CO_2$-fixing source in Arabidopsis (Bartrina et al. 2011). In contrast, a significant positive correlation between the expression of *TaCKX2* genes and grain number was observed in wheat (Zhang et al. 2010b). This differential regulation of CKX genes on yield components in both crops is unclear. Auxins (IAA) and abscisic acid (ABA) are key regulators of grain sink activity (Asli and Houshmandfar 2011; Pudelski et al. 2012), and a higher CK and IAA levels and lower ABA levels (higher CK/IAA and ABA ratio) are beneficial at early grain-filling period to increase the sink activity in order to attract more assimilates.

Higher ethylene levels were shown to reduce grain weight (Beltrano et al. 1994; Yang et al. 2006a) through accelerating kernel abortion (via PCD and DNA fragmentation) in wheat (Young and Gallie 1999; Hays et al. 2007). Ethylene metabolism operates in endosperm transfer cells, where PCD initiates and progress stochastically in wheat endosperm; whereas it initiates within the upper central endosperm and expands outwards in maize (Young and Gallie 1999), indicating the complex nature of regulation of ethylene. Despite these acknowledged studies, the precise regulation of several of these hormonal effects on grain development and fertility is largely unknown.

The optimal balance of spatial and temporal generation of hormones is important for proper grain filling. Certain hormones such as GAs and kinetin improve growth and development more on the basal branches than on the apical branches, in contrast to IAA, which accelerates growth of the spikelets on the apical branches only (Mohapatra et al. 2011). Such spatial production of hormones affects the assimilate partitioning to the spikelets resulting inferior and superior spikelets. For example, the slow rate of grain filling of the inferior grains was attributed to the low contents of zeatin, zeatin riboside, IAA and ABA and the higher levels of ethylene (Zhao et al. 2007). Higher concentrations of ethylene were more detrimental to the spikelets in the lower part of the panicle, as they stay longer in the boot of the flag-leaf sheath. Moreover, the compact arrangement of spikelets in the panicle axis increase ethylene production (Panda et al. 2009), and high levels of ABA was proposed to antagonise the negative effects of ethylene on spikelets (Yang et al. 2006b). Polyamines (spermidine and spermine) show negative interaction with ethylene, and a high ratio of polyamine and ethylene improves grain filling of spikelets (Wang et al. 2011). Hormones are known to affect the activities of carbohydrate metabolic enzymes and cell-cycle genes. Higher levels of ethylene were shown to repress the activities of SUS, INV and starch synthesis enzymes such as AGPase and soluble starch synthase (Naik and Mohapatra 2000; Zhu et al. 2011), and high levels of ABA reduce SUS activity (Tang et al. 2009; Zhu et al. 2011); while high concentrations of cytokinins could enhance the activities of cell-cycle genes (Morris et al. 1993). Cytokinins could improve assimilate unloading from the phloem in the developing seeds. Overall, these studies suggest that plant hormones are well connected to grain yield physiology, and an appropriate levels of these hormones through either phenotypic selection or biotechnological interventions would be necessary to improve grain yields in the future given clear evidence for sink limitation even in the modern cultivars that are presumably associated with conservative hormone-mediated responses to the environment (Reynolds et al. 2009).

### *Molecular regulation of grain development*

Grain development is associated with massive changes in gene expression, proteomics and transcriptomics (Wan et al. 2008b; Meziani et al. 2012; Pont et al. 2011), which largely coincide with specific developmental phases in order to improve carbon accumulation and its conversion efficiency (Vensel et al. 2005; Nadaud et al. 2010). Proteomic maps of wheat grain development have revealed that all genomes (A, B and D) carry different proportions of proteins during grain development (Kim et al. 2010a, b), suggesting that altering the portion of any of the genomes would alter certain seed-specific proteins during the grain development. For example, the removal of D genome from hexaploid constitution substantially affected the expression of nonstorage proteins (Islam et al. 2003).

