Chapter 11
Wheat-Perennial Triticeae Introgressions: Major Achievements and Prospects

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11.1 Introduction

Species belonging to the Triticeae tribe of the grass family (Poaceae) have constantly played a decisive role in development and livelihood of mankind. In addition to about 100 annual such species, including some of the most important domesticated cereal crops (e.g., wheat, barley, and rye), the tribe encompasses around 400 perennials. The latter group comprises several species, commonly referred to as wheatgrasses and wildryes, which, either as natural invaders or purposefully introduced and even selected by man, represent excellent sources of forage and habitat for livestock and wildlife, and also contribute to soil upkeep and to many other aspects of environmental management. In addition to their utility as species per se, many perennial grasses have been successfully hybridized with cultivated, annual cereal crops and notably wheat, for which they have worked as highly valuable sources to improve resistance to biotic and abiotic stresses, as well as quality and yield-related traits, and even to try conferring a perennial habitus to the typically annual wheat.

The relative ease with which hybridization, both natural and man-made, and transfer of desirable attributes has been accomplished from several perennial Triticeae into wheat is due to the existence of sufficient cytogenetic and cytogenomic affinity between the former group of species, belonging to the wheat tertiary gene pool (Harlan and de Wet 1971), and the cultivated forms of *Triticum*. Based on this, not only complete or partial wheat-perennial Triticeae amphiploids, but also addition and substitution lines of single alien chromosomes, and even radiation-induced--> translocation or recombinant lines with segmental introgressions have

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been developed. In recent years, several extensive reviews have dealt with this ample field of basic and applied research (see, e.g., Li and Wang 2009; Wang 2011; Mujeeb-Kazi et al. 2013; Ceoloni et al. 2014a; Chaudhary et al. 2014). The present contribution will focus on major achievements and latest advances in gene transfer from those perennial Triticeae species that have more significantly contributed, or have the potential, to enhance the breeding performance of cultivated wheats, both bread wheat (*Triticumaestivum* L., $2n=6x=42$) and durum wheat (*Triticum durum* Desf., $2n=4x=28$), in the light of a changing ecological and socioeconomic agricultural perspective.

11.2 A Brief Survey on the Cytogenomic Makeup of Perennial Triticeae

Depending on the taxonomic treatment, between 200 and 250 wheatgrass and wild-rye species have been described worldwide, the majority being native to Eurasia and a few to North America, but, as a whole, spread and adapted to the most different environmental conditions of all continents (reviewed in Wang 2011). Not differently from the other representatives of the Triticeae tribe, perennial grasses represent fascinating and puzzling examples of reticulate evolution, in which besides polyploidization, hybridization and interspecific introgression among polyploid lineages and/or their diploid progenitors played a key role in shaping their genomes (e.g. Mahelka et al. 2011; Mason-Gamer 2013; Sun 2014). The resulting genomic heterogeneity has made taxonomic treatment of this ample group of species quite challenging, and often controversial. Moreover, as for other species groups, rather different criteria have animated classification systems through the years (e.g. Barkworth et al. 2009). Even the many genetic and cytogenetic approaches used to investigate intra- and interspecific genome relationships, from classical analyses of chromosome pairing in hybrids, to their "modern" version, with differentially painted genomes, based on genomic in situ hybridization (GISH), up to the ever increasing use of gene/sequence comparisons, and of the many other molecular tools recently available, in several cases still require a thorough interpretation. Thus, although the genome-based classifications proposed by Dewey (1984) and Löve (1984) remain important reference points, subsequent literature revealed them insufficient or incongruent in the face of new findings, and novel interpretations for some controversial biosystematics questions concerning perennial Triticeae species have been recently proposed (see, e.g., Mahelka et al. 2013; Wang and Lu 2014; Wang et al. 2015). As a matter of fact, it is quite obvious that, as more and robust information becomes available, taxonomic treatments change to reflect this information; however, extent and timing of their acceptance and adoption remain subjective. As a consequence, often multiple taxonomic treatments are in use at any given time (Barkworth and von Bothmer 2009). Because taxonomic consideration are not within the scopes of this chapter, in line with what stated by Yen et al. (2005), taxonomy will be used here as "a tool for species recognition," and, perhaps primarily, as "a guide for germplasm utilization, and

a common language for communication." In this view, the currently most-used nomenclature will be employed here, both for genera and species names, and for their genomic formulas. Table 11.1 summarizes this information for perennial Triticeae species that are representatives of pivotal genomes and/or of genome combinations. In the following sections of the present chapter, those that, at various levels, have been involved in alien gene transfer into wheat will be recalled. Species of *Hordeum* genus (H genome) will be treated in a different chapter (Chap. 12).

Most recent classifications identify ~10 basic genome types represented among perennial Triticeae species, the majority of which are contained in varying combinations (and most likely, for what above said, in variously rearranged forms) in the numerous polyploid representatives (Table 11.1). Among them, genome P identifies the current *Agropyron* genus, formerly reported to comprise about 20 genera and 400–500 species, and now universally restricted to the "crested wheatgrasses" such as *A. cristatum* (Wang 2011). Diploid, tetraploid, and hexaploid species in this genus form a common gene pool, in which gene flow occurs among cross-pollinating species of the three ploidy levels. Tetraploid *A. cristatum*, the most common of the three crested wheatgrasses, represents a case of segmental autosomy, in that it probably originated from hybridization between diploid *A. cristatum* and *A. mongolicum*,

Table 11.1 Perennial Triticeae species representatives of pivotal genomes or genome combinations

Genus	Basic genome(s)	Ploidy	Representative species	Genomic formula
Agropyron	P	2*x*, 4*x*[a], 6*x*	*A. desertorum*; *A. cristatum*	P
Australopyrum	W	2*x*	*A. pectinatum*; *A. retrofractum*	W
Dasypyrum	V	2*x*, 4*x*	*D. breviaristatum*	V^b
Elymus	St, H, Y, P, W	4*x*, 6*x*		
		6*x*	*E. rectisetus*	StWY
		6*x*	*E. repens*	StStH
Leymus	Ns, Xm	4*x*	*L. racemosus*; *L. multicaulis*; *L. mollis*	NsXm or Ns_1Ns_2
Psathyrostachys	Ns	2*x*, 4*x*	*P. huashanica*	Ns
Pseudoroegneria	St	2*x*, 4*x*	*Ps. spicata*; *Ps. stipifolia*	St; StSt or St_1St_2
Thinopyrum	E (≅J), St or S	2*x*–10*x*		
		2*x*	*Th. bessarabicum*	J or J^b or E^b
		2*x*	*Th. elongatum*	E or E^e or J^e
		4*x*	*Th. curvifolium*	EE or J^eJ^e or J^bJ^e
		6*x*	*Th. junceum*	$E^bE^bE^e$ or JJE
		6*x*	*Th. intermedium*	E^eE^bSt or E_1E_2St or JJ^sS or $J^{vs}J^vSt$
		10*x*	*Th. ponticum*	$E^eE^bE^xStSt$ or JJJ^sJ^s

For comments and references, particularly on alternative genomic formulas of a given species, see text

[a]The most frequently detected ploidy level within a given genus is underlined

both containing the same basic P genome, but distinguished from each other by structural rearrangements (see Han et al. 2014 and references therein; see also Sects. 11.3.2 and 11.3.3).

An important genus is *Pseudoroegneria*, whose St genome (designated S before Wang et al. 1995) characterizes its taxa, with diploid and auto- or near-autopolyploid representatives. *Pseudoroegneria* species have been prolific contributors, most probably as maternal parents (Zhang et al. 2009a; Mahelka et al. 2011), to many allopolyploids of different genera, notably *Thinopyrum* and *Elymus* (Table 11.1), hence St is definitely a core genome of the Triticeae tribe (Wang et al. 2010a, 2015; Mason-Gamer 2013).

Noteworthy is then the E genome of *Thinopyrum* species, whose symbol was differentiated into E^e and E^b to designate the haplomes of two diploid representatives of the genus, i.e., *Th. elongatum* and *Th. bessarabicum*, respectively (Wang et al. 1995). Alternative symbols, namely J, or J^e, and J^b for the respective diploid species, are used, and also included in the genome formulas of *Thinopyrum* polyploids (Table 11.1; see also Chen et al. 1998; Fedak and Han 2005; Chang et al. 2010; Wang 2011). In fact, the genus encompasses a large number of perennial species and a wide range of ploidy levels, from diploidy up to decaploidy. As several examples will illustrate in the following sections, both the diploids and many polyploids, particularly the hexaploid *Th. intermedium* and the decaploid *Th. ponticum*, have been among the most extensively exploited in wheat breeding, not only among perennial Triticeae, but among wheat relatives as a whole (see Sect. 11.3). Consequently, many cytogenetic and cytogenomic aspects of their chromosome makeup have been extensively analysed. Relatively close relationships have been established for the genomes of diploid *Th. elongatum* and *Th. bessarabicum* (reviewed in Wang and Lu 2014), although accompanied by various types of chromosomal rearrangements, which differentiate their karyotypes and reduce interspecific pairing (see, e.g., Jauhar 1990; Wang and Hsiao 1989; Wang 1992). As expected, the level of intricacy of intergenomic relationships increases in polyploid representatives of the genus, making interpretation of their origin and definition of their genomic constitution highly debated (Zhang et al. 1996a, b; Chen et al. 1998; Chen 2005; Wang 2011; Wang and Lu 2014; Wang et al. 2015). A shared conviction is that the St (or S) genome from the *Pseudoroegneria* genus definitely enters in the genomic composition of both *Th. intermedium* and *Th. ponticum*. The St/S genome, in turn, shows close relatedness with the E (= E^e) and J (= E^b) genomes, as proved by extensive autosyndetic pairing (Wang 1989a, b, 1992; Jauhar 1995; Cai and Jones 1997) and cross-hybridization in Southern and GISH experiments (Zhang et al. 1996a; Liu et al. 2007). Thus, a conclusive definition of the genomic composition of *Th. intermedium* and *Th. ponticum* has been difficult to reach. The former has been described with various genome formulas, including E^eE^bSt (Wang and Zhang 1996) and E_1E_2St (Zhang et al. 1996b) or JJ^sS (Chen et al. 1998), while $E^eE^bE^xStSt$ (reviewed in Li and Zhang 2002) or JJJ^sJ^s (Chen et al. 1998) have been indicated for the latter. The controversy has particularly dealt with distinction between chromosomes considered on one hand of fully St/S-genome derivation (Zhang et al. 1996a), and, on the other, hypothesized to result from intergenomic

rearrangements in the course of polyploid evolution, with presence of St/S genomic DNA confined to pericentromeric regions (as in J^s type chromosomes, see Chen et al. 1998). In any case, hybridization to the St/S genomic DNA, whether complete or segmental, represents a distinctive mark of the genomic origin of the *Thinopyrum* chromosome(s) involved. However, the picture has been further complicated by evidence of hybridization of J^s chromosomes with either genomic DNA or a repetitive sequence of the V genome of the genus *Dasypyrum* (see ahead), suggesting the involvement of V genome in the evolution of the J^s genome (Kishii et al. 2005; Mahelka et al. 2011; Deng et al. 2013). Very recently, comprehensive reassessments have been provided for some of the most controversial issues of biosystematics and evolutionary relationships of perennial Triticeae species (Wang and Lu 2014; Wang et al. 2015, and references therein). One of them concerns the origin and genome constitution of *Th. intermedium*, which appears to be now nearly resolved. Presence of the St genome from *Pseudoroegneria* is substantiated by all studies, hence considered unequivocal. Moreover, based on assays with EST-SSR primer sequences derived from the putative diploid progenitor species carrying the St, J^b, and J^egenomes, the St genome in *Th. intermedium* results the least modified from the present-day *Pseudoroegneria* diploids. On the other hand, the same assays showed both J and J^s to differ from present day J^e (*Th. elongatum*) and J^b (*Th. bessarabicum*) genomes, respectively: the former distinction (J vs. J^e) would be based on presence of long-terminal repeat sequences of rye (R genome) origin, the latter (J^s vs. J^b) on presence of repetitive sequences of *Dasypyrum* (V genome) derivation. Taking into account such evidence, a novel designation has been proposed for the *Th. intermedium* genome formula, that is $J^{vs}J^rSt$, with J^{vs} and J^r representing ancestral genomes of J^b and J^e (Wang et al. 2015).

