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REVIEW

Diploid and tetraploid tall wheatgrasses: valuable wild relatives of wheat at risk from taxonomic lumping, assumptions in gap analyses, and habitat loss

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Abstract Wild genetic resources for tetraploid (*Triticum turgidum* L.) and hexaploid (*T. aestivum* L.) wheats include diploid and tetraploid taxa from the tall wheatgrass morphological complex, which, along with the wheats, are in the Triticeae grass tribe. These wild taxa are caespitose perennials with a littoral circum-Mediterranean distribution and they present several traits increasingly useful for wheat improvement in response to challenges precipitated by climate change. The active taxonomic history of the Triticeae has provided these taxa with a rich synonymy, but in general, they have been lumped, and thus camouflaged, under a single binomial along with two other tall wheatgrass taxa (an octoploid and a decaploid). The diploid and tetraploid taxa are extremely underrepresented or completely missing in germplasm collections. Global concern for security of crop wild relatives has generated efforts at gap analyses for conservation purposes, but issues with underlying distribution data for these taxa have excluded them from lists of threatened species. Their native habitats of saline marshes are being increasingly impacted by development and conversion. For the goal of securing these species in nature with access to their genetic diversity for wheat improvement, the optimum strategy is a combination of documenting the present distribution of these taxa in nature, determining whether they occur in currently protected areas of salt-marsh habitat, and sampling for ex situ conservation. It is in the interest of several national, regional, and international wheat improvement programs and crop wild relative conservation projects that these wheat genetic resources be recognized and conserved appropriately.

Keywords In situ conservation · Ex situ conservation · Genetic resource · Genebank collection · *Lophopyrum* · *Thinopyrum*

Introduction

The descriptive name ‘tall wheatgrass’ has been applied to taxa in the tribe Triticeae (Poaceae) united by the following morphological characters: tall, caespitose plants with elongate, nonfragile spikes with a single spikelet per node, and truncate glumes about half the length or less of the spikelet length. Tall wheatgrasses comprise diploid, tetraploid, octoploid, and decaploid taxa. The taxonomic issues and history involving this group, including relationships to the rhizomatous beach or dune and intermediate wheatgrasses are complex. For comprehensive taxonomic reviews and differing conclusions, see Melderis (1978) and Jarvie (1992) and for a review of the

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taxonomic issues in Triticeae in general (although with a surprising omission of genus *Lophopyrum*) see Barkworth and von Bothmer (2009).

From the standpoint of utilizing crop wild relatives for crop improvement, the key unit is the gene pool in the sense of Harlan and de Wet (1971). The focus of this review is on the diploid and tetraploid tall wheatgrass species in this context and on their utility for crop improvement, rather than dwelling on formal taxonomy. The genus *Lophopyrum* Á.Löve was here adopted for tall wheatgrasses because it sets them unambiguously apart from other wheatgrass taxa. *Lophopyrum* includes diploids ($2n=14$) *L. elongatum* (Host) Á.Löve and *L. haifense* (Melderis) Á.Löve; tetraploids ($2n=28$) *L. scirpeum* (C.Presl) Á.Löve, *L. flaccidifolium* (Boiss & Heldr.) Á.Löve, *L. curvifolium* (Lange) Á.Löve, *L. corsicum* (Hackel) Á.Löve, *L. caespitosum* (C.Koch) Á.Löve, and *L. nodosum* (Nevski) Á.Löve; octoploid ($2n=56$) *Lophopyrum turcicum* (McGuire) McGuire; and decaploid ($2n=70$) *L. ponticum* (Podp.) Á.Löve. All of them have been included at some point in other genera (for example, *Agropyron* Gaertn., *Elymus* L., *Elytrigia* Desv., *Thinopyrum* Á.Löve, and *Triticum* L.). Useful cross-referencing of synonyms can be found in the encyclopedic reports of Löve (1984) and Dewey (1984).

In the context of utilizing tall wheatgrass gene pools as sources of genetic diversity for wheat improvement, it is not realistic to rely on the taxonomic premise of the fixed morphology of a single desiccated type specimen to serve as a proxy for what is a dynamic interplay of genetic diversity and environmental selection pressures relevant to genes for adaptation (the "first artificial deception of systematics", Darlington 1963, p. 133). Boreau (1868) already noted that the primary characters (for example, green versus glaucous color, smooth versus rough rachis, absence, presence, or length of awns) used in taxonomic descriptions of taxa of the genus *Agropyron* in the broad sense of his day might be useful in some determinations, but that they were not likely to be suitable for characterizing species. It will be shown that the reliance on taxonomy for identifying gene pools of tall wheatgrasses has actually impeded capture and evaluation of the genetic diversity of these taxa.

There appear to be at least ten gene pools among tall wheatgrasses: two at the diploid level, six at the tetraploid level, and one each at the octoploid and decaploid levels. Each gene pool reflects its own history of adaptation to specific habitat(s). Following Harlan and de Wet (1971) and Feldman and Levy (2023), the diploid and tetraploid *Lophopyrum* taxa (and likely the octoploid and decaploid taxa as well) can be considered in the secondary gene pool for tetraploid and hexaploid wheat (*Triticum turgidum* L. and *T. aestivum* L., respectively). This is a crucial distinction because the relegation of these taxa to the tertiary gene pool for wheats (e.g., by Landucci et al. (2014)) is one factor that has caused them to be excluded from crop wild relative priority lists (see gap analysis section below).