Modifying the expression of cell division and expansion genes may alter grain filling (Laudencia-Chingcuanco et al. 2007). Extending the activation of cell division genes would allow both cell division and expansion processes simultaneously, which might produce more, but also larger cells, which could increase the sink activity. Recently, an overexpression of a cell-cycle gene, CYCD7; 1, promoted overgrowth of both embryo and endosperm through increased cell division and enlargement (Collins et al. 2012), and an overexpression of TRANSPARENT TESTA GLABRA 2 (*TTG2*, Ohto et al. 2009) increased cell expansion and thus seed growth in Arabidopsis. In wheat, the activity of CDK genes is linked to *Ph1* locus as *Ph1* locus suppresses cdk2-type activity in hexaploid wheat (Griffiths et al. 2006), suggesting that cell division during grain development is tightly linked to the genetic factors (*Ph1*) associated with the polyploidization.

In rice, three cell wall invertase genes, *OsCIN1-3*, play complementary roles in assimilate unloading (Wang et al. 2008a); while *INV3*, *Sus3* (SuSase) and *AGPL-1 and 2* (AGPase) expressions were higher in superior spikelets (Ishimaru et al. 2005b). Recently, an overexpression of a gene, *GIF1* (grain incomplete filling1), has been shown to improve carbon deposition during early grain filling and increase grain weight (Wang et al. 2008a). Indeed, the natural variation for grain size was linked to a gene, *GS3* (grain size 3; Mao et al. 2010). A gene, *indica Gn1*, differentiates grains on secondary and tertiary rachis in indica rice, which increased grain number by 40 % in japonica rice (Yoshida et al. 2006). Several transcription factors such as *Carbon Starved Anther* (*CSA;* Zhang et al. 2010a), *Rice Starch Regulator1* (*RSR1*; Fu and Xue 2010) and seed storage proteins (AACA, Zhu et al. 2003) were shown to be linked to nutrient and carbon partitioning during zing; however, they have not so far been explored. These studies suggest that these genes could be useful to increase assimilate partitioning and grain architecture in both crops.

### *Lodging resistance*

Lodging resistance is an important factor to reduce yield loss under field conditions and is associated with stem strength and crown root spread depending on conditions (Foulkes et al. 2011). Previous studies suggest that the second internode play an important role in wheat lodging resistance (Zuber et al. 2001). Several QTLs for lodging resistance have been mapped on several chromosomes (Keller et al. 1999; Hai et al. 2005; Marza et al. 2005; McCartney et al. 2005; Huang et al. 2006; Verma et al. 2008; Ma 2009). QTL mapped on 5A was consistently reported in all these studies suggesting that this QTL might be more closely linked to lodging resistance (Keller et al. 1999; Marza et al. 2005; McCartney et al. 2005; Huang et al. 2006; Verma et al. 2008; Ma 2009). A gene on chromosome 3B was mapped, which was shown to be one of the locations of a stem solidness gene (Lanning et al. 2006) and for stem strength and diameter (Hai et al. 2005), suggesting that different genetics may control lodging resistance traits. Recently a gene, STRONG CULM2 (*SCM2*) was identified, and a near-isogenic line carrying *SCM2* showed enhanced culm strength in rice (Ookawa et al. 2010). This gene has a pleiotropic effect on yield components and increased spikelet number. This indicates that many of the genes controlling plant traits have pleiotropic effects on other traits, and such genes should be identified and explored in crop improvement programmes.