A complex history of genome rearrangements has been also described for species of the genus *Elymus* (Mahelka and Kopecky 2010; Zeng et al. 2013b; Sun 2014; Wang et al. 2014; Wang and Lu 2014), the largest genus in the Triticeae tribe, including, in its broadest sense, around 200 species that are widely distributed all over the world. *Elymus* is an exclusively allopolyploid genus, in which five basic genomes (St, H, Y, P, and W; Table 11.1) have been identified (Wang 2011; Wang and Lu 2014). Among them, the St genome is recognized as common to all *Elymus* species, while Y, another pivotal genome of the genus, is still of debated origin (Sun 2014; Wang and Lu 2014).

Chromosomal rearrangements were also frequently detected in species of the polyploid *Leymus* genus, such as tetraploid *L. racemosus* and *L. multicaulis* (Qi et al. 1997; Jia et al. 2002; Zhang et al. 2010; see Sect. 11.3.2). All *Leymus* species are based on the Ns-genome from *Psathyrostachys* (see ahead) and the Xm-genome of still unknown origin, with genomes P of *Agropyron* and F of *Eremopyrum triticeum* hypothetically considered in its ancestry (reviewed in Wang and Lu 2014). However, a different genomic constitution has been recently proposed (Anamthawat-Jónsson 2014). The study, based on FISH experiments with *Leymus* specific dispersed retroelement-like repeats as probes, showed them to be distributed over all *Leymus* chromosomes, without any differentiation between chromosomes. The same repeats were also abundant in the Ns genome progenitor in *Leymus*, i.e.,

Psathyrostachys. Experiments on *Leymus* chromosomes using *Psathyrostachys* genomic DNA as probes further supported the proposal of NsNs (Ns_1Ns_2) genome constitution for *Leymus*. The possibility that an Xm genome might have been involved in the beginning of the allopolyploidization process was not discarded, but in this case, the Ns genome specific elements would have spread predominantly and rapidly across genomes, leading to genome homogenization.

As mentioned, the Ns genome characterizes the predominantly diploid species of the small *Psathyrostachys* genus, containing species, such as *P. huashanica*, endemic to the Shaanxi Province of China, which has provided a number of desirable genes for wheat improvement (see Sect. 11.3.3.2).

Finally, the V^b genome is included in Table 11.1, which symbolizes the perennial representative of the *Dasypyrum* genus, currently considered to comprise two species only, the other one being the annual *D. villosum*, with a V^v genome designation (Gradzielewska 2006a; De Pace et al. 2011). *D. breviaristatum* is largely tetraploid, while *D. villosum* is strictly diploid. The origin and genomic constitution of 4*x D. breviaristatum* is debated. A general consensus exists on its autotetraploid origin. However, a direct derivation from *D. villosum* appears to contrast with the results of various types of investigations (reviewed in De Pace et al. 2011). Thus, the most likely candidate for the diploid species in which the genome duplication event occurred to give rise to the current 4*x D. breviaristatum* genome seems to be 2*x D. breviaristatum* rather than *D. villosum* (reviewed in De Pace et al. 2011). Nonetheless, several morphological and cytomolecular features are definitely indicative of a common ancestry of the two species, with differentiation between them probably due to adaptability to diverse ecogeographic areas occupied by the common ancestor. In comparison with *D. villosum* (Gradzielewska 2006b; De Pace et al. 2011), research on *D. breviaristatum* and, hence, exploitation of its positive attributes in wheat breeding, is very limited. However, some examples are given in Sect. 11.3.2.

11.3 Exploitation of Useful Traits

As above anticipated, exploitation of the ample variability present in perennial Triticeae germplasm has been accomplished through incorporation into the wheat genome of as much as the entire alien genome, particularly in the form of chromosome-doubled hybrids, i.e., amphiploids, down to a single chromosome or chromosome arm pair (either added or substituted), or just a small chromosomal segment. As expected, the relative degree of success has been strongly correlated with several factors, primarily interspecific and consequent intergenomic relatedness, but also degree of crossability, as well as stability of cross combinations and of their derived lines. For all these aspects, species belonging to the *Thinopyrum* genus turned out to be the most amenable (see, e.g., Jiang et al. 1994; Mujeeb-Kazi and Wang 1995; Wang 2011; Mujeeb-Kazi et al. 2013; Ceoloni et al. 2014a), hence the most extensively used in the production of one or more types of assembly with

the wheat genome. Several examples of wheat–alien combinations will be illustrated in the following, both involving *Thinopyrum* spp. and also more distant wheat relatives among perennial Triticeae species, gathering them on the basis of the amount of alien genome(s) contribution.

11.3.1 Hybrids and Amphiploids

A plentiful array of hybrids and complete or partial amphiploids was obtained with representatives of many species and genera of perennial Triticeae (Wang 1989a, 1989b, 1992, 2011; Jiang et al. 1994; Mujeeb-Kazi and Wang 1995; Fedak and Han 2005; Mujeeb-Kazi et al. 2013; Ceoloni et al. 2014a, and references therein). Such hybrid combinations have provided fundamental knowledge of the intergenomic affinities between the donor species and the recipient wheat, and, as in most wide crosses, represented the first step in the course of targeted introgression of desired alien traits, generally associated with alien transfers of limited entity (see ahead, Sects. 11.3.2 and 11.3.3).

Moreover, amphiploids involving *Thinopyrum* species, sometimes referred to as "Tritipyrums" (e.g., Marais et al. 2014) or "Trigopiros" (e.g., Fradkin et al. 2012), obtained from colchicine-induced or even spontaneous doubling of the F_1's chromosome number, probably represent the only other case, besides that of the well-known triticale (× Triticosecale Wittmack; Larter 1976), that may have practical utility. In fact, as an alternative route to direct domestication of some perennial species, such as *Th. intermedium* and *Th. ponticum* (see, e.g., Cox et al. 2010; Bell et al. 2010; DeHaan et al. 2014), derivatives from hybridization of *Thinopyrum* species with either durum or bread wheat have long been looked to as possible gateways to development of a perennial wheat. Unlike conventional wheat, that requires tilling and seeding the soil every growing season, develops shallow roots and grows on soil exposed to wind and water erosion for much of the year, perennial wheat would be planted once and harvested several times, would take greater advantage of precipitation during its longer growing seasons, and, thanks to deeper and larger roots, would also reduce soil erosion, nitrogen losses and salinization, as well as sequester carbon from the atmosphere. It would also require fewer farming operations and less herbicide supply, additional key features for sustainability of cereal cropping in less developed regions and marginal lands. Furthermore, greater complexity of the perennial cereal crown may act as a barrier to soil diseases, and this, coupled with ample resistance to foliar diseases conferred by genes of the perennial donor species, can greatly reduce challenges that perennial wheat production might face in terms of disease control (e.g., Cox et al. 2005a, b; Hayes et al. 2012; Turner et al. 2013). Therefore, breeding programmes aimed at capitalizing on perenniality-associated traits, yet providing agronomically and economically acceptable yields, are being conducted in the United States, Australia and other countries, also pointing at a dual-purpose perennial wheat, able to produce grain and additional forage during summer and autumn, hence representing a sustainable and profitable option

for mixed crop–livestock farming systems (Cox et al. 2006, 2010; Bell et al. 2010; Ward et al. 2011; Larkin et al. 2014).

Perennial habit embodies a highly complex suite of traits, expected to be largely quantitative in nature. Therefore, notwithstanding the evidence of a gene or genes on chromosome 4E of diploid *Th. elongatum* determining some ability of post-harvest regrowth (Lammer et al. 2004; see also Sect. 11.3.2), it is not surprising that a common outcome from studies on perennial wheat is that plants derived from intergeneric combinations tend to be perennial only when the proportion of their total genome derived from the perennial parent is conspicuous (Cox et al. 2002; Hayes et al. 2012; Larkin et al. 2014). As a matter of fact, similarly to the regrowth phenotype conferred by chromosome 4E, which results less strong and more environmentally dependent than that observed in the *T. aestivum-Th. elongatum* complete amphiploid (Lammer et al. 2004), in wheatgrass derivatives reasonable capacity to regrow post-harvest and yield grain over successive years are only observed when many chromosomes are added to wheat from the perennial donor species (Hayes et al. 2012; Larkin et al. 2014). On reviewing the genomic composition of the most promising wheat-perennial derivatives, it has been recently suggested that the best prospects for a productive breeding program in the medium term would derive from complete amphiploids between wheat (either tetraploid or hexaploid wheat) and a diploid perennial donor, such as *Th. elongatum*, contributing, as in the triticale case, a whole-genome equivalent (Mujeeb-Kazi et al. 2008; Larkin et al. 2014). Providing the necessary chromosomes for the desired "package" of perenniality traits are present, other possibilities for generating perennial wheat amphiploids are of course possible; in fact, besides *Th. elongatum*, successful donor perennial parents have largely included the polyploid *Th. ponticum* and *Th. intermedium*. Also in these cases, if the wheat parent was a hexaploid, an entry required at least 56 chromosomes to achieve any substantial post-harvest regrowth, and even this was no guarantee of a capacity to survive post-harvest (Cox et al. 2010; Hayes et al. 2012; Larkin and Newell 2014; Larkin et al. 2014). Clearly, it is the presence, not solely numerical, of critical alien chromosomes to assure perenniality traits, as the expression of robust perennial habit in partial amphiploids derived from various hybridization strategies demonstrates. One notable case is that of MT-2 lines, derived from an original *T. durum/Th. intermedium* decaploid amphiploid and, following chromosome loss, averaging $2n = 56$, with around 30 *Thinopyrum* chromosomes (2:1 ratio between E (or J)-genome and St-genome chromosomes, see Table 11.1) and 26 wheat chromosomes (Jones et al. 1999). This genomic constitution contrasts with that of other octoploid partial amphiploids, such as OK-906 and Agrotana, having 40 wheat and only 16 *Thinopyrym* (E/J + St) chromosomes, characterized by an annual habit (Jones et al. 1999). In all cases, including primary types, as well as derivatives from their inter-crossing or even from backcrossing to the perennial parent, several rounds of breeding cycles and heavy selection will likely be required for the novel wheat type to achieve the desired performance and stability of all target traits. Such stability is expected to correspond to achievement

of an inter-genomic "equilibrium," following a variety of "revolutionary" changes triggered by newly established allopolyploid conditions (Ma and Gustafson 2008; Feldman and Levy 2012; Wang et al. 2014).