Ultimately, the value of a crop wild relative does not necessarily derive from concepts of gene pools and taxonomy. That depends on utility of its germplasm for genetic improvement of the crop and factors affecting introgression of the germplasm into the crop, such as prezygotic and postzygotic reproductive barriers, and degree with which chromosomes of the wild relative can be recombined with those of the crop. By these measures, diploid and tetraploid tall wheatgrasses are valuable wild relatives for wheat, as they can be relatively easily hybridized with wheat, their chromosomes can be introgressed into the wheat genome and can be induced to recombine with wheat homoeologous chromosomes (Dvořák 1979). Furthermore, the seven *L. elongatum* chromosomes have conserved the 1:1 homoeologous relationship to the seven chromosomes of the progenitor of the tribe Triticeae (Xu et al. 2020) and can serve, along with the genome of hexaploid wheat parent *Aegilops tauschii* as a reference in comparative genomic research. These properties set the E genome of *L. elongatum* apart even from the closely related J genome of *Thinopyrum bessarabicum* (Săvul. & Rayss) Á. Löve (Wang and Hsiao 1989).

The primary focus of this review is the taxonomic history of the tall wheatgrass complex, utility of the diploid and tetraploid species for wheat improvement, and causes that have led to their underrepresentation in genebanks and in protected habitats. The strategies of gap analyses pursued to prioritize crop wild relatives for conservation are discussed, and it is shown that pitfalls in this approach have the consequence that diploid wheatgrasses receive no or low conservation priority. Finally, strategies for improving the

conservation status of the diploid and tetraploid tall wheatgrasses are considered.

Taxonomic background

Diploid taxa

In 1802, Nicholas Thomas Host described a grass under the binomial *Triticum elongatum*. He collected it from "dry places and places flooded with sea water" along the southeast shores of the Gulf of Trieste between Trieste, in what is now Italy, and Piran, in what is now Slovenia (Host 1802). It was perennial and caespitose with fibrous, 'not-creeping' roots. This taxon journeyed from *Triticum* to *Agropyron* (Palisot de Beauvois 1812) where it remained for about 120 years. During that time, a number of taxa that were somewhat similar morphologically to Host's description were subsumed by many workers under the *Agropyron elongatum* binomial. The *elongatum* specific epithet (in the broad sense that it had assumed over these years) was subsequently transferred to *Elytrigia* (Nevski 1934) and then to *Elymus* (Heneen and Runemark 1972). In contrast, keeping strictly to the description by Host, the *elongatum* epithet was transferred by Löve (1980) to a new genus *Lophopyrum*. Subsequently Dewey (1984) transferred all *Lophopyrum* taxa into *Thinopyrum*, broadening Löve's concept of *Thinopyrum*, but continuing to recognize the difference between the *Lophopyrum* taxa of Löve and the other taxa for which Löve had created the genus *Thinopyrum*, by sequestering the *Lophopyrum* taxa in a new section (section *Lophopyrum*) of *Thinopyrum*. Even workers who followed this enlarged use of *Thinopyrum* continued to recognize the morphological distinctions between the two sections, referring to "the Junceum complex and the Elongatum complex of the genus" (Liu and Wang 1992).

It has been known since 1935 that the taxon matching Host's description and distribution is diploid ($2n = 14$) (Simonet 1935a). Plants of this taxon appear to be primarily autogamous. Diploid plants associated with this name have been reported from other coastal sites in Mediterranean countries (Italy, Greece, southeastern mainland France and Corsica, Crete, Tunisia, and Algeria) and on the Black Sea coast of Bulgaria (Supplementary file 1).

A second diploid taxon, from Israel, was described in 1952 as a variety of *Elytrigia elongata* (*E. elongata* (Host) Nevski var. *haifense* Melderis) in a determination by A. Melderis in Rechinger's documentation of the specimens from the 1930s of G. Samuelsson (Rechinger 1952). The specimen was collected by E. Wall, a colleague of Samuelsson in 1932 in Palestine (now Israel) (Rechinger 1952, p. 304). Subsequently, as part of the move of *Elytrigia elongata* to genus *Elymus*, the taxon became *Elymus elongatus* ssp. *haifensis* (Melderis) Heneen & Runemark and was shown to be diploid ($2n = 14$) (Heneen and Runemark 1972). Subspecies *haifensis* was distinguished from subspecies *elongatus* by shorter glumes, pubescent palea (versus glabrous palea), and pubescent ribs on leaves (versus mostly glabrous leaves) (Rechinger 1952). Löve (1984) elevated the subspecies to a species in *Lophopyrum*, *L. haifense* (Melderis) Á.Löve. In addition to having these morphological distinctions, this taxon is strictly allogamous, lending support to its status as a separate species (McGuire, unpublished).

A third binomial, *Triticum rigidum* Schrad. enters the literature involving tall wheatgrasses beginning with Schrader's description in Flora Germanica (Schrader 1806), but it does not represent another distinct taxon. The type specimen (http://plants.jstor.org/specimen/bm001043973) has been annotated as *Elytrigia elongatum* Nevski in 1990 by JK Jarvie, but by the distribution given by Schrader and those of subsequent floras which report it, it appears that specimens at other ploidy levels are being included under the binomial using the specific epithet *rigidum*.

Tetraploid taxa

In 1820, Carl Bořivoj Presl described a grass under the name of *Agropyron scirpeum* from the coast (in moist peaty places by the sea) at Mondello (near Palermo) in Sicily (Presl 1820). He characterized the roots as creeping (*radice repente*), but Gussone (1827), moving *A. scirpeum* to *Triticum scirpeum* referenced Presl's description, but noted that roots are only slightly creeping (*radice subrepente*). Gussone also added locations in Sicily, not only on the coast at Mondello but also at Termini and inland at Serra di Falco on damp, clayey, salty soils. Later Gussone (1842) elaborated on this taxon and reported that roots were fibrous, scarcely creeping (*radix fibrosa,*

vix repens) and added two more sites in Sicily: at the coast at Catania and on Maretimo Island, just west of Sicily.