In rice, plant height has been the main target for improving lodging resistance, and several genes were identified such as *Heterotrimeric G protein* (*RGA1*, Ashikari et al. 1999; Fujisawa et al. 1999), *OSH15* (Sato et al. 1999) and *sd-1* (Monna et al. 2002; Sasaki et al. 2002; Spielmeyer et al. 2002). Since most dwarfing genes inherit in an autosomal recessive pattern as recessive alleles (Mackill and Rutger 1979) and exhibit pleiotropic effects on other traits (*OSH15* reduce panicle length; Sato et al. 1999), these cannot be used yet in practical agriculture or breeding (Kashiwagi and Ishimaru 2004). A QTL (*prl5*) on chr. 5 (Kashiwagi and Ishimaru 2004; Kashiwagi et al. 2010), a QTL for culm strength (*STRONG CULM2*) on chr. 6 (Ookawa et al. 2010) and several QTLs for stem diameter (*sdm*) on chr. 1, 7, 8 and 12 (Kashiwagi et al. 2008) were mapped. Since some of these QTLs were co-localized with QTLs for panicle structure and plant height (Huang et al. 2009; Ookawa et al. 2010), these QTLs might be useful for the rapid development of lodging resistance genotypes using a marker-assisted selection approach.

## Metabolomics-assisted plant breeding

Metabolomics-assisted plant breeding has been emerged as an 'additional' route towards crop improvement, despite genomics and genetics-based approaches, in which metabolites are used as biomarkers in plant breeding (Herrmann and Schauer 2013). Metabolites show extensive genetic diversity in many (crop) plant species such as rice (Degenkolbe et al. 2013), wheat (Beleggia et al. 2013), maize (Frank et al. 2012), tomato (Schauer et al. 2006), potato (Carreno-Quintero et al. 2012), rapeseed (Wagner et al. 2012) and Arabidopsis (Sulpice et al. 2010), and thus reflect a selective force linking genotype and phenotype (Fiehn 2002). Several techniques (GC–MS, LC–MS, CE–MS and NMR, Obata and Fernie 2012) are commonly used in plant metabolomics research, and recent advances in metabolomics allow monitoring of the whole metabolite inventory of an organism, or even of a specific cell type, in a high-throughput approach under both stress and non-stress conditions.

The use of metabolites as biomarkers in plant breeding is strongly debated and has not yet been commercially exploited. Nevertheless, an expanding catalogue of metabolite QTLs (mQTLs) is available, and several prototype studies assessing the combination of marker-assisted selection/association mapping at the metabolomics level are currently underway worldwide (mQTLs for lipid metabolism in rice grains, Ying et al. 2011; mQTLs for a wide range of metabolites in rice grains, Matsuda et al. 2012; mQTLs for amino acid contents in wheat, Jiang et al. 2013; several mQTLs for several metabolites in wheat flag-leaf, Hill et al. 2013). These studies demonstrate that specific regions of genome that affect agronomic traits and biomass also have distinct effects on specific combinations of metabolites (Meyer et al. 2007; Hill et al. 2013), strongly supporting the association between metabolites and yield traits. However, mQTLs tended to be less heritable, and numerous mQTLs show moderate effect on phenotype structure due to epistatic interaction (Rowe et al. 2008). Given the low heritability of yield traits (~10 %) that have been successfully incorporated into breeding programmes, the mQTLs with the heritability of 25–35 % are encouraging enough to include this metabolic approach in future breeding programmes (Fernie and Schauer 2008; Hill et al. 2013). In this perspective, the development of hybrid cultivars instead of open-pollinated cultivars could potentially increase certain metabolites without any yield penalty (Fernie and Schauer 2008).

Metabolite levels are more closely linked to phenotype than genes (Fiehn 2002; Herrmann and Schauer 2013), and thus the epistatic, epigenetic or post-translational effects on a specific trait evolution can be directly linked to metabolite profiles (Herrmann and Schauer 2013). Although metabolite changes are species-, stress- and environment-specific, they respond rapidly to even short episodes of environmental changes (Stitt et al. 2010), making them very likely candidates as early stress markers for studying plant stress responses. Metabolomics-assisted breeding could be more useful for breeding polyploidy crops especially for crops for which hardly any genomic information is available or for the traits showing high genetic and environmental complexity (Steinfath et al. 2010). In this respect, Gartner et al. (2009) proposed the combination of genetic and metabolic markers as promising approach for traits having complex molecular bases. The investment in the technology could be expensive; however, several metabolic markers could be identified simultaneously in one measurement that can dramatically reduce the cost of biomarker selection. Certain trait responses may not be linked to metabolite dynamics, for example no mQTL was identified on homologous group 2 chromosomes in which the photoperiod response (*Ppd*) genes are located (Hill et al. 2013). The presence of inherent feedback metabolic loops for maintaining homeostatic nutrient levels in plants may pose problems in increasing expression levels of anabolic biosynthetic genes (Tang et al. 2007). Therefore, the practical usage of metabolomic approach is not a trivial task, and much information needs to be generated before this technology becomes a practical tool in future plant breeding programmes.