Apart from the "perenniality" suite of traits, the numerous amphiploids, both complete and partial types synthetized through the years, represent a key step to early assess expression into the recipient wheat background of the valuable attributes identified in perennial Triticeae germplasm. As for closer gene pools, mostly stress resistance genes, particularly those against fungal and viral diseases, with a frequently monogenic control, have been more easily detected and, through subsequent steps, handled for targeted transfer. Genes of this kind were shown to provide excellent resistance to leaf, stem and stripe rust, powdery mildew, karnal bunt, spot blotch, *Stagonospora nodorum* blotch, Fusarium head blight (FHB) or scab, tan spot, eyespot, barley yellow dwarf virus (BYDV), wheat streak mosaic virus (WSMV) and its vector, wheat curl mite (WCM), and aphids (see, e.g., Oliver et al. 2006; Li and Wang 2009; Chang et al. 2010; Wang 2011; Zeng et al. 2013a). Remarkable tolerance to abiotic constraints, notably salinity, has also been detected in various amphiploid combinations involving various perennials, such as *Th. elongatum*, *Th. bessarabicum* and *Th. distichum*, and both bread and durum wheat (e.g., Dvorak and Ross 1986; King et al. 1997b; Colmer et al. 2006; Mujeeb-Kazi et al. 2013; Marais et al. 2014). Although major genes have been sometimes identified also for such more complex traits and eventually transferred into wheat (see Sects. 11.3.2 and 11.3.3), it was not infrequent to detect a truly quantitative type of inheritance, with several alien genes scattered on different chromosomes acting in an additive manner (Zhong and Dvorak 1995; Colmer et al. 2006; Mujeeb-Kazi et al. 2013). A similar outcome was observed for FHB resistance conferred by genes on *Th. junceum* chromosomes (McArthur et al. 2012), and for BYDV resistance from *Th. elongatum* (Anderson et al. 2010). In these instances, a "genome-wide" approach of transfer promotion can be profitably applied, by introducing into the hybrid or amphiploid genotype a recessive condition at the main wheat locus normally suppressing homoeologous chromosome pairing, i.e., *Ph1* (reviewed in Ceoloni and Jauhar 2006; Qi et al. 2007; see also Sect. 11.3.3). This strategy is not only effective in capturing the most of the alien donor genetic determinants for a given polygenic trait, but also when multiple genes/quantitative trait loci (QTLs) for various desirable attributes are scattered in the alien genome(s). In fact, this was proved to be the case for a large number of complete or partial amphiploids (see, e.g., Chen 2005; Fedak and Han 2005; Wang 2011; Zeng et al. 2013a), and for some of these (e.g., for a *T. aestivum-Th. bessarabicum* amphiploid, Kazi 2011) extension of pairing and recombination promotion to potentially all wheat-alien homoeologous partners was successfully exploited in parallel with the more frequently pursued strategy of backcrossing the *Ph1* amphiploid to a normal wheat genotype, to "scale down" the alien donor genomic component to single chromosome additions and substitution lines, and leaving the *ph1* mutant effect to be active only on single, specific alien chromosomes (see Sect. 11.3.3).

11.3.2 Chromosome Addition and Substitution Lines

In general, starting from a hybrid or a complete/partial amphiploid combination with one or more appealing attributes for potential enhancement of wheat performance, a step forward for reduction of unwanted alien genetic material is the isolation of single alien chromosome addition and substitution lines into the wheat background. Molecular and phenotypic evaluation of these materials enables chromosomal assignment of gene(s) of interest, besides that genome and homoeologous group attribution of the specific alien chromosome(s). To this respect, sometimes the picture may be complicated by intergenomic rearrangements not seldom occurring in hybrids and amphiploids, as it is in the case of related genomes of polyploid *Thinopyrum* species (reviewed in Fedak and Han 2005), and hence maintained in derived addition and substitution lines. Various examples are illustrative of this phenomenon, including *Th. junceum* chromosomes in AJDAj5 and AJDAj6 addition lines, which, based on EST-SSR (Wang et al. 2010b) and RAPD (Wang et al. 2003) markers, appear as complexly restructured chromosomes, carrying portions with segmental homoeology to groups 1 + 5 and 2 + 5 + 1, respectively. Such complex patterns of homoeology with wheat chromosomes (Moustakas 1991; Wang et al. 2010b; Wang 2011) are likely the result of structural rearrangements differentiating the E^b and E^egenomes which make up the hexaploid *Th. junceum* genome (Table 11.1), and of the complex, reticulate evolution characterizing polyploid lineages of these and all Triticeae species (see Sect. 11.2).

The same reasoning can explain what observed in combinations with wheat of *Thinopyrum* chromosomes belonging to polyploid species, containing, besides E/J--type genomes, one or more St genomes, consistently proved to be closely related to E/J genomes (Zhang et al. 1996a; Fan et al. 2007; Liu et al. 2007; Wang 2011). Thus, the *Th. intermedium* chromosome present in addition line L1, derived from the TAF46 partial amphiploid with *T. aestivum*, was interpreted as a prevailingly St chromosome, with pericentromeric chromatin of E-genome derivation (Wang and Zhang 1996). The BYDV resistance gene present in TAF46 and L1 was allocated to the distal 7St region of the long arm of such a chromosome (Zhang et al. 1996b). Carrier of an St-E translocation was also considered one of the seven *Th. intermedium* chromosomes present in the Zhong 5 partial amphiploid, and from it incorporated into disomic additions Z1, Z2 and Z6, and substitutions Yi 4212 and HG 295 (Tang et al. 2000; Zhang et al. 2001; Ayala-Navarrete et al. 2009). All lines carrying this chromosome, showing group 2 homoeology, showed high resistance to BYDV.

The array of disease resistance phenotypes assigned to given *Thinopyrum* spp. chromosomes via evaluation of addition or substitution lines is indeed plentiful. Among the most relevant for having represented starting materials for subsequent use in breeding of their gene content, are various examples in which *Th. ponticum* chromosomes are involved. One notable case is that of the 6Ag chromosome, containing the durable and wide-spectrum stem rust resistance gene *Sr26*. Remarkably, since its identification in the 1950s (Shebeski and Wu 1952), *Sr26* remains still effective against all known races of the causing agent, including all pathotypes

belonging to the Ug99 lineage (FAO 2015). After several backcrosses with bread wheat cv. Thatcher of an original *T. aestivum-Th. ponticum* partial amphiploid with $2n = 56$ (Shebeski and Wu 1952), addition and substitution lines were obtained. These, besides proving that the strong resistance was fully associated with the alien 6Ag chromosome, also showed the latter to be homoeologous to wheat group 6, and to compensate well for wheat 6A, consistently replaced by 6Ag in the substitution lines (Knott 1964). Since the 1960s, the long-lasting *Sr26*-based resistance was introduced in Australia in the form of a radiation-induced 6AgL-6AL translocation, derived from a 6Ag addition line (Knott 1961), which has been widely used commercially, in spite of the 6AgL-associated yield penalty (The et al. 1988). Further 6Ag manipulations subsequently undertaken to obviate this defect will be described ahead (Sect. 11.3.3).

Another valuable *T. aestivum-Th. ponticum* pre-breeding material is the 7Ag(7D) substitution line called Agrus. Initially the line was used as a source of the highly effective leaf rust resistance gene *Lr19*, and, as illustrated in the following section (Sect. 11.3.3), through different strategies (Sharma and Knott 1966; Sears 1973, 1978; see also ahead), 7Ag was engineered to give wheat translocation and recombinant lines carrying *Lr19*. In rather close linkage with *Lr19*, along the 7AgL arm, the *Sr25* stem rust resistance gene was also found to be located (McIntosh et al. 1977, and both genes still provide strong resistance to the respective rust disease (e.g., Gennaro et al. 2009; Liu et al. 2010; FAO 2015). Of somewhat lower efficacy in time and space (Friebe et al. 1996; FAO 2015) has been the resistance to leaf and stem rust conferred by the *Lr24* and *Sr24* gene, respectively, located on a *Th. ponticum* 3AgL arm of a 3Ag *Th. ponticum* chromosome, substituted for wheat chromosome 3D in the TAP67 derivative line from the (*T. aestivum* × *Th. ponticum*) × *T. aestivum* cross (Bakshi and Schlehuber 1959). TAP 67, showing normal vigor and fertility and reasonably good yield, was used as donor of the *Lr24* gene to a series of bread wheat recombinant lines mostly involving the homoeologous wheat 3DL arm (Sears 1973, 1978). Similarly to the *Lr19* + *Sr25* case, it was later discovered that *Lr24* was linked to *Sr24* in all recombinant and translocation lines of the same 3Ag chromosome (McIntosh et al. 1977). Based on GISH evidence, the 3Ag chromosome appears to belong to a J^s (= St) genome of the donor species (Li et al. 2003).

As to valuable resistance sources associated to chromosomes of other *Thinopyrum* species, resistance to stem rust, including Ug99 strains (Xu et al. 2009), was found to be conferred by a *Th. junceum* chromosome, largely homoeologous to wheat group 4, present in the addition line HD3505 (Wang et al. 2010b). Besides this, a group 2 *Th. junceum* chromosome in the AJDAj3 addition line contained an effective gene(s) for resistance to FHB (McArthur et al. 2012).

Further, considering wheat cv. Chinese Spring-*Th. elongatum* disomic substitutions, chromosomes 2E and 3E provided excellent resistance to cereal yellow dwarf virus (CYDV), while substitution lines for 1E and 6E were significantly more resistant to *Septoria tritici* blotch compared to Chinese Spring (Anderson et al. 2010). However, neither chromosome by itself conferred resistance as high as that of several wheatgrass accessions; similarly, genes on multiple *Th. elongatum* chromosomes were apparently required for complete resistance to BYDV. On the other

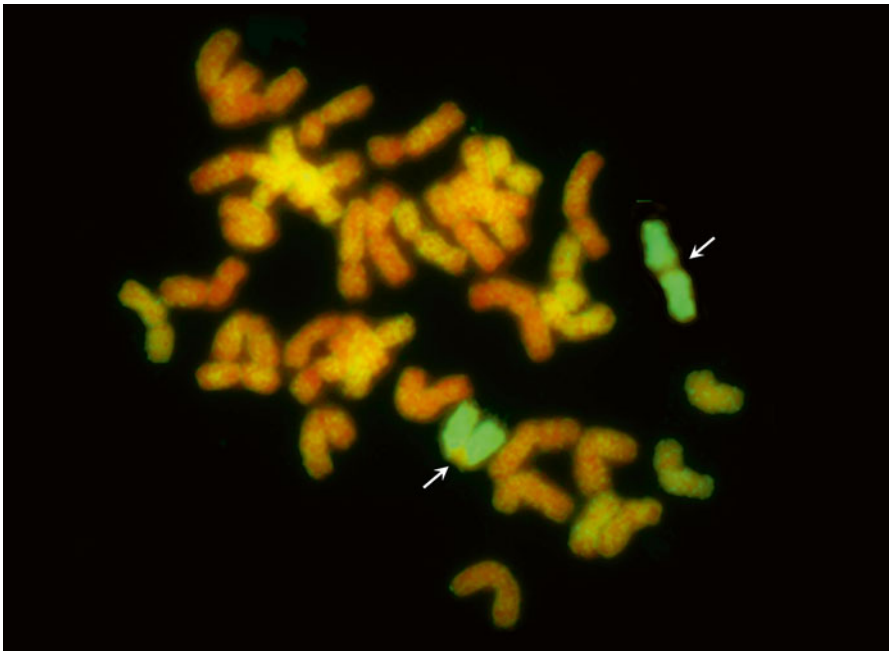

Fig. 11.1 Partial somatic metaphase plate of a bread wheat-*Thinopyrum elongatum* 7E(7D) substitution line, subjected to fluorescence GISH, as described in Forte et al. (2014). Total *Th. elongatum* DNA, used as one probe, is marked by green fluorescence (FITC fluorochrome), which highlights the two 7E chromosomes (*arrowed*). Total wheat DNA, used as the other probe, was labelled by Cy3 (red fluorescence). The more greenish wheat chromosomes belong to the D genome, with which the *Thinopyrum* DNA cross hybridizes more intensely (i.e., shares higher homology) than with those of the A and B genomes

hand, the excellent resistance to FHB observed in 7E(7A), 7E(7B), and 7E(7D) substitution lines (Fig. 11.1), was shown to be due to the presence of a gene(s) for type II resistance on the 7EL arm (Shen et al. 2004; Shen and Ohm 2006). Transfer of this effective gene in both bread and durum wheat has been recently undertaken (Forte et al. 2011 and unpublished).