The first determination of chromosome number on plants matching the Presl description in morphology and origin was by Breton-Sintes and Cauderon (1978) in plants grown from seeds provided by a botanic garden in Catania, Sicily. Subsequent confirmation came from plants from two locations in Syracuse Province in Sicily (Bartolo et al. 1981). Both investigations reported $2n=28$ for what each called *Agropyron scirpeum,* and Bartolo et al. (1981) emphasized that it should be a species distinct from the morphologically related diploid, *A. elongatum*. Plants with the morphology associated with this name have been reported from other Mediterranean coastal sites in Italy (Supplementary file 1).

While this tetraploid taxon might be derived from one or more diploid taxa, it is not currently typically sympatric in nature with a diploid taxon. This tetraploid taxon has been described in the literature for almost as long as the diploid *L. elongatum*. The two subgenomes making up the genome of tetraploid *L. scirpeum* are diverged from each other so that heterogenetic chromosome pairing in meiosis is rare (Breton-Sintes and Cauderon 1978; Dvořák 1981). The plants are autogamous. Heneen and Runemark (1972) submerged '*Agropyron scirpeum'* (the Sicilian material) to a subspecies of *Elymus elongatus* (*E. elongatus* ssp. *flaccidifolius* (Boiss. & Heldr.) Heneen & Runemark, which also includes tetraploid material they studied from the Aegean. Until more is known about these taxa, it seems best to follow Löve (1984) and let the morphological distinctions used by Heneen & Runemark for subspecies characterization be used to distinguish the tetraploids as separate species: *L. flaccidifolium* (Boiss & Heldr.) Á.Löve, strictly from the Aegean, and *L. scirpeum* with Sicilian and, possibly, also Aegean distributions. Clearly further study of these tetraploids is needed, but unfortunately there is no gene-bank source of accessions of *L. flaccidifolium*.

Autotetraploids apparently arise in nature in diploid tall wheatgrass populations (Charpentier et al. 1986; Jarvie 1989), but meiotic analysis of such plants revealed bivalent-only pairing (Charpentier et al. 1986). In contrast, autotetraploids produced de novo in laboratories from diploid wheatgrasses with the use of colchicine are not fully fertile and show multivalents in meiosis (Charpentier et al. 1986).

Accession PI 547326 in the US NPGS (additional designations Jarvie-15–4 and W6 6985) needs further discussion. It originated from a collection by J. Jarvie in 1988 along the Mediterranean Coast of mainland France and was assumed by him to be diploid (Jarvie 1989). It was one of eight accessions of *Elytrigia elongata* (as he termed it then) that he collected and imported to the USDA ARS Forest and Range Research Laboratory, Logan Utah USA, but only this one (with the Logan designation MA-3–55-69) was accessioned by the US NPGS, as PI 547326. One user of this accession reported it as diploid (Li et al. 2004), but it cannot be determined from that paper whether this was an assumption or whether a chromosome count was made. The earliest documented chromosome number report is $2n=28$ for an early generation of the material at Logan (designated as MA-3–55) that become PI 547326 (Liu and Wang 1993b). Root-tip chromosome counts for two plants grown by the author from seed of accession PI 547326 received from US NPGS in 2012 are also tetraploid, $2n=28$ (see Cytological characterization section below) and both selfed and open-pollinated progeny of those plants and plants from other 2012 seed not counted were stable at $2n=28$.

Jarvie (1989, 1992) noticed in the field during his 1988 collection trip that some sites seemed to have *E. elongata* in two sizes. He suggested the more robust plants were autotetraploid and that they could be mistaken for *E. scirpea* (*Lophopyrum scirpeum*). However, the site of PI 547326 (his site 15) was not one of the sites where he noted the apparently spontaneous autotetraploids (Jarvie 1989). One explanation for the tetraploid chromosome number is that the sample that has been increased and distributed as PI 547326 by the US NPGS came from autotetraploid seeds from the original collection site. Alternatively, if the diploid taxon is prone to production of unreduced gametes and even if this accession was originally diploid, it is possible that with any seed increase taking place from the time it was imported to the USDA ARS Forest and Range Research Laboratory, Logan or following its deposition in the US NPGS, spontaneous autotetraploidy has occurred and the seed currently being distributed from the US NPGS as PI 547326 is tetraploid for that reason.

The other tetraploids, *L. curvifolium*, *L. corsicum*, *L. caespitosum*, and *L. nodosum*, have been very little studied and the investigations that have been done involved only one or two accessions of each species. One accession of *L. curvifolium*, five of *L. caespitosum*, and two of *L. nodosum* were screened for salt tolerance but were not found to be appreciably tolerant (McGuire and Dvořák 1981). *Lophopyrum curvifolium* and *L. corsicum* are endemic and do not have coastal distributions, but are found inland at higher elevations in Spain (Lange 1860) and Corsica (Briquet 1910), respectively. Contandriopoulos (1962) suggested that these two taxa might represent vicarious corresponding taxa in the sense of Löve (1954), having dispersed and diversified from an earlier common origin. Perhaps *L. nodosum*, which also has an inland, higher elevation distribution could be included too. *Lophopyrum caespitosum* does have a coastal distribution in the Crimea along the Black Sea.