## Similarities and differences between wheat and rice yield-associated traits

Wheat and rice, being largely a temperate and tropical species, differ for environmental factor responses. Winter wheat requires vernalization, while rice does not; and wheat requires long days, while rice requires short days. The genetic loci controlling these responses appear to be located on different genomic regions in both species (Cockram et al. 2007; Colasanti and Coneva 2009: Yano et al. 1997; Yamamoto et al. 2000; Lin et al. 2006). However, certain *Vrn* loci share sequence similarity with photoperiod loci in rice. For example, vernalization loci, *VRN-B3*, has been shown to be collinear with *OsFT* in rice, which underlies the photoperiod gene, *Hd3a* (Yan et al. 2006). Similarly, *Vrn-A1* shares high synteny with *Hd6* in rice (Kato et al. 1999). While *eps* genes are shown to be absent in rice (Faricelli et al. 2009), two photoperiod alleles, *Hd1* and *2* located on chr. 6 and 7, respectively, were proposed to be associated with earliness in rice (Nakagawa et al. 2005). The distal regions of the long arm of wheat chromosome 1 were showed to be undergone numerous changes that differentiated wheat and rice genomes, which are thought to be a part of an ancient duplication between rice chr. 5 and 1 (Valárik et al. 2006).

Genetic analyses have identified both common and distinct QTLs regulating photosynthetic traits. Few QTLs located on the same chromosomes regulating flag-leaf characteristics (Coleman et al. 2001; Wang 2009) and chlorophyll content (Quarrie et al. 2006; Zhang et al. 2009; Yan et al. 2010a, b) were identified. In wheat, QTLs on chr. 4 were linked to chlorophyll fluorescence traits (Zheng-Bin et al. 2010), while QTLs on chr. 4 was shown to control photosynthesis rate in rice (Adachi et al. 2011). Although QTLs regulating Rubisco content in wheat is unknown (but in barley QTL on chromosome 4 was mapped for Rubisco content; Becker and Heun 1995; Forster et al. 2000), QTLs located on chr. 8, 9 and 10 were shown to control Rubisco content in rice (Ishimaru et al. 2001b; Kanbe et al. 2009). These studies highlight a common and distinct genetic control of photosynthetic traits in both species.

Although wheat and rice operate similar C3 photosynthetic mechanisms, they differ in many aspects involved in photosynthesis processes. Both chloroplast and mesophyll cell area are high in rice as compared to wheat, which increases $CO_2$ diffusion into the stroma. The balance between the capacities of Rubisco and RuBP regeneration does not differ between two species (Sudo et al. 2003); wheat allocates higher leaf N to Rubisco with greater $K_{cat}$ compared to rice (Makino et al. 1992, 2011) and thus exhibit higher photosynthesis than rice in cool temperature conditions (<25 °C). The RuBP regeneration capacity is also higher in wheat than in rice due to greater electron transport rate, which is closely related to a greater Cyt *f* content (Sudo et al. 2003). Higher RuBP regeneration capacity is also supported by enzymes such as NADP-G3PDH, PGAKinase and cpFBPase activities per unit leaf N, which are higher in wheat than in rice (Sudo et al. 2003).