Molecular and cytogenetic techniques were used to identify a new wheat-*Th. intermedium* ssp. *trichophorum* substitution line from the cross of TE-3 partial amphiploid and the Chinese wheat line ML-13 (Hu et al. 2011). The *Thinopyrum* derived St-chromosome, substituting for wheat chromosome 1D, was proved to contain new gene(s) for stripe rust resistance. Furthermore, wheat-*Th. intermedium* lines carrying a group 4 homoeologous chromosome or its short arm were resistant to eyespot (Li et al. 2005). Eyespot resistance was similarly associated to a group 4 chromosome of *Th. ponticum*, but the same was not true for group 4 chromosomes of the diploid *Th. elongatum* and *Th. bessarabicum* species (Li et al. 2005).

On the other hand, taking into account tolerance to abiotic stresses, chromosomes of diploid *Thinopyrum* species with different homoeology to wheat chromosomes

were shown to harbour genes enhancing wheat salt tolerance (Colmer et al. 2006). Dissection of this complex trait by use of addition or substitution lines, revealed *Th. elongatum* chromosome 3E to have a major dominant effect on salt tolerance, with 3E substitution lines showing superior "exclusion" of Na+ and better maintenance of K+ in flag leaves, higher dry mass and grain yields when compared with wheat cv. Chinese Spring (Omielan et al. 1991). It was, instead, the $5E^b$ of *Th. bessarabicum* to confer higher ability to "exclude" Na+ from both mature and newly developed leaves to substitution, and to a lesser extent, addition lines compared to normal wheat (Mahmood and Quarrie 1993). Although other *Th. bessarabicum* chromosomes are likely involved in fuller expression of the trait, attempts to transfer the $5E^b$ gene(s) were undertaken (King et al. 1997a). Partly homoeologous to wheat group 5 is also the *Th. junceum* chromosome ($5E^b$ or 5J) present in the AJDAj5 addition line (see also above), resulting salt tolerant (Wang et al. 2003).

Another interesting trait that could allow wheat to better respond to environmental constraints, namely waterlogged conditions, was identified in diploid *Th. elogatum* chromosomes homoeologous to groups 2 and 4. In fact, presence of 2E and 4E in *T. aestivum* addition lines was associated with a positive effect on root growth and penetration in waterlogged soil (Taeb et al. 1993).

Investigation of addition lines of *Th. bessarabicum*, *Th. elongatum* and *Th. intermedium* chromosomes, mostly homoeologous to wheat group 1, have also provided interesting information as to the presence of several novel alleles for high molecular weight glutenin subunits (HMW-GS), known to play an important role in determining end-use quality in wheat (Niu et al. 2011). Novel HMW-GS have been also identified and fully characterized in *Th. ponticum*: some of them contain extra cysteine residues in their amino acid sequences, a feature that makes them potentially able to exert a positive influence on wheat dough properties (Liu et al. 2008). Similarly, good potential for improvement of wheat end-quality was shown for a HMW-GS gene located on a group 1 St chromosome of *Th. intermedium* ssp. *trichophorum*, present into spontaneously occurred substitution and homoeologous recombinant bread wheat lines (Li et al. 2013). The genomic sequence of the *Thinopyrum*-derived HMW-GS was characterized and designated *Glu-1St#2x*, since it closely resembled x-type wheat glutenins. Phylogenetic analysis revealed that *Glu-1St#2x* subunit clearly clustered with *Glu-R1* from *Secale cereale* and *Glu-E1* from *Th. elongatum*, and evolved earlier than the split of wheat *Glu-1* homoeologous genes.

A peculiar trait that *Thinopyrum* species, besides that other Triticeae, showed to possess is blue aleurone. The blue pigmentation of aleuronic layer is due to the presence of anthocyanins, one of the major groups of flavonoid compounds that differ from those in red or white wheat grains, and play active roles in several human metabolic activities, such as antioxidant activity, anti-inflammatory, anticancer, and hypoglycemic effects (Abdel-Aal et al. 2006). Development of synthetic blue-seeded wheats from intergeneric crosses with *Thinopyrum* species has a long history in North America, Europe, and Asia (Morrison et al. 2004; Zheng et al. 2009). Blue aleurone represents an easily scorable marker, used in various genetic studies and breeding practice of wheat (reviewed in Zheng et al. 2009). Moreover, increased

interest in health beneficial flavonoids, has attracted attention to the accumulation of anthocyanin pigments in blue-grained wheat as a new dietary source of these compounds, whose biosynthesis might be upregulated during seed development by blue-aleurone (*Ba*) genes. Analysis of substitution and addition lines of *Thinopyrum* chromosomes into wheat backgrounds showed effective *Ba* genes to be consistently associated with homoeologous group 4. A *Th. ponticum* 4Ag chromosome pair was found to substitute for a 4D pair in the blue-grained Blue Dark wheat developed in Canada and in Blue 58 produced in China (Zheng et al. 2009). Crossing the substitution line Blue 58 with euploid *T. aestivum*, Li et al. (1986) isolated monosomic substitution plants ($2n=41$), in whose selfed progeny distinct seed colors (dark blue, medium-light blue, and white) were observed: dark blue seeds corresponded to disomic substitutions ($2n=42$), seeds of medium-light blue color were of monosomic substitutions, whereas white seeds belonged to nullisomic plants ($2n=40$). Thus, a clear-cut association between the grain color and the dosage of the *Th. ponticum* blue-grained gene (named *Ba1*) on 4Ag was established. A strong dosage effect was similarly observed for a gene, designated *BaThb*, on chromosome 4 J ($=4E^b$) of diploid *Th. bessarabicum* (Shen et al. 2013). By molecular cytogenetic and marker analyses of spontaneous or induced translocation lines, the *Ba* genes of the two *Thinopyrum* species were assigned to non-colinear positions along the long arms of the respective group 4 chromosomes (Zheng et al. 2009; Shen et al. 2013).

Although in much more limited number, and never as complete sets, addition and substitution lines of chromosomes of perennial grasses more distantly related to wheat than the *Thinopyrum* genus have been obtained. Some involve species of the large *Elymus* genus, such the allohexaploid *Elymus rectisetus*, an apomictic species carrying the St, W, and Y genomes (Table 11.1). In backcross progeny from crosses with bread wheat, also attempted to transfer apomixis into wheat (Liu et al. 1994), a disomic addition for a 1Y chromosome was identified, exhibiting moderate resistance to both tan spot and Stagonospora nodorum blotch (Oliver et al. 2008), as well as a 1St addition with a good level of resistance to FHB (Dou et al. 2012; McArthur et al. 2012).

Chromosomes of another polyploid, mostly tetraploid, group of perennials, belonging to the *Leymus* genus (Table 11.1), were also shown to possess valuable traits for wheat improvement. Particularly noteworthy is the biological nitrification inhibition (BNI), i.e., the capacity of root exudates to suppress NO_3^- formation and keep the largest part of soil's inorganic-N in the NH^+_4-form, found to be highly expressed in Volga or mammoth wildrye, *L. racemosus*, while virtually lacking in wheat. Analysis of wheat *L. racemosus* addition lines revealed that such BNI capacity is expressed in the genetic background of wheat cv. Chinese Spring, and is mostly controlled by one *L. racemosus* chromosome, named Lr#n, whose presence increases by about fourfolds that of the Chinese Spring control (Subbarao et al. 2007). However, the same Lr#n chromosome, recently shown to be homoeologous mostly to group 2 wheat chromosomes (Larson et al. 2012), does not provide tolerance to NH^+_4, which appears to be under the control of chromosome 7Lr#1-1, showing group 7 homoeology. Both attributes would be beneficial for a sustainable wheat production, since while NH^+_4 could represent the necessary signal to make the BNI

capacity responsive to the environment, the ability to combat nitrification in intensive wheat farming systems has the potential to reduce nitrogen pollution from such systems (Subbarao et al. 2007).

Furthermore, two of the several wheat-*L. racemosus* addition lines developed in China showed high resistance to FHB (Wang and Chen 2008). From pollen irradiation of the MA7Lr monosomic addition line, with the alien chromosome showing homoeology to wheat group 7 chromosomes, a ditelosomic substitution line was isolated, where a pair of 7Lr#1S telocentric chromosomes, to which the FHB resistance gene(s) could to assigned, replaced wheat chromosome 7A.

Another attribute that could profitably be introgressed from *L. racemosus* into wheat is tolerance to Aluminium (Al) toxicity, a key factor limiting its production in acidic soils, which represent 40 % of the world's cultivated land. Recently, two addition lines, for chromosome A (group 2 homoeology) and E (unknown homoeology) were shown to significantly enhance wheat Al tolerance in terms of relative root growth (Mohammed et al. 2013). The markedly increased tolerance conferred by chromosome E was attributed to improved cell membrane integrity. The same study also showed the importance of wheat chromosome 2B in the expression of the Al tolerance of *L. racemosus* chromosome A, not detected in the substitution line lacking this chromosome, and also the negative effect of other *L. racemosus* chromosomes on the same trait, evidently resulting from interaction between wheat and alien genes. Targeted chromosome engineering with the two positively contributing lines is expected to allow attainment of Al-tolerant wheat cultivars.

In the search for sources of tolerance to heat stress, one of the major factors limiting wheat production in tropical and subtropical environments, the same set of *L. racemosus* addition and substitution lines was evaluated under controlled and field stressful conditions (Mohammed et al. 2014). Chromosomes A, 2Lr#1 and 5Lr#1, added to lines TAC1, TAC12 and TAC13, showed early heading and maturity, which enabled these lines to fill their grains normally and escape the late heat stress occurring at the end of the season. In addition to this avoidance mechanism, the most tolerant TAC12 line probably possesses a heat tolerance mechanism correlated with a more efficient mitochondrial electron transport activity, hence cell viability (Mohammed et al. 2014). Higher mitochondrial efficiency under heat stress conditions also appeared to underlie the heat tolerance of TAC6 addition line, harboring a *Leymus* chromosome of homoeologous group 5. Yield-related traits were also observed in the various lines, among which TAC14, carrying the group 7 chromosome 7Lr#1, stood out for its considerable yield potential, resulting from both high tiller number and kernel weight. Interestingly, group 7 chromosomes of wheat (Quarrie et al. 2006) and *Th. ponticum* (Kuzmanovic et al. 2014), also carry genes for yield-contributing traits (see Sect. 11.3.3).