Despite the apparent morphological affinity of these four tetraploids with the tall wheatgrass complex, meiotic chromosome pairing and molecular marker analyses indicate that genomes of species outside this group are involved along with the E genome. Karyotype and meiotic analysis (Liu and Wang 1989) indicated that *L. caespitosum* is an allotetraploid with the E genome of the tall wheatgrass complex and the *Pseudoroegneria* genome (designated S at this point by Liu & Wang). More recently this was confirmed by Wang et al. (2017), who, with a molecular probe (designated St_2-80), found tetraploid *L. caespitosum* (*Trichopyrum caespitosum* in their work) was an allotetraploid, having both the St genome (as they designated it, in contrast to the S designation of Liu and Wang 1989) from genus *Pseudoroegneria* and the E genome. The *L. caespitosum* accession used in that work was PI 565003, maintained by the US NPGS as *Thinopyrum caespitosum*, from the Crimean peninsula. Wang et al. also screened *L. scirpeum* with their St_2-80 marker, but this tetraploid involved only the E genome as earlier concluded by Dvořák (1981).

Meiotic chromosome pairing analysis led McGuire (1984) to suggest that *L. curvifolium* was an E-genome tetraploid. Later, building on the premise of Wang and Hsiao (1989) that the E genome of *L. elongatum* and the J genome of *Th. bessarabicum* were two versions of the same basic genome, designating them J^e and J^b, respectively, and with meiotic analyses of additional hybrid combinations, Liu and Wang (1993b) concluded that the genomes of *L. curvifolium* were closer to the J^b genome than to the J^e genome.

Löve (1984) suggested that *L. nodosum* was an E-genome autotetraploid; however, karyotype and meiotic analysis by Liu and Wang (1993a) indicated that *L. nodosum*, like *L. caespitosum,* possesses S and E subgenomes. At this point, *L. scirpeum* and *L. flaccidifolium* appear to be the only E-genome-only tetraploid members of the tall wheatgrass complex.

Octoploid and decaploid taxa

Robust tall wheatgrasses not from the coastal Mediterranean were shown to be decaploid ($2n=70$) (Peto 1930) and octoploid ($2n=56$) (Sapegin 1935). Both the decaploid and octoploid taxa have been crossed with hexaploid wheat (Sapegin 1935; Vakar et al. 1934; Peto 1936) and while the octoploid taxon is understudied, the decaploid is an important source of genes and traits for wheat improvement (for example, resistance to stripe rust (Jiang et al. 2025), *Fusarium* head blight (Yang et al. 2024), and powdery mildew (Yang et al. 2022)). The earliest description and herbarium specimen that unequivocally matched the plants known to be decaploid was that of *Triticum ponticum* as reported by Podpěra (1902). This epithet was adopted for the decaploid taxon first into *Elymus* as a subspecies of *E. elongatus* by Melderis (1978) and as a species in *Lophopyrum* by Löve (1984) with a subsequent transfer to *Thinopyrum* sect. *Lophopyrum* by Dewey (1984).

Multiple authors have noted differences among the diploid, tetraploid, and decaploid tall wheatgrasses in morphology and distribution. Podpěra (1902) in publishing *Triticum ponticum* as a species distinct from the *Triticum elongatum* of Host (1802) emphasized the differences in habitat (steppe versus coastal, respectively) and morphology (glume enervation, leaf blades, and auricles). Simonet (1935a,b) recognized that the diploid plants from the brackish marshes of the Camargue Region of France matched the type description of *Triticum elongatum* of Host (1802), while decaploid plants were stronger and taller and were found in non-coastal regions of the Crimea and Caucasus among other continental locations. Simonet also identified morphological distinctions: the decaploid plants had fewer florets in the spikelets than the diploid plants,

had pubescent internodes, large-anthers, squarely truncated glumes, and weak venation compared to the diploid plants, concluding that the decaploid plants warranted a taxonomic rank other than lumping them within the diploid taxon (Simonet 1935b). Contandriopoulos (1962) distinguished between diploid and decaploid tall wheatgrass taxa on the basis of leaf anatomy, arguing that such differentiation was sufficient for species-level classification. Dewey (1984) recognized morphological differences between the diploid and decaploid taxa and the ecological differences between their habitats and considered it appropriate to have different specific epithets. In contrast, Heneen and Runemark (1972), while noting that the decaploid tall wheatgrass had a distribution (wide ecologic amplitude including loess soils of southern Russia) distinct from that of the diploid and tetraploid (salinic soils at seashores), argued for the continued combining of the decaploid with the diploid and tetraploid taxa as subspecies in *Elymus elongatus* only because they found it hard to tell them apart morphologically, although they did acknowledge that the three taxa (diploid, tetraploid, and decaploid) may ultimately warrant separate species designations.

The octoploid taxon could not be matched unequivocally to any previously published binomial and a specimen grown from seed obtained from US NPGS (PI 179162, originating from Turkey) was described and published as *Elytrigia turcica* (McGuire 1983). This epithet for the octoploid taxon was subsequently transferred to *Lophopyrum* (McGuire in Löve 1984).

Despite the morphological similarities and apparent overlapping of habitats for the octoploid and decaploid taxa, there is no confirmed identification of the sources of the subgenomes of either taxon. However, the E genome of the diploid tall wheatgrass is closely related to two subgenomes of the decaploid (Dvořák 1981) and the St genome seems to be implicated once (Zhang et al. 1996; Wang et al. 2017). Chen et al. (1998) reported that genomic DNA probes from the diploid tall wheatgrass species, the diploid beach or dune wheatgrass species (*Thinopyrum bessarabicum*), and the diploid *Pseudoroegneria strigosa* species in genomic in situ hybridization (GISH) analyses showed *L. ponticum* has three pairs of *L. elongatum* or *Th. bessarabicum* genomes and two pair of genomes related to the S genome of *Ps. strigosa* (equivalent to the St genome of Wang et al. 2017).