The carbohydrate metabolic enzymes operate in similar manner in both species. However, they differ for reserve carbohydrates storage; wheat synthesizes fructans, while rice do not, due to the lack of enzyme, fructosyltransferase in rice (Ji et al. 2007). Some of the sucrose enzymes share sequence similarity. For example, wheat SSIV cDNA shows synteny and shares a similar exon–intron arrangement with rice SSIVb (Leterrier et al. 2008). The enzyme isoforms required for starch biosynthesis in rice are proposed to be not found in other cereal tissues or non-cereal plants (James et al. 2003; Mohapatra et al. 2011). In wheat, the SPS activity (Castleden et al. 2004), while in rice, starch synthase activity (SSIII, Sehnke et al. 2001) was observed to be limited due to their interaction with 14-3-3 proteins. The isoforms of cytokinin oxidase/dehydrogenase gene (*CKX2*) have proposed to be undergone a *Triticeae*-specific gene-duplication event in wheat and barley compared to rice (Mameaux et al. 2012). They were consistently showed to increase grain number per panicle in rice (Ashikari et al. 2005) and per spikelet in wheat (Zhang et al. 2010b). A gene, GW2, increases grain weight in both crops (Su et al. 2011; Bednarek et al. 2012; Zhang et al. 2013), and it shows differential influence on yield components. In rice, GW2 decreases grains per spike by 30 % and increases panicles per plant by 27 %, while it shows no effect on yield components in wheat (Bednarek et al. 2012).

## Promises in translational biology between rice and wheat

A list of research gaps identified at the molecular level in both crops is presented in Table 3. Modifying phenological phase durations, particularly stem elongation period, has been highlighted to increase wheat yield potential (Slafer et al. 2001). In this sense, the dominant early flowering *TaFT* allele may be viable as it is associated with the insertion of a retroelement in the promoter. In barley, polymorphisms within the first intron are associated with the early allele. Recently, a novel retrotransposon inserted in the dominant *Vrn-B1* allele confers spring habit in tetraploid wheat (Chu et al. 2011). The limited germplasm screens completed to date suggest that the early *Vrn-B3* allele has not been extensively used in commercial varieties and represents a novel source to modulate wheat

**Table 3** Proposed research gaps to fill using a translational biology-based approach between wheat and rice

| Trait | Wheat | Rice |
|---|---|---|
| Developmental phase modifications | *Vrn-A1* (stem elongation period)<br>*Ppd-D1* (heading time)<br>*Vrn-D3* (maturity)<br>(*Chen* et al. 2010) | ? |
| | ? | *OsPRR37* gene<br>(*Koo* et al. 2013) |
| Earliness per se | *Eps* genes<br>(*Gouis* et al. 2011) | ? (Hd1&2) |
| Increased light interception | ? | Low Chl *b* contents or high Chl *a*/*b* ratio<br>(*Zhu* et al. 2010) |
| | | *Chlorina-1* gene<br>(*Zhang* et al. 2006) |
| Increased intercellular $CO_2$ concentration | *QTL* on chr. 5B<br>(*Yan* et al. *2010*) | ? |
| Increased net photosynthesis | ? | *PsbS, SBPase, FBPase*<br>(*Feng* et al. 2007, 2009*; Hubbart* et al. *2012*) |
| Rubisco protein polymorphism at position 309 (Met—C3; Ilo—C4)<br>(*Christian* et al. *2008; Whitney* et al. 2011) | ? | ? |
| Increased Rubisco content | ? | *RbcS* gene<br>(*Suzuki* et al. 2007*; Ishikawa* et al. 2011) |
| Increased electron transport rate | *pFNRII* proteins<br>(*Bowsher* et al. 2012) | ? |
| Delayed leaf senescence and lower ethylene production | ? | *SUB1A* gene<br>*(Fukao* et al. 2012*)* |
| Increased assimilate mobilization | ? | *GIF1* gene (Wang et al. 2008a)<br>*Rg5* (Ishimaru et al. 2005a) |
| Increased grain assimilate accumulation | ? | Higher number of large vascular bundles of spikelets<br>(*Xing and Zhang,* 2010) |
| Increased grain length and weight | ? | *SS7* (*Qin* et al. *2012*) |
| | | *GS3* (*Takano-kai* et al. 2009) |
| Increased grain number | ? | *Gn1* (*Yoshida* et al. 2006) |
| Increased granule-bound starch synthase thermostability | ? | Single-nucleotide polymorphism in GBSS protein (G vs. T)<br>(*Larkin and Park,* 1999) |
| Increased starch accumulation | *AGPase* structural modifications<br>(*Meyer* et al . 2007) | ? |
| Increased culm strength | ? | *SCM2* gene<br>(*Ookawa* et al. 2010) |