Analysis of addition/translocation lines of another *Leymus* species, i.e., *L. multicaulis*, into Chinese bread wheat cultivars, showed different *Leymus* chromosomes as capable to confer resistance to FHB, CYDV and stem rust (Zhang et al. 2010). Where revealed by use of SSR markers, homoeology of these chromosomes corresponded to wheat groups 1 and 3, to which most of the 24 tested lines appeared to be ascribable (Jia et al. 2002; Zhang et al. 2010). Both RFLP and SSR markers

revealed as well rearranged chromosomes, of frequent occurrence in cross-pollinated species like *L. racemosus* (Qi et al. 1997) and *L. multicaulis* (Jia et al. 2002; Zhang et al. 2010; see Sect. 11.2). Curiously, all the added/translocated chromosomes of the 24 lines illustrated above appeared to belong to only one of *Leymus*genomes, namely Xm, of yet unknown origin (Wang 2011). Conversely, of Ns genome likely derivation are the three *L. mollis* chromosomes substituted into the $2n=42$ line selected among F5 progenies from the cross of an octoploid *Tritileymus* amphiploid (*T. aestivum*×*L. mollis*, $2n=56$) with *T. durum* (Zhao et al. 2013). The retained *L. mollis* chromosomes belong to homoeologous groups 1, 5 and 6. The triple alien substitution line, meiotically stable and well compensated, is remarkably resistant to stripe rust and of convenient short stature; thus, it can be employed as a bridge parent in wheat breeding via chromosome engineering.

Desirable genes for wheat improvement have also been identified in species of the genus *Agropyron* (P genome, Table 11.1) (Han et al. 2014 and references therein). A series of disomic addition lines was obtained from the cross of a Chinese accession of tetraploid *A. cristatum* with common wheat cv. Fukuhokomugi (Wu et al. 2006; Han et al. 2014). In all of them, SSR, EST-SSR and STS markers specific to the *Agropyron* chromosome were primarily related to homoeologous group 6; however, the group 6 markers, mainly located in the 6P pericentromeric region, were not completely identical among the different addition lines. Moreover, there were several markers belonging to other homoeologous groups distally located along the various 6Ps. Such rearrangements, probably differentiating the two P genomes of *A. cristatum* (see Sect. 11.2), led to distinguish four 6P types ($6P_I$–$6P_{IV}$) with different genetic make-up. Among them, $6P_I$ was proved to carry a gene(s) conferring high grain number per spikelet and per spike and also gene(s) for resistance to wheat powdery mildew (Han et al. 2014).

Various novel disease resistance genes have been also identified on specific V^b chromosomes of the perennial tetraploid *D. breviaristatum*. Addition and substitution lines were isolated in the progeny of wheat-*D. breviaristatum* amphiploids crossed with cultivated wheat, including different addition lines carrying genes for stripe rust (Yang et al. 2008), as well as stem rust and powdery mildew (Liu et al. 2011) resistance. Marker data indicated that the V^b chromosomes in the latter two addition lines were rearranged with respect to wheat homoeologous groups. On the other hand, various molecular markers confirmed a group 2 homoeology for the V^b chromosome substituted into a Chinese bread wheat in place of chromosome 2D, able to confer stripe rust resistance at the adult plant stage (Li et al. 2014). Interestingly, FISH, C-banding, and PCR-based molecular marker analyses indicated that the $2V^b$ of *D. breviaristatum* was completely different from $2V^v$ of *D. villosum*, in line with the current view about the origin of 4*x D. breviaristatum* (see Sect. 11.2).

All the addition and substitution lines described above were obtained in the hexaploid background of *T. aestivum*. Development and maintenance of intra- and interspecific aneuploid types is known to be much more difficult at the tetraploid level (reviewed in Ceoloni and Jauhar 2006). Thus, a very limited number of chromosomes of alien species belonging to the secondary and tertiary gene pools (containing

genomes that are nonhomologous to those of wheat) could be stably added to the *T. durum* genome or substituted for its component chromosomes. With the only notable exception of the complete set of D-genome disomic substitution lines, of which a complete set was developed in the variety Langdon, the remaining ones were mostly incomplete and/or of a monosomic type (reviewed in Ceoloni et al. 2005a). However, four out of the seven chromosome pairs of diploid *Th. elongatum* were added to *T. durum* cv. Stewart (Mochizuki 1960, 1962). Isozyme analysis allowed identification of the homoeology of the added chromosomes with those of wheat, showing individual relationship to group 1, 6, 3 and 4 (Ono et al. 1983). More recently, from an initial F_1 hybrid between durum wheat cv. Langdon and a *Th. elogatum* accession tolerant to Fusarium heat blight, subjected to several backcrosses with the durum parent and selfings, a disomic addition line with $2n = 30$ was obtained (Jauhar et al. 2009; Jauhar and Peterson 2011). Molecular markers allowed identification of group 1 homoeology of the added chromosome, hence named 1E, and will be useful in the transfer of the FHB resistance into durum wheat in a more stable chromosomal condition.

11.3.3 Segmental Introgression Lines

The excessive amount of alien genetic material makes the type of cytogenetic stocks described above still unsuited for practical breeding use; they represent, however, potent resources from which further chromosome manipulations can give rise to exploitable products where undesired linkage drag is largely minimized.

Although none of the wheat-alien transfers so far produced has probably equalled the worldwide success of the spontaneous 1BL.1RS wheat–rye translocation (Mujeeb-Kazi et al. 2013), for an appreciable number of the beneficial traits originating from perennial Triticeae the transfer into wheat has reached the final step, i.e., that of a segmental introduction(s) of sub-chromosomal entity, well harmonized with the wheat genomic environment. The most significant progress has been registered in the last few years, in coincidence with the great advancements in molecular genetic, cytogenetic, and genomic tools, and consequent ability to precisely monitor the alien introduction process and finely target the desired outcomes.

As with other alien sources not sharing with wheat completely homologous genomes, various methods have been used to induce translocations or recombination events between wheat chromosomes and those of perennial wheatgrasses and wildryes. While in the early attempts of chromosome engineering the use of radiation-induced-->translocations was almost invariably adopted (e.g., Sharma and Knott 1966; Knott 1968), genetic promotion of intergenomic homoeologous pairing and recombination has been later the method of election, particularly after the isolation of mutants at the *Ph1* locus in both bread (Sears 1977) and durum wheat (Giorgi 1983). In a few instances, exchanges associated with cell culture-induced breakage and fusion (Banks et al. 1995), or the ability of *Aegilopsspeltoides* Ph^I gene(s) to partly inhibit the wheat *Ph1* effect (Wang et al. 2003), were the way followed to

promote transfer of BYDV resistance and, respectively, salt tolerance from addition lines for a group 7 *Th. intermedium* chromosome (7Ai-1) and for a group 5 *Th. junceum* chromosome (AJDAj5). On the other hand, in a number of cases (see ahead) exchange products of potential breeding value have spontaneously occurred, probably as a result of the action of pairing promoting genes present in perennial Triticeaegenomes, which, to various extent, appear to counteract the suppressing effect of wheat *Ph* genes (Dvorak 1987; Zhang and Dong 1995; Jauhar and Almouslem 1998; Jauhar and Peterson 2000; Kang et al. 2008; Mullan et al. 2009). Whatever the method adopted for promoting exchanges, segmental introductions that involved homoeologous chromosomes and were of relatively more limited length gave rise to the best compensating and hence useful products for breeding exploitation.

11.3.3.1 Transfers Involving *Th. intermedium* and *Th. ponticum*

Favoured by the close relationships of their E/J and St basic genomes (Table 11.1) with those of wheat, particularly D and A, *Th. intermedium* and *Th. ponticum*, and so diploid species of the same genus, result the most valuable species contributing to wheat cultivar development among perennial Triticeae, and probably among wild relatives altogether (e.g., Li and Wang 2009; Wang 2011; Mujeeb-Kazi et al. 2013). As for other alien donors, among the many useful genes that have been stably transferred from *Thinopyrum* species into compensating wheat translocation/recombinant lines, the more easily manageable genes conferring disease resistance prevail. Many of these were described in previous extensive reviews (e.g., Mclntosh et al. 1995; Friebe et al. 1996; Li and Wang 2009). In recent years, the list of exploitable resistance sources has widened, with addition of several new genes, and of genes previously included in transfer types unsuitable for breeding use (e.g., associated with excessive alien chromatin amount).

Introgressions from *Th. intermedium*

As to *Th. intermedium*, transfers into wheat include *Pm40* (Luo et al. 2009) and *Pm43* (He et al. 2009) for resistance to wheat powdery mildew, a disease toward which the donor species shows complete immunity (Wang et al. 2000). Both transfers appeared to consist of a spontaneously occurred cryptic translocation (the former on wheat 7BS, the latter on 2DL), giving rise to cytologically and phenotypically suitable bread wheat lines for use in breeding, especially in humid Chinese environments, where the disease is constantly epidemic. From the same wheat-*Th. intermedium* partial amphiploid used as donor material of the *Pm43* gene, an additional, spontaneous translocation product was recently obtained, consisting of a bread wheat line with a pair of chromosomes 6A carrying a *Th. intermedium* segment which occupies most of the short arm, and contains a gene with dominant inheritance, determining an immune reaction to powdery mildew races collected from

wheat fields of the Southwestern China (Tang et al. 2014). GISH analyses revealed the alien segment to originate from an St chromosome of the *Thinopyrum* donor species, which likely carries numerous *Pm*-type genes on different chromosomes and genomes. Various genes for resistance to rusts were also incorporated into wheat chromosomes within *Th. intermedium* chromosome segments. One such cases is that of the stem rust resistance gene *Sr44* (initially designated as *SrAgi*, Mclntosh et al. 1995), which confers resistance to the Ug99 race complex (Pretorius et al. 2010), and, starting from addition and substitution lines for the complete 7Ai (or 7J) chromosome, has been incorporated into a compensating 7DL.7JS (=7DL.7Ai-1S) Robertsonian translocation (Liu et al. 2013a), as well as into 7AL.7AS-7Ai-1S *ph1b*-induced homoeologous recombinant lines (Khan 2000). Distally located on the long arm of the same 7Ai chromosome, the *Bdv2* gene conferring BYDV resistance is located; several subchromosomal introgressions containing *Bdv2* were obtained, as either cell culture- or radiation-induced translocations (Banks et al. 1995; Crasta et al. 2000), or *ph1b*-induced homoeologous recombinants (Xin et al. 2001) into wheat 7DL. Lines carrying the shortest alien segment (particularly TC14, with just 20 % distal 7DL replaced by 7AiL, see e.g Ayala-Navarrete et al. 2009) have been deployed in breeding in China and Australia (Zhang et al. 2009b; Ayala-Navarrete et al. 2013). Multi-environment yield trials conducted in Australia showed the impact of TC14 on various genetic backgrounds to be generally benign, except for a frequent delayed maturity, which makes this translocation useful in BYDV-prone areas that experience a less pronounced terminal drought (Rosewarne et al. 2015).

An additional highly effective gene toward this relevant viral disease, named *Bdv4*, is located on a *Th. intermedium* chromosome with group 2 homoeology incorporated into the Zhong 5 partial amphiploid and derived substitution lines (see Sect. 11.3.2). A combination of translocations containing *Bdv2* and *Bdv4* is being endeavoured, which would likely confer to wheat an even stronger and more durable resistance than either gene alone, like that expressed by the wheatgrass donor species (Ayala-Navarrete et al. 2009).