Other taxa

While the focus of this review is on the members of the morphologically defined tall wheatgrass polyploid complex, it is possible that the tetraploid, octoploid, and decaploid members may involve other genomes in addition to the E genome of the diploid tall wheatgrass species *L. elongatum* and the S or St genomes noted above. Closely related to the genome of *L. elongatum* is the genome of the diploid species *Thinopyrum bessarabicum* in the beach or dune wheatgrass polyploid complex characterized by rhizomatous dune and shore plants with elongate, fragile spikes with single spikelets per node, and lanceolate glumes greater than half the length of the spikelets. Tetraploid, hexaploid, and octoploid taxa are also known from the beach wheatgrass complex. There have been successful efforts at crossing *Th. bessarabicum* to wheat and creating amphiploids, addition and substitution lines, and introgression lines (Singh et al. 2020). During the searches of genebank holdings for accessions of the diploid and tetraploid tall wheatgrass complex described below, it was apparent that accessions of the diploid beach wheatgrass were also strikingly absent from genebanks. A case can be made for the need for enhanced conservation efforts for *Th. bessarabicum* parallel to this case study of the diploid and tetraploid tall wheatgrasses.

There has been debate on just how close is the relationship between the genomes of *Th. bessarabicum* and *L. elongatum*. Wang and Hsiao (1989) advocated that they are modifications of the same genome based on meiotic pairing data in hybrids involving each diploid to several other taxa. This conclusion of close relationship between these two genomes, led Dewey (1984) as noted above, to combine taxonomically all taxa of both the beach wheatgrass group and the tall wheatgrass group into genus *Thinopyrum*, but as different sections (Dewey 1984). However, the alternative that the two diploid genomes should be considered distinct has been advocated based on meiotic chromosome pairing and chiasma frequency in hybrids between the two diploid species and in amphiploids derived from them (Jauhar 1988) and based on molecular and cytogenetic analyses of the *Th. bessarabicum* genome (Badaeva et al. 2019). Löve's (1984) taxonomic treatment assumed the genomes were distinct and grouped the tall wheatgrasses as taxa of *Lophopyrum* and grouped the beach

wheatgrasses as taxa of *Thinopyrum* and that treatment has been followed here.

Habitats and geographic distributions of diploid and tetraploid tall wheatgrasses

Beginning with the initial descriptions of the taxon subsequently determined to be diploid (Host 1802) and the first-described taxon subsequently determined to be tetraploid (Presl 1820), a number of resources were reviewed from which historical and current distributions and associated habitats of these taxa were obtained (see Supplementary file 1 for details): current and historical floras and species checklists and species descriptions (Host 1802, 1827; Marschall von Bieberstein 1819; Presl 1820; De Visiani 1826; Gussone 1827, 1842, 1843; Bertoloni 1833; Koch 1848; Parlatore 1848; Grenier and Godron 1856; Boissier 1859, 1881; Lange 1860; Willkomm and Lange 1870; Arcangeli 1882; Battandier and Trabut 1902; De Halácsy 1904; Briquet 1910; Rouy 1913; Fiori 1923–1925; Hayek 1932–1933; Nevski 1934; Rechinger 1952; Cuénod 1954; Löve and Löve 1974; Bartolo et al. 1981; Pignatti 1982; Jeanmonod and Gamisans 2013), collection reports (McGuire 1988, unpublished; Jarvie 1989), and research publications (Stebbins and Pun 1953; Contandriopoulos 1962; Schulz-Schaeffer and Jurasits 1962; Heneen and Runemark 1972; Löve 1980; Charpentier et al. 1986, 1988; Balduzzi 2012; Margiotta et al. 2013, 2020; Sciandrello and Tomaselli 2014; Veronico et al. 2017; Sciandrello et al. 2019). As noted earlier, these investigations use differing classifications for these taxa, but in instances where a specimen can be confidently assigned to the type descriptions, a consistent pattern emerges of the habitats and geographic distributions of the taxon.

The diploid tall wheatgrass taxon, *L. elongatum*, is found in circum-Mediterranean and Black Sea littoral zones: coastal marshes and wetlands, edges of brackish lagoons, saline dry places, and places subject to inundation with sea water. The countries in which it was found are Algeria, Croatia, Egypt, France (mainland and Corsica), Greece, Iraq, Italy, Lebanon, Slovenia, Tunisia, Turkey, Ukraine (Crimea), and in the Transcaucasia region (Caucasus from the Black Sea to the Caspian Sea). This latter location and those in Iraq and Crimea seem anomalous in the context of the other geographic locations. All three of these locations came from the *Flora Orientalis* (Boissier 1881), which does not distinguish between *Agropyrum elongatum* and *A. scirpeum*, giving an inclusive geographic range for both, and may also be including specimens of what should be the decaploid tall wheatgrass.

The other diploid tall wheatgrass taxon, *L. haifense*, with morphological characters and a breeding system distinct from *L. elongatum* has a very discrete geographic range in what is modern Israel: coastal salt marshes between Haifa and Acre and at an inland spring (Einot Gibton) and wetland area (Rechinger 1952; Charpentier et al. 1986).