flowering time (Yan et al. 2006; Cockram et al. 2007). *VRN-A1, VRN-D3* and *PPD-D1* are shown to be linked to specific developmental phases, stem elongation period, heading time and physiological maturity, respectively (Chen et al. 2010); however, the effects of these loci on modifying developmental phases are yet to be explored. The effects of earliness genes on flowering-time variation remain poorly characterized in both species (Colasanti and Coneva 2009). Progress in defining and utilizing *eps* loci will rely on the development of backcross lines to isolate individual QTLs, an approach that has proven highly successful in rice (Yano et al. 1997; Ebitani et al. 2005). As cereals possess relatively large number of *eps* loci and exhibit variation between both winter and spring types, *eps* loci represent an untapped potential for targeted breeding for fine-tuning flowering time in both species (Cockram et al. 2007).

Grain yields are dependent on three interacting traits: source, sink and assimilate flow to sink organs. The genetic regulation of traits comprising the sink is better understood than source and assimilates flow, and thus these should be the targets for future work (Xing and Zhang 2010). In both species, the genetic variability for photosynthetic capacity in cultivated and wild relatives is yet to be explored, although limited studies have already been attempted using a few genotypes in both species (Teng et al. 2004;

Matsumoto et al. 2005). In rice, one allele of OsBRI1, *d61-7*, confers two important agronomic traits—semidwarf stature and erect leaves—and led to 30 % more grain yield than wild type at high temperature (Morinaka et al. 2006). Although modern wheat has partially erect leaves and the genes for the erect leaves likely exist in most current crops (Richards 2000), searching for *d61-7* like genes may be important to design leaf posture of all leaves of the canopy for improving light conversion efficiency (Zhu et al. 2010).

In both species (being C3 species), the $CO_2/O_2$ specificity of Rubisco could be modified using the variation in nucleotide diversity. For example, in Rubisco nucleotide sequence, at position, 328, many C3 species exhibit C4 dominant serine residue and mutation at this site could alter $CO_2/O_2$ specificity of the Rubisco (Christin et al. 2008). Recently, the evolution of phosphoenolpyruvate carboxylate—enhanced feedback inhibitor tolerance in C3 and C4 plants—was shown to be determined by a single residue, Arg884 (Paulus et al. 2013). The catalytic switch, the key residue of faster carboxylation rate, is yet to be identified in C3 species (isoleucine 309 in C4 species, Whitney et al. 2011). Also, the exact interaction between Rubisco activase and Rubisco is unclear in both species, although models predict that amino acids between 89 and 94 of the L-subunits are important targets of interaction with Rubisco (Portis et al. 2008). Exploring the nucleotide diversity of Rubisco and its mode of interaction with Rubisco activase would greatly improve the Rubisco activity in both species.

As QTLs regulating Rubisco content have been reported to vary with the developmental stage in rice (Ishimaru et al. 2001b; Kanbe et al. 2009), developmental stage-specific QTLs should be identified and explored. Any pleiotropic effects on other traits should be analysed. For example, a QTL on chromosome 4, which regulates several photosynthetic traits in rice, was shown to increase leaf N content and hydraulic conductance by increasing root surface area and root hydraulic conductivity (Adachi et al. 2011). Light use and conversion efficiency could be increased using *Chl1* gene in both crops (Larkum and Kühl 2005; Chen and Blankenship 2011).