Introgressions from *Th. ponticum*

Perhaps even more impacting on breeding are transfers originating from *Th. ponticum*. Among the many genes introduced from this species into the wheat background (see, e.g., Li and Wang 2009; Ceoloni et al. 2014a), one illustrative case of how chromosome engineering can be the key to effective exploitation of desirable alien variation is that of the stem rust resistance gene *Sr26*. As above anticipated (Sect. 11.3.2), a radiation-induced 6AgL-6AL (=6Ae#1) translocation was introduced in Australia and from that many wheat cultivars carrying *Sr26* have been released. However, although *Sr26* still remains effective against all known races of stem rust, including all currently described pathotypes of the Ug99 lineage (FAO 2015), its resistance has only been used commercially in Australia, where use of 6Ae#1-bearing cultivars has been declining over the past two decades. The reason

probably lies in the up to 15 % yield reduction associated with the presence of the 6Ae#1 segment carrying the target gene (Knott 1968; The et al. 1988), a segment that occupies about 90 % of 6AL (Friebe et al. 1996; Dundas et al. 2015). Work was therefore undertaken to reduce the segment size of the 6Ae#1 translocation present in the Australian cv. Eagle by induced recombination with its wheat homoeologues (Dundas and Shepherd 1998; Dundas et al. 2007). By use of biochemical and molecular markers, over 1400 critical individuals were effectively screened, and among them 11 were found to have reduced size of 6Ae#1 chromatin (Dundas et al. 2015). Of the seven proved to carry *Sr26*, five involved chromosome 6A, one 6D and the last an unidentified wheat chromosome. GISH-based physical mapping placed the *Sr26* gene at the distal end of the *Th. ponticum* chromosome arm, and selected recombinant lines with around 30 % of distal 6AgL chromatin have already shown higher grain yields than the recurrent wheat cultivars in preliminary field evaluations (Dundas et al. 2015).

As mentioned before (Sect. 11.3.2), some *Th. ponticum* chromosome regions present the interesting occurrence of more than one useful gene for potential use in wheat. One such case concerns the distal portion of 3AgL arm, harbouring the *Lr24* and *Sr24* genes. Cultivars have been developed mostly from Agent, a spontaneous, compensating translocation carrying both genes in its terminal 3AgL segment, spanning about 30 % of the wheat 3DL arm (Friebe et al. 1996); however, several recombinant lines, involving mostly chromosome 3D but also 3B, were also obtained by genetically induced homoeologous recombination (Sears 1973, 1978). One of the 3BS.3BL-3AgL recombinant lines, carrying about 20 % of distal 3AgL, has been employed in recent years to introduce the two genes on a 3B chromosome of durum wheat (Ceoloni, unpublished). In contrast with the short-term protection provided in North America and South Africa, breakdown of leaf rust resistance conferred by *Lr24* was only detected in Australia after almost 20 years of its extensive exploitation (Park et al. 2002), and the gene can still be useful in resistance gene combinations (Bariana et al. 2007). On the other hand, *Lr24* confers complete immunity to all leaf rust pathotypes spread in China, where was recently tagged by a STS marker for MAS breeding (Zhang et al. 2011b), and in India (Kumar et al. 2010). As to *Sr24*, the gene maintains its efficacy in Australia and in many wheat producing regions worldwide, although some Ugandan "Ug99" pathotypes mutated in recent years to acquire virulence toward *Sr24* (FAO 2015).

Transfers Involving *Th. ponticum* Group 7 Chromosomes

Amongst *Sr* genes effective against all Ug99 races emerged so far, besides *Sr44* and *Sr26* already described, *Sr25* and *Sr43*, both from *Th. ponticum*, have to be recalled. The latter was originally introduced into common wheat in the form of chromosome substitution and translocation lines involving the alien group 7 chromosome, designated $7el_2$, and wheat chromosome 7D (Knott et al. 1977; Kibiridge-Sebunya and Knott 1983). However, even the best of the translocation lines (e.g., KS24-1 or KS24-2 in Kim et al. 1993), turned out to be 7DS.$7el_2$L Robertsonian

translocations, with the complete $7el_2L$ arm determining undesirable linkage drag. Therefore, to eliminate unwanted alien genes, such as one enhancing yellow flour pigmentation (*Yp*) of the recipient bread wheat, a *ph1b*-mediated chromosome engineering strategy was applied to the 7DS-$7el_2S$.$7el_2L$ KS10-2 initial translocation line (Niu et al. 2014). To identify new wheat lines carrying *Sr43* on shortened alien segments, several stem rust resistant plants were screened for dissociation of *Sr43* from one or more of the six codominant SSR markers located on 7DL, and two recombinants with *Th. ponticum* segments of limited size, interstitially located in the subterminal region of 7DL, were eventually isolated. GISH revealed the $7el_2L$ portions to be inferior to 20 % of the recombinant 7DL; however, in both lines the yellow pigmentation was still higher than in wheat control lines, though inferior to the KS10-2 initial translocation line. Moreover, the *Sr43* gene they contain could have a limited deployment because of its temperature-sensitive expression, making the gene largely ineffective at 26 °C (Niu et al. 2014).

No doubt, the most extensively targeted group 7 *Thinopyrum* chromosome is the one originally named 7Ag (Sears 1973) but also $7el_1$ (Sharma and Knott 1966; Knott et al. 1977), because of its nearly complete homology with $7el_2$, as probably deriving from a different accession of the same species. In fact, $7el_1$ and $7el_2$ not only show almost complete pairing (Dvorak 1975; Forte et al. 2014), but also exhibit considerable correspondence in gene content, particularly at the L arm level. Both arms possess genes controlling resistance to leaf rust (*Lr19* on $7el_1L$ and a weaker, unknown *Lr* gene on $7el_2L$), and to stem rust (*Sr25* and *Sr43*, respectively), as well as genes determining yellow flour pigmentation (*Yp*) and Segregation distortion (*Sd*) (reviewed in Ceoloni et al. 2014a). Contrasting phenotypes for reaction to *Fusarium* head blight (FHB) differentiate the two 7el sources, $7el_1$ being susceptible and $7el_2$ bearing a major QTL in the distal end of its long arm (Shen and Ohm 2007; Forte et al. 2014).

The extensive work addressed to traits of $7el_1$ derivation, of both theoretical and practical value, has been enabled by availability of a wide array of translocation and recombinant lines involving this chromosome, produced both in bread and in durum wheat backgrounds. The consistent interest for $7el_1$ transfers was primarily addressed to the *Lr19* gene, conferring a largely effective resistance to wheat leaf rust across time and space (Gennaro et al. 2009 and references therein). Using the $7el_1$(7D) substitution line, named Agrus, as starting material (Sect. 10.3.2), *Lr19* was incorporated into bread wheat cultivars through both irradiation (Sharma and Knott 1966; Knott 1968) and induced homoeologous recombination (Sears 1973, 1978). Among the radiation-induced translocations, the one named T4 (= Agatha), consisting of a 70 % long $7el_1L$ segment inserted onto the wheat 7DL arm (Fig. 11.2a; Dvorak and Knott 1977; Friebe et al. 1996), proved to have a good compensating ability (Friebe et al. 1994).

An additional resistance gene, namely *Sr25*, conferring resistance to several races of wheat stem rust (McIntosh et al. 1976; Knott 1989a), and recently shown to be effective even against Ug99 (Li and Wang 2009; Liu et al. 2010), enhanced the validity of T4. As such, this sizable translocation has been incorporated into several bread wheat varieties, including the CIMMYT cultivar Oasis 86 and various

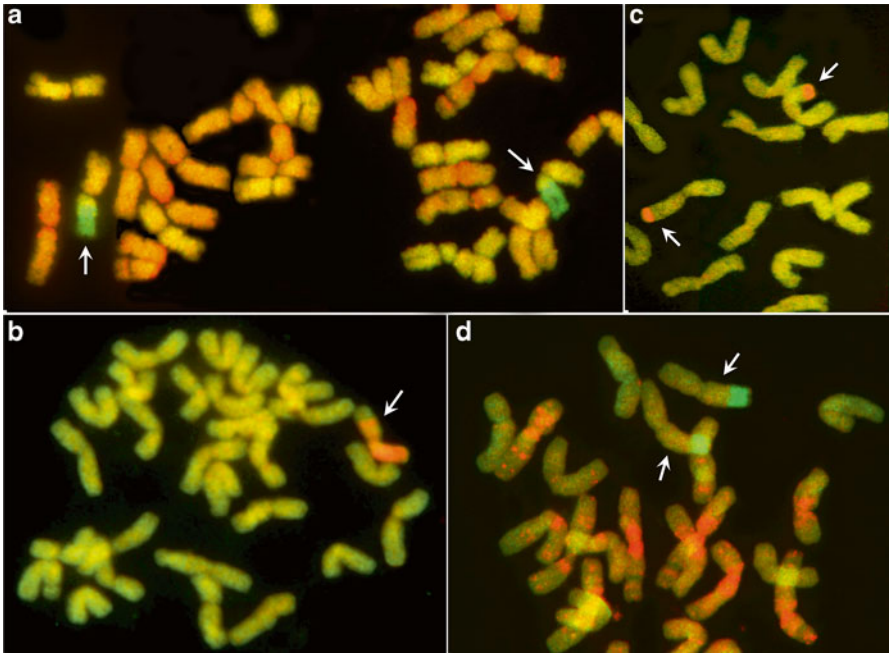

Fig. 11.2 Somatic chromosomes of wheat translocation and *ph1*-induced recombinant lines, carrying different segments of *Thinopyrum ponticum* chromosome 7Ag, subjected to fluorescence GISH, as described in Forte et al. (2014). Total DNAs of wheat and *Th. ponticum* were labelled with different fluorochromes in separate experiments; as a result, *Th. ponticum* DNA is marked by green fluorescence in **a** and **d**, and by red fluorescence in **b** and **c**. In all *plates*, the wheat-*Th. ponticum* chromosomes are *arrowed*. (**a**) Partial metaphase *plate* of the bread wheat T4 translocation line, carrying a pair of 7D chromosomes with 70 % of 7AgL on their long arms; (**b**) Complete metaphase *plate* of a primary durum wheat recombinant, hemizygous for a 7A chromosome with 7Ag chromatin encompassing the entire long arm and about half of the short arm; (**c**–**d**) partial metaphase *plates* of secondary 7A-7Ag durum wheat recombinants, with shortened amounts of 7Ag chromatin compared to the primary recombinant type: R5-2-10, with 23 % 7AgL on distal 7AL (**c**), and R23-1, with 40 % 7AgL on its 7AL arms (**d**)

derivatives still bred in several world Countries endangered by Ug99 (e.g., DRRW 2011), and the Sweden cultivar Sunnan (Mclntosh et al. 1995). In India, the second largest wheat producer in the world after China, with about 12 % share in total world wheat production, cultivars with *Lr19* + *Sr25* have become popular, and besides the rust protection, this alien transfer seems to be associated with slow leaf senescence and increased yield (Sivasamy et al. 2010).