In terms of habitats and distribution, there are four main patterns for tetraploid tall wheatgrass taxa: A. Coastal, brackish marsh and wetland Mediterranean areas of France (mainland and Corsica), Italy (especially on Sicily), and Aegean islands of Greece and coastal Black Sea regions of Bulgaria and Ukraine (*L. scirpeum*); B. Coastal marshy and sandy areas of Greece and its Aegean islands (*L. flaccidifolium*); C. Dry plains and stony slopes of the Crimean peninsula of Ukraine (*L. nodosum*); and D. Inland higher elevation, drier sites in Spain (*L. curvifolium*), the French island of Corsica (*L. corsicum*), and Turkey and the Caucasus region (*L. caespitosum*). Finally, there have been tetraploids described from one of the same habitats in Israel where the diploid *L. haifense* was found (Einot Gibton) as well as at an inland oasis site (Ein Avdat) in the Negev desert. These tetraploid examples were designated as 'tetraploid *Agropyron elongatum*' by Charpentier et al. (1988) and are entered in Supplementary file 1 as "*4x elongatum*".

Lophopyrum elongatum and *L. scirpeum* are the diploid and tetraploid (respectively) tall wheatgrass taxa about which we have the most information as useful crop wild relatives of wheat and their primary habitats are coastal marshes and wetlands. However, these habitats are increasingly at risk from human pressures of agriculture intensification and urban and tourism development (for example, Balduzzi 2012; Veronico et al. 2017; Margiotta et al. 2020). When collecting specifically in 1988 for Triticeae germplasm along the Mediterranean coast of mainland France, Jarvie (1989) noted that land development for tourism was shrinking that coastal habitat for the *elongatum* taxon (*Elytrigia elongata*). Similarly, the author visited sites in 1988 in search of *L. elongatum* along the Adriatic coast of Italy and Slovenia

identified in floras and in the original description of *Triticum elongatum* (Host 1802) and instead of salt marshes found dikes and agricultural production or urban development (McGuire 1988, unpublished collection report). Of the many sites at which the diploid and tetraploid tall wheatgrass taxa were historically found (Supplementary file 1), it is clear that there are fewer sites in which these taxa can be found today. This habitat deterioration or loss means the amount of geographic diversity (and potential genetic diversity) that could have been studied and accessed for these crop wild relatives has been eroded.

Traits of diploid and tetraploid tall wheatgrasses valuable for wheat

Very little screening work has been done on the diploid and tetraploid taxa themselves and most results identifying useful traits have come from investigations beginning with an octoploid amphiploid created in the 1950s between hexaploid wheat and a diploid *L. elongatum* species (Rommel and Jenkins 1959). This amphiploid was widely circulated for cytogenetic and genetic research. Rommel and Jenkins (1959) designated it as 8A206, but it became known as AgCS (Ag for *Agropyron elongatum*, as the diploid wheatgrass parent was known in the 1950s, and CS for Chinese Spring, the hexaploid wheat parent of the amphiploid) (Dvořák and Knott 1974). The E genome in the AgCS amphiploid was the source of addition and substitution lines of the diploid tall wheatgrass chromosomes in hexaploid wheat (Dvořák and Knott 1974; Dvořák 1980; Dvořák and Chen 1984; Tuleen and Hart 1988) that have been used to elucidate the relationships of the *L. elongatum* chromosomes. Unfortunately, Rommel and Jenkins (1959) did not identify the origin of the accession of *L. elongatum* they used in producing the AgCS amphiploid. The unidentified accession could be either an accession of *L. elongatum* from Tunisia which was known to be available in several research labs during the period when the amphiploid AgCS was produced or an accession of *L. elongatum* from Mediterranean mainland France which was also available at the University of Manitoba. The former accession was acquired before 1950 by G.L. Stebbins at the University of California from Y. Cauderon, INRA, France, but originated from 'Ariana, Tunisia' (Stebbins and Pun 1953). As cited by Heneen and Runemark (1972), the second accession was one they studied and had obtained from Jenkins at Manitoba. A further clue comes from McDonald et al. (2001) who report that the *L. elongatum* accession they called 'D', which they obtained from the University of Manitoba to screen for waterlogging tolerance, was definitely not the accession which was the parent of the Rommel and Jenkins 1959 amphiploid (AgCS). However, it cannot be discerned whether the D accession is the same as the accession referenced by Heneen and Runemark (1972). No matter what is the identity of the diploid tall wheatgrass parent of AgCS, every trait identified for it was the result of research done with AgCS or its derivatives.

Traits of diploid and tetraploid tall wheatgrasses useful for wheat are summarized in Table 1. These results are from at most six different accessions of one diploid taxon (*L. elongatum*; see notes a, d, e, h, and j in Table 1) and one accession each of possibly four tetraploid taxa (*L. curvifolium*, *L. scirpeum*, a tetraploid derived from *L. elongatum* from the mainland French Mediterranean coast, and a tetraploid derived from *L. haifense* in Israel; see notes b, c, f, g, and i in Table 1). Accession PI 287739 of *L. curvifolium* used in crosses to wheat by Mujeeb-Kazi et al. (1987) was identified by them as being maintained in the caespitose perennial wheatgrass nursery of Douglas Dewey at Logan Utah USA as *L. curvifolium* from Spain. (Seed from PI 287739 is still available from the US NPGS, however, in that database, even though it has a recorded chromosome number of $2n=28$, it is misidentified as *Thinopyrum intermedium*, which otherwise is a hexaploid species.) A comparison of the limited geographic representation represented by these tetraploid accessions with the wide distributions documented for these taxa in the preceding section (and in Supplementary file 1) emphasizes the very limited extent of the potential genetic diversity that has been investigated.