Currently, there is still large knowledge gaps on the genetic and molecular control of the biological processes related to yield traits, particularly for grain development. None of the major QTLs for grain number were cloned in Triticeae (McIntyre et al. 2010; Sreenivasulu and Schnurbusch, 2012). Grain weight is known to be unaltered in modern wheat compared to old cultivars. Many QTLs located on chr. 4 and 7 were identified for seed weight in wheat (McCartney et al. 2005; Huang et al. 2006; Mir et al. 2012). In rice, seed weights of QTLs were identified on chr. 1, 3, 5 and 6 (Aluko et al. 2004; Li et al. 2004; Fan et al. 2006; Xing and Zhang 2010), and rice chr. 3 and 6 represent parts of wheat chr. 4 and 7, respectively (Gale and Devos 1998; ter Steege et al. 2005). These studies highlight the importance of chr. 4 and 7 for improving seed weight, and thus grain yield in wheat more than in rice as single grain weight is genetically constant in rice irrespective of N application and growth environments (Yoshida 1981). To improve the assimilate transport capacity, genotypic variation for the translocation efficiency of carbohydrates and nutrients among the available germplasm should be explored in both species. In this sense, vascular systems, enzymes and assimilate transporters should be considered (Cui et al. 2003; Xing and Zhang 2010).

The increased grain number and grain weight have been consistently reported to be linked to increasing endosperm cell number and aleurone cell size in both species (Brocklehurst 1977; Radley 1978; Chojecki et al. 1986; Yan et al. 2010a, b). The determination of grain number, which is associated with number of fertile florets per spikelet, appears to be due to heterochronic initiation of the floret meristem development from the spikelet meristem and is strongly ploidy dependent in wheat (Shitsukawa et al. 2009). Identification of the genes controlling heterochronic development of the floret meristem and their functional analysis of the homoeologous genes should be performed in the future (Shitsukawa et al. 2009). In addition, the parental genome imbalance was shown to be one of the major determinants of endosperm development in Arabidopsis. For example, increasing the parental genome ratio (e.g. 2 m:4p) in endosperm delays endosperm cellularization and produce larger seeds, while increasing the maternal genome ratio (e.g. 4m:2p) leads to precocious endosperm cellularization and smaller seeds in Arabidopsis (Tiwari et al. 2010). This suggests that maternal genomic dosage play a key role in endosperm development (Lu et al. 2012). Understanding such parental genomic regulation of grain development in both species particularly in polyploidy species such as wheat would undoubtedly helps to increase grain size (Dupont 2008; Wan et al. 2008b; Nadaud et al. 2010; Martínez et al. 2011; Tasleem-Tahir et al. 2011; Lesage et al. 2012; Meziani et al. 2012). In both species, altering aleurone cell developmental fate would alter grain weight potential. While the transcription factors regulating aleurone cell development is unknown in wheat, GAMYB in barley (Gubler et al. 2002) and MRP-1 in maize (Gomez et al. 2009) were shown to control aleurone cell development.

In both species, hormonal regulation of grain filling has been emphasized. Higher CK, GA and IAA levels and lower ABA and ethylene levels appear to be beneficial at early grain-filling period to increase the sink activity to attract more assimilates. While such hormonal regulation in rice is relatively comprehensive (Mohapatra et al. 2011), this has been largely unexplored in wheat. The hormonal regulation (e.g. ethylene) in cereal grains is strongly cultivar dependent (Eastmond and Jones 2005); thus, the selection of, screening for, genotypes with optimal flag-leaf or grain ethylene might be a viable option for yield improvement.

To summarize, conventional approaches to crop improvement have maintained genetic gains to the present day; recent technological advancements have led to the emergence of high-throughput tools to explore and exploit plant genomes for crops improvement. These have deciphered both conserved as well as species-specific genes linked to yield traits in both crop species. Genomics-based translational approaches can open new perspectives not only for plant biologists to understand crop diversification but also to assist in designing new strategies for crop improvement.

**Conflict of interest** The authors declare that they have no conflict of interest.

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