As to the *Yp* gene(s), also associated with *Lr19* and S*r25*, as it is one of its most likely candidates, i.e., *Psy1* (coding for phytoene synthase, required for endosperm carotenoid accumulation, see Gallagher et al. 2004; Pozniak et al. 2007), the current perception by breeders and consumers seems to be changing as compared to the past. In fact, higher carotenoid content in the wheat grain is becoming a desirable trait for the multiple beneficial health effects determined by these compounds,

leaving the aesthetic aspect of the increased flour yellowness of relatively minor importance (Ravel et al. 2013). However, reduction of pigmentation was attempted by various means in past years. By subjecting Agatha (=T4) to EMS treatment, Knott (1980, 1984) produced mutant lines with reduced flour pigment levels but poor agronomic performance (Knott 1984, 1989b): one (Agatha 28-4) was found to carry a point mutation for the *Psy1*-7el$_1$ gene (Zhang and Dubcovsky 2008), the other (Agatha 235-6) has apparently lost a terminal portion of the original 7el$_1$L segment, also including *Sr25* (Friebe et al. 1994), but retains an intact *Psy1*-7el$_1$ gene. A second *Yp* gene, more proximally located along the T4 7el$_1$L segment, is possibly mutated in Agatha 235-6 (Zhang and Dubcovsky 2008). In a recent study (Rosewarne et al. 2015), Australian adapted genetic backgrounds carrying the original T4 translocation or each of Knott's two mutant T4's, were trialled over a wide range of Australian environments and growth conditions. The effects of T4 and mutant 28-4 on yield in the different sites were similar to those of previous reports by CIMMYT, indicating they provide a yield advantage in high yielding, particularly non-moisture-stressed, environments. For both lines the percentage effect of the translocation in comparison to non-T4 lines increased as the site yield increased. By contrast, the mutant 235-6 translocation was not found to provide a yield increase, but rather to cause depression of several yield-related traits even under water-favourable conditions, which suggests the loss of yield contributing gene(s), besides that yellow pigmentation and *Sr25* resistance, in its rearranged 7el$_1$L segment.

Additional white-endosperm, T4 derivatives were also obtained by gamma-ray irradiation (Marais 1992a), and via *ph1b*-induced recombination (Marais 1992b; Prins et al. 1997; Marais et al. 2001; Somo et al. 2014). Through the latter strategy, repeated rounds of homoeologous recombination eventually resulted in production of recombinants with the desired endosperm phenotype, but with their differently sized alien segments relocated from the wheat 7DL arm to 7BL. This event was accompanied by structural aberrations in the region of exchange, which, even in the absence of the *Sd* gene (named *Sd1*, see ahead), might be partly responsible for some detrimental effects on the breeding performance of the carrier lines. However, one recombinant line showed to have the aberrant region replaced by normal wheat chromatin, thus being potentially suitable for breeding exploitation (reviewed in Somo et al. 2014). In all such lines, a second *Sd* gene (named *Sd2*, see Groenewald et al. 2005) was hypothesized to be retained and to cause, similarly to *Sd1*, aberrant segregation of the recombinant chromosomes, particularly through the male germline, as well as negative effects on fertility and seed set. These undesirable *Sd*-associated effects were, however, manifested in heterozygotes only.

In a separate attempt (Zhang et al. 2005), Sears' Transfer#1 primary recombinant line (Sears 1973, 1978) instead of the T4 translocated chromosome was fractionated into various 7D/7el$_1$ secondary recombinant chromosomes. One of the selected recombinants was proved to have lost the very distal *Yp* gene, yet retaining *Lr19* and the proximally associated *Sd1* gene.

Genetic and physical mapping of all the breakpoints present in the several 7D/7el$_1$ translocation/recombinant lines, by means of various molecular markers and genes/phenotypes assigned to deletion bins or chromosome segments revealed

by GISH (e.g., Groenewald et al. 2005), showed substantial synteny and colinearity between the *Th. ponticum* and wheat group 7 chromosomes, and the critical alien genes, with a centromere-*Sd1-Lr19- Yp/Sr25* order, to reside in the distal half of the arm, with the *Lr19*-to-telomere portion spanning about a quarter of it. This type of information is also instrumental to selection of the most suited lines for breeding applications, i.e., in principle, those that possess the minimum amount of alien chromatin exceeding the gene(s) of interest. Such a selection criterion becomes particularly stringent when the recipient species is durum wheat, markedly less tolerant to genic and chromosomal imbalances than hexaploid bread wheat (reviewed in Ceoloni et al. 2005a). For the same reason, chromosome engineering in this *Triticum*species poses more difficulties and has provided, as a whole, a relatively limited number of transfer lines of breeding value (Ceoloni et al. 2014b).

Nonetheless, the *Lr19* + *Sr25* + *Yp* association looked very appealing for a multi-targeted improvement of the durum wheat crop. Therefore, a chromosome engineering strategy, based on the use of the *ph1c* mutant of durum cv. Creso (Giorgi 1983), was specifically targeted to the concomitant incorporation of the three genes into durum wheat (Ceoloni et al. 2005b). Through this approach, assisted by proper selection tools (molecular markers, FISH/GISH), the excessive length of $7el_1$ chromatin present on chromosome 7A of a primary recombinant line (Fig. 11.2b) was sufficiently shortened to give secondary and tertiary recombinant types still carrying all target genes and being well tolerated by the recipient durum genome (Fig. 11.2c, d; Ceoloni et al. 2005b, 2014a). From one of them, named R5-2-10 (Fig. 11.2c), with its 23 % of distal $7el_1$L including *Lr19* + *Sr25* + *Yp* but no *Sd* gene, exhibiting very good agronomic and quality performance (Gennaro et al. 2003, 2007), a variety was released in Italy in 2010 with the name of Cincinnato.

The 7AL-$7el_1$L durum wheat recombinants, for several of which near-isogenic lines (NILs) have been obtained, represented a highly valuable tool to carry out a variety of studies, from integrated genetic and physical mapping of the 7L critical arms, with assignment of numerous markers and genes to several 7L sub-regions, to the analysis of some structural and functional characteristics associated with defined $7el_1$L portions. Among the most meaningful *Th. ponticum* traits that could be detected and precisely evaluated are traits with a great potential to positively impact on yield. Effects on yield parameters started to be associated to $7el_1$L introgression following field trials of NILs carrying the T4 translocation introduced by CIMMYT into the cultivar Oasis 86 and various other bread wheat cultivars (Singh et al. 1998; Reynolds et al. 2001; Monneveux et al. 2003). In all backgrounds, 10–15 % increase in biomass, grain yield and grain number/spike was observed compared to controls lacking the translocation. Through CIMMYT lines, such material has been extensively used in many breeding programs worldwide. However, no precise notion was available on the location along the sizable $7el_1$L segment of the multiple genes/QTL likely underlying the yield-contributing traits. NILs of some of the durum wheat-Th. *ponticum* recombinants developed in the background of the well adapted but rust-susceptible cv. Simeto, helped in gaining this knowledge. NILs of recombinant lines R5-2-10, R112-4 and R23-1, carrying 23, 28 and 40 % distal $7el_1$L, respectively, on the corresponding 7AL arms (Fig. 11.2c, d), have been field-tested in a

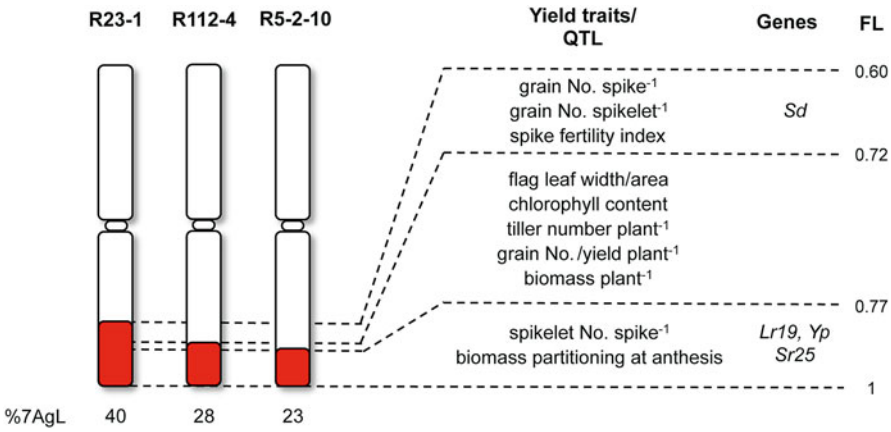

Fig. 11.3 Structural–functional dissection of 7A-7Ag chromosomes representing three durum wheat-*Th. ponticum* recombinant lines. Within the 7AgL regions defined by the different 7AL-7AgL breakpoints in the three chromosome types, known genes (*Lr19*, *Sr25*, *Yp*, *Sd*), and putative genes/QTL for yield-contributing traits could be assigned (adapted from Kuzmanovic et al. 2014 and unpublished). *White background* = 7A, *red background* = 7AgL. *FL* fractional arm length of the breakpoint to centromere distance, from 0 = centromere to 1 = telomere

central Italy environment where durum wheat is typically grown. Significant and differential impacts on relevant yield traits could be detected in homozygous carriers (HOM+) vs. non-carriers (HOM−) of the different $7el_1L$ segments (Ceoloni et al. 2014b; Kuzmanovic et al. 2014). $7el_1L$ genes/QTL determining positive effects on grain and tiller number, grain and biomass yield, flag leaf dimensions and chlorophyll content, were found to be all located within the distal 40 % of the alien arm. Most of them turned out to reside within the 28 %-long $7el_1L$ segment of line R112-4, except for the locus/i controlling grain number per spike and per spikelet, present in the most proximal $7el_1L$ portion of the total 40 % assayed, specific to R23-1 (Fig. 11.3).

Many of the valuable loci detected and confirmed across years appear to be readily exploitable in durum wheat breeding, as they are included in the R112-4 $7el_1L$ segment that has no undesirable linkage drag for the recipient species. Less straightforward may turn out to be the harnessing of the grain number per spike/spikelet locus, in most instances found to be associated with considerably decreased kernel weight and, at times, also depending on the wheat genotype, with other abnormal plant phenotypes. These have been tentatively attributed to the presence, in the same R23-1-specific $7el_1L$ segment, of a *Sd* gene (probably *Sd1*, see also above), determining in durum wheat backgrounds a more or less severe segregation distortion of such a recombinant chromosome, always in the direction of self-elimination through the male germline (Ceoloni et al. 2014a).

Taking advantage of the $7el_1$-$7el_2$ homologous relationships, via homologous recombination in hybrids between translocation/recombinant lines carrying the two long arms or portions of them, useful genes originally present in either one have

been recently assembled in novel combinations in both bread wheat (Shen and Ohm 2007; Zhang et al. 2011a; Forte et al. 2014) and durum wheat backgrounds (Forte et al. 2014). Thus, both species have been equipped not only with *Lr19* + *Yp* + *Sr25* and yield-contributing QTLs of $7el_1L$ origin, but also with a $7el_2L$-derived effective FHB resistance gene/QTL (named *Fhb-7el*$_2$ in Forte et al. 2014). The latter can considerably reinforce resistance to a disease which, favoured by climate changes, has recently become a threat also in unusual environments and toward largely susceptible species, such as durum wheat. In both transfer schemes, the bread wheat 7DS.$7el_2L$ centric translocation line (KS24-1 genotype, see above) was employed as donor of *Fhb-7el*$_2$, while, depending on the target wheat species, the bread wheat T4 translocation onto 7D or durum wheat recombinant lines onto 7A were used as source of the $7el_1L$ genes. In contrast to the nearly complete pairing and recombination between the $7el_1L$ and $7el_2L$ portions shared by the two cross parents of the bread wheat transfer, in *T. aestivum* × *T. durum* pentaploid F_1s considerable reduction in pairing and recombination frequency was observed, mostly ascribable to the location of the parental 7elL portions on otherwise homologous 7D chromosomes vs. 7D and 7A homoeologs in the two F_1 types. Nevertheless, pyramiding of target genes/QTL from the two *Th. ponticum* accessions into both wheat species, greatly assisted by use of advanced selection (MAS) and characterization (GISH) tools, was successfully achieved. Such materials, already exhibiting highly satisfactory agronomic performance (Forte et al. 2014), are expected to lead in the short-term run to durum and also bread wheat cultivars with potential to greatly contribute to enhanced security and safety of the wheat crop.