Representation of tall wheatgrass taxa in genebanks

To assess the representation of tall wheatgrasses in genebanks, three search platforms were used: that of the US NPGS, the Genesys platform, and the Nordic Baltic Genebanks Information System (GeNBIS) (for details of methods and results, see Supplementary file 2). Both the US NPGS and the GeNBIS employ the GRIN-Global database system and search engine. The Genesys platform uses a different search engine

Table 1 Traits and characteristics of *Lophopyrum elongatum* and tetraploid *Lophopyrum* taxa (*L. scirpeum*, *L. curvifolium*, and "*x Th. elongatum*") useful for wheat improvement

Trait	Species	Reference
Stripe rust resistance	*L. elongatum*	Ma et al. 2000[a]; Yang and Ren 2001[a]
	"4x Th. elongatum"	Li et al. 2019[b]; Gong et al. 2023[b], 2024[b]
	"Th. scirpeum"	Gong et al. 2022[b]
Powdery mildew resistance	*"Th. scirpeum"*	Gong et al. 2022[b]
Stem rust resistance, esp. Ug99	*L. elongatum*	Zheng et al. 2014[c]
Fusarium head blight resistance	*L. elongatum*	Shen et al. 2004[a]; Jauhar et al. 2009[d]; Wang et al. 2020[c]; Guo et al. 2023[a]
Cephalosporium gramineum resist	*L. elongatum*	Mathre et al. 1985[e]
Helminthosporium leaf blight resist	*L. curvifolium*	Mujeeb-Kazi et al. 1987[f]
Wheat streak mosaic resistance	*L. scirpeum*	Sharma & Gill 1983[g]
Barley yellow dwarf resistance	*L. elongatum*	McGuire et al. 1995[a,h]; Anderson et al. 2010[a]
	L. scirpeum	Sharma & Gill 1983[g]
Cereal yellow dwarf resistance	*L. elongatum*	Anderson et al. 2010[a]
Mycosphaerella graminicola resist	*L. elongatum*	Anderson et al. 2010[a]
Salt tolerance	*L. elongatum*	McGuire & Dvořák 1981[h]; Dvořák et al. 1988[a]; Omielan et al. 1991[a]
	L. scirpeum	McGuire & Dvořák 1981[i]
Seedling salt stress tolerance	*"4x Th. elongatum"*	Zeng et al. 2023[b]
Waterlogging tolerance	*L. elongatum*	Taeb et al. 1993[a]; McDonald et al. 2001[h]
Perennial life history	*L. elongatum*	Lammer et al. 2004[a]
High molec. weight glutenin variants	*L. elongatum*	Dvořák et al. 1986[a]; Liu et al. 2008[d]; Margiotta et al. 2020[j]

[a]Used *L. elongatum* single-chromosome addition/substitution lines derived from the amphiploid AgCS (Rommel & Jenkins 1959) widely available in North America since the 1950s, which was produced from a cross between hexaploid wheat cultivar Chinese Spring and an unidentified accession of *L. elongatum*

[b]Both "*4x Th. elongatum*" and "*Th. scirpeum* " are designations used for the same tetraploid E-genome source identified by Charpentier et al. 1988 as accession Ae41 of '*4x Agropyron elongatum*' (a wild tetraploid tall wheatgrass) from Ein-Avdat, Negev, Israel that was used in the production of the hexaploid partial amphiploid '8801' (Guo et al. 2015) that was the source of all derived lines studied by Li et al. 2019; Gong et al. 2023, 2024; and Zeng et al. 2023 (calling it "*4x Th. elongatum*") and Gong et al. 2022 (calling it "*Th. scirpeum*")

[c]The "*L. elongatum*" accession was PI 547326, from the Mediterranean coastal area of mainland France, collected by Jarvie 1989 and presumed diploid, but subsequently found to be a tetraploid, possibly autotetraploid. Zheng et al. 2014 specifically noted that accession PI 531718, from Tunisia, showed no resistance to wheat stem rusts. This accession was sequenced by Wang et al. 2020 and was the only true diploid accession among those Zheng et al. screened as "*L. elongatum*" accessions

[d]The *L. elongatum* accession was PI 531719, from the Mediterranean coastal area of mainland France

[e]Two *L. elongatum* accessions were screened, one identified as C3-5–7 from France and the other as '? (diploid) United States', it is possible that the latter was the Ariana Tunisia accession, available in North America since the 1950s

[f]The *L. curvifolium* accession was PI 287739, from Spain, accessed in Dewey's caespitose perennial nursery, Utah; PI 287739 is erroneously identified by the US NPGS as *Thinopyrum intermedium*, an otherwise hexaploid taxon

[g]The *L. scirpeum* accession was identified as *Agropyron scirpeum* from 'Dewey from Europe'

[h]The *L. elongatum* accession was designated D (originally sourced from the University of Manitoba, Winnipeg) and reported by McDonald et al. 2001 not to be the same accession used by Rommel & Jenkins 1959 in the production of the octoploid amphiploid, later to be known as AgCS

[i]The *L. scirpeum* accession was from the Aegean islands (TS-2–21, Dewey)

jWild *Thinopyrum elongatum* populations from southeast Italy (Apulia) coastal sites

and it collects and presents data from providers which include genebanks of the centers and institutes of the CGIAR and other international organizations and national and regional genebanks. The GeNBIS covers the national genebanks in all the Nordic and Baltic countries. In all three systems, the searches were made with all possible specific and subspecific epithets and their orthographic permutations as taxa of the several genera historically used for tall wheatgrass taxa (*Agropyron*, *Agropyrum*, *Elymus*, *Elytrigia*, *Lophopyrum*, *Thinopyrum*, and *Triticum*). A summary of results is presented in (Table 2). There were no available diploid or tetraploid accessions resulting from searches via the Genesys platform or at the GeNBIS.

The US NPGS holds a very small representation of diploid and tetraploid wheatgrass taxa. The two taxa with the most widespread historical and current distribution (coastal marshy habitats in many countries bordering the Mediterranean Ocean, Supplementary file 1) have the most limited current availability: only two accessions for the diploid *L. elongatum* (PI 531717 from France and PI 531718 from Tunisia), one accession for a possible autotetraploid derived from *L. elongatum* (PI 531526, from France), and two accessions of the tetraploid *L. scirpeum* (PI 531749 from Italy-Sicily and PI 531750 from Greece-Aegean islands). Even though the Spanish endemic *L. curvifolium* has a limited geographic range, it is underrepresented with only a single, and taxonomically misidentified, available accession (PI 287739). The five available accessions of *L. nodosum*, endemic to Crimea, may perhaps be considered a modest geographic sampling and the nine available accessions of *L. caespitosum*, ranging from Transcaucasia into Turkey may also be a modest representation. The other target taxa, diploid (*L. haifense*) and tetraploids (*L. flaccidifolium*, *L. corsicum*, and the tetraploid accessions known from Israel), have much more limited geographic distributions, but no available accessions of any of them were found in the US NPGS (Table 2).

Cytological characterization of accessions in genebanks

Seed of accessions designated *Thinopyrum elongatum* (Host) D.R.Dewey, *Th. scirpeum* (C.Presl) D.R.Dewey, *Th. caespitosum* (K.Koch) Zhi W.Liu & R.R.-C.Wang, and *Th. ponticum* (Podp.) Barkworth & D.R.Dewey were requested and received from the US NPGS at various times between 1978 and 2024. Seeds were germinated, root tips were excised, fixed, and stained, and condensed chromosomes in mitotic metaphase cells were counted (based on protocol in Dvořák 1971). For the most part, accessions received from the US NPGS had chromosome numbers corresponding to those provided in the Observation field of the Genetic Resources Information Network (GRIN) database (Table 3). For accessions lacking a chromosome number in the GRIN database, data in Table 3 provided new information. In some cases, new chromosome counts differ from the GRIN-reported chromosome numbers (Table 3). Accession PI 179162 exemplifies the latter situation. It was received as an accession of *Th. elongatum* in the late 1970s and it had a chromosome number of $2n=56$ (Table 3 and McGuire and Dvořák 1981) matching what was reported in the GRIN database. A plant grown from seed of that accession was used as the type specimen for determination of the octoploid species *Elytrigia turcica* (McGuire 1983, synonyms *Lophopyrum turcicum* and *Thinopyrum turcicum*). However, seed from a second distribution of that accession from the US NPGS, in 2012, had the chromosome number $2n=70$. A second example of differing counts is accession PI 229914 received as an accession of *Th. caespitosum* in the late 1970s. It had a chromosome number of $2n=28$ (Table 3 and McGuire and Dvořák 1981), which is expected since *Th. caespitosum* is considered to be a tetraploid species. However, the GRIN-provided chromosome number was $2n=42$, which is not found among the chromosome numbers of species of the tall wheatgrass morphological complex.

Efforts to identify and prioritize crop wild relatives by gap analysis

The case for the value of crop wild relatives (CWRs) for crop improvement has been made many times. The Global Crop Diversity Trust (now Crop Trust), with funding from the Government of Norway, managed a Crop Wild Relatives Project, from 2011 to 2021 (GCDT 2021), with emphasis on the importance of CWRs and the need to collect them in the face of threats in the wild. The CWR Project focused on CWRs of crops covered under the Multilateral System of the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA

Table 2 Accessions likely in the tall wheatgrass morphological complex available from the US National Plant Germplasm System (NPGS) and genebanks of the Genesys platform

Search term[a]	Chromosome number as provided by genebank, determined by author, or inferred from description or distribution	Count of accessions
	US National Plant Germplasm System	
elongata/um/us	$2n=70$	32
	$2n=56$	11
	$2n=42$ (misidentified, not a tall wheatgrass)	11
	$2n=28$	1
	$2n=14$	2
	Unknown, but likely $2n=70$	7
	Total elongata/um/us	*64*
scirpea/um/us	$2n=28$	2
nodosa/um/us[b]	$2n=28$	5
caespitosa/um/us[c]	$2n=28$	9
curvifolia/um/us[d]	$2n=28$	1
corsica/um/us; *flaccidifolia/um/us*		0
pontica/um/us	$2n=70$	6
	$2n=28$	1
	Unknown	2
	Total pontica/um/us	*9*
Thinopyrum sp.	$2n=70$, likely *L. ponticum*	1
	$2n=42$, not likely tall wheatgrass	9
	$2n=28$, likely *L. caespitosum*	1
	$2n=28$, not likely tall wheatgrass	3
	$2n=14$, likely *Pseudoroegneria tauri* ssp. *libanotica*	1
	Unknown, not likely tall wheatgrass	3
	Total Thinopyrum *sp.*	*18*
	Genesys platform[e]	
elongata/um/us	$2n=70$	17
scirpea/um/us; *nodosa/um/us*; *caespitosa/um/us*; *curvifolia