A highly significant example of multiple *Th. ponticum* gene introgressions with proved positive impact on breeding is that of the Chinese cultivar Xiaoyan 6, in which at least two wheat chromosomes (2A and 7D) carry chromosomal segments from *Th. ponticum* with genes contributing durable resistance to stripe rust and *Septoria tritici* blotch, wide environmental tolerance to high temperature, strong light, and hot-dry winds during grain-filling stages (Li et al. 2008 and references therein). Because of its superior performance under both drought and irrigated conditions, its strong yield stability under diverse environments and good bread-making quality, Xiaoyan 6 was cultivated as the main variety in Shaanxi Province for 16 years (1980–1995). Moreover, Xiaoyan 6 has been used as a core parent for wheat breeding in China in the past 20 years, with more than 50 wheat varieties apparently involving it in their pedigree. These varieties have been grown in more than 20 million hectares, and increased wheat grain production by 7.5 billion kg in total. Thus, Xiaoyan 6 provides an unparalleled example of successful wheat breeding through segmental alien introgression.

11.3.3.2 Additional Introgressions with Actual or Potential Impact on Wheat Improvement

Additional wheat-*Thinopyrum* derivatives have been used in breeding programs to combat major wheat production constraints. One such case concerned the Mayoor and Chirya lines, selected from the intergeneric combination between *T. aestivum*

and *Th. curvifolium* (the latter containing two modified E or J^e/J^bgenomes, see Table 11.1; see also Liu and Wang 1993; Wang 2011), used to develop wheat varieties resistant to the spot blotch disease, caused by *Bipolaris sorokiniana*, in various parts of the world, particularly Central-Southern America and South Asia (Duveiller et al. 1998; Mujeeb-Kazi et al. 2013). Another interesting case is that of a wheat-*Th. disticum* derivative (the latter with a similar genome to that of *Th. curvifolium*, see Liu and Wang 1993), able to confer remarkable salt tolerance to Pakistani and Mexican varieties (see Mujeeb-Kazi et al. 2013).

A potentially appealing resource for wheat breeders has been recently produced which combines genes from two *Thinopyrum* species, namely the already mentioned *Lr19* + *Sr25* from $7el_1L$ of *Th. ponticum*, and the *Bdv2* gene from the closely homoeologous arm 7AiL of *Th. intermedium* (Ayala-Navarrete et al. 2013). Donors of the respective genes to the recombinant translocations were T4 mutant 28-4 (lacking the *Yp* gene, see above), with 70 % of wheat 7DL replaced by *Th. ponticum* chromatin, and TC14, with 20 % distal 7DL replaced by 7AiL (Ayala-Navarrete et al. 2009). Thus, from recombination in a *ph1b* background, desired recombinants were selected by MAS, containing all genes within a single block of alien chromatin as short as the distal 20 % of 7DL chromosome arm (Ayala-Navarrete et al. 2013).

Of similarly limited size was found to be the *Th. elongatum* 3EL segment replacing the most distal 3AL portion in the best of a series of recombinant lines (named 524–568) developed to improve bread wheat salt tolerance (Mullan et al. 2009). Thanks to high-resolution genetic and physical mapping of wheat-alien chromosome breakpoints, coupled with phenotypic analysis of the 3D-3E and 3A-3E recombinant set, the gene(s) responsible for the Na^+ "exclusion" mechanism, previously ascribed to the alien 3E chromosome, turned out to be confined to the distal end of 3EL. This makes line 524–568 a good candidate to obviate or at least alleviate yield penalties caused by high accumulation of Na^+ that modern commercial wheat varieties experience under salinity stress. Interestingly, a comparable level of 3E-wheat group 3 homoeologous recombination was detected in the absence of the wheat *Ph1* gene and under the pairing promoting effect of gene(s) on *Th. elongatum* chromosome 3E, combined with absence of other *Ph* wheat genes on chromosomes 3A and 3D, as in 3E(3A) and 3E(3D) substitution lines (Mullan et al. 2009).

Also in a normal *Ph1* background of the cross progeny to wheat of a wheat-*Th. bessarabicum* amphiploid, a T2JS-2BS·2BL translocation line was recovered (Qi et al. 2010). This, when compared to normal wheat lines, showed enhancement of many yield-related traits, namely more fertile spikes per plant, longer spikes, more grains per spike, and higher yield per plant. At the same time, the quite syntenic replacement included the wheat dominant allele for the *Ppd-B1*, controlling photoperiod response and determining early heading date (Snape et al. 2001). Thus, the T2JS-2BS.2BL translocation line headed considerably later than control lines. However, the size of the 2JS segments could be further engineered to eliminate the undesirable trait(s), and only exploit the positive yield attributes.

Transfers onto wheat of subchromosomal segments from perennial Triticeaegenomes more distantly related to the former than those of *Thinopyrum* spp. have been documented in recent years. One interesting example concerns tetra-

ploid crested wheatgrass, *Agropyroncristatum* (Table 11.1), which, besides genes for disease resistance and stress tolerance, was shown to harbour genes/QTL able to enhance wheat yield performance. Already in addition lines (Wu et al. 2006; Han et al. 2014; see Sect. 11.3.2), and, in translocations lines later obtained (Luan et al. 2010), several useful genes were allocated to *A. cristatum* chromosome 6P; Song et al. 2013; Ye et al. 2015). In particular, genes/QTL enhancing relevant traits such as number of fertile tillers and of grains per spike could be ascribed to specific 6P subregions, and were expressed in translocation lines with minimal amount of 6P chromatin (Luan et al. 2010; Ye et al. 2015). Precise characterization of these lines, including identification of 6P-specific markers, provides a good basis for the utilization of multiple *A. cristatum* genes in wheat improvement.

The same applies to a highly effective stripe rust resistance gene present on chromosome arm 3NsS of *Psathyrostachys huashanica* (Table 11.1), an endemic and endangered wild species in China, stably transferred onto wheat arm 3BS (Kang et al. 2011). The 3BL.3BS-3NsS translocation had a spontaneous occurrence in the selfed progeny of a 3Ns monosomic addition line into wheat. Of spontaneous occurrence were also numerous translocations detected in advanced backcross/selfed generations from a *T. aestivum* x *Elymusrepens* cross, several of which fully expressed the high FHB resistance of the wild parent (Zeng et al. 2013b).

11.4 Concluding Remarks and Future Prospects

The examples above illustrated provide ample evidence of the richness of perennial Triticeae gene pools in beneficial traits for wheat improvement. Recent progress has also been described for many such traits in the path of their stable incorporation into the wheat genome, and, hence, of their well advanced "state of art" in view of practical exploitation as novel breeding materials. Although the history of distant hybridization involving this large group of wheat relatives goes back to the 1930s (Tsitsin 1960), the major progress, as, indeed, for wheat relatives in general, is concentrated in the very last years, in parallel with remarkable advancements in the amount of information and tools for Triticeae genomics and related fields of knowledge. Not only these extraordinary developments have speeded up and made much more effective characterization and selection procedures, but also have considerably increased the ability to capture novel variability for much more complex traits, e.g., yield-related traits, than those almost exclusively targeted in past years. Thus, the answer is now ready to Cox's question of some years ago (Cox 1997), concerning the perspectives for deepening the wheat primary gene pool. He, in fact, while appreciating the fact that "humans have resorted to interspecific crossing to improve wheat's pest resistance," at the same time wondered "…why should wheat's progenitors not be regarded as sources of useful genetic variation for all economic traits?" The rather obvious answer is in the above statements, that is to say we now can manipulate genomes with knowledge and tools virtually inconceivable just a few years ago. As a result, also the overall success of cytogenetic strategies in finely

engineering the genomes of cultivated wheat species has been greatly enhanced. Thus, although the route from the trait identification stage to the output of practical products, ending with varietal release, may well remain relatively long and complex, a holistic and highly effective approach is nowadays applicable; no doubt, this will help to better cope with current and future environmental and social changes, and to meet the requirements for food security and safety sustainably.

In a broader and longer-run perspective, other approaches are expected to complement and even succeed in effecting finer manipulations than those currently achievable by chromosome engineering. In this context, disregarding a number of limitations, the transgenic approach, or perhaps better, where applicable, its cisgenic "version" (Holme et al. 2013), has the advantage of avoiding "linkage drag" potentially associated with cytogenetics-based manipulations. A cisgenesis-mediated transfer of a gene coding for a MYB transcription factor isolated from *Th. intermedium* and conferring to the transformed wheat enhanced resistance to the take-all disease was recently described (Liu et al. 2013b). The number of "wild" genes available for this kind of transfer is expected to rapidly increase in a short-term run, as whole genome sequences of the wild donors of the A and D genomes to polyploidy wheats are already available (Jia et al. 2013; Ling et al. 2013). Further, to preferentially target genic regions and greatly reduce the repetitive sequence content of large Triticeaegenomes, reduced representation-based approaches are available (Hirsch et al. 2014), and, among them, exome capture has been recently demonstrated to be a powerful approach for variant discovery in cultivated barley and related species (Mascher et al. 2013), as well as in rice and in polyploid wheat species (Saintenac et al. 2011; Winfield et al. 2012; Henry et al. 2014). For species with large genome size, such as cultivated wheats and the many polyploid perennial taxa discussed in the present context, an exome-wide basis can be cost-effective and high-throughput. In fact, even if a reference sequence is not available, a transcriptome assembly can be performed at relatively low cost and can serve as a starting point for the design of capture targets for any species (Henry et al. 2014). Furthermore, progress in chromosome genomics, i.e., genome analysis using chromosome-based approaches, allowed by high-throughput flow sorting technology and recently empowered by the high discriminatory capabilities of FISH labeling (Giorgi et al. 2013), enables isolation of pure chromosome fractions from virtually any genome, including the complex ones of polyploid wheats and of related Triticeae species (reviewed in Doležel et al. 2014; see also Chap. 13 in this book). Thus, specific alien chromosomes, or even recombinant/translocated wheat-alien chromosomes as those described in Sect. 11.3.3, can be the "substrate" for a highly focused exome capture or other gene-targeted approaches. Desirable variant alleles from a given donor species thus identified, can, on one hand, be made available for cisgenic manipulations, although these will retain their inherent drawback of random insertion and unpredictable expression of the delivered gene in the recipient genome. On the other hand, they can also serve as externally supplied DNA templates for targeted gene/allele correction or replacement via recent "genome editing" approaches, holding good promise also in a breeding perspective (reviewed in Podevin et al. 2013).

In conclusion, there is ample consensus on the absolute need that intensification of agricultural production necessary to "close the yield gap," particularly crucial in the wheat case, has to imply a package of measures that only a changing landscape of breeding strategies can successfully harness. Technical or other types of limitations will have to be overcome before the latest ground-breaking strategies will be in place. Fortunately, however, several novel wheat materials, many reinforced with valuable genes from perennial Triticeae, have been developed in which yet untapped potential for breeding gains has been effectively unlocked, and many more are expected to be readily available in the near future. This effort, coupled with the ever paramount contribution of traditional breeding to incorporate the beneficial transfers into elite and adapted cultivars, will hopefully soften the highly complex scenario threatening mankind's staple wheat crop.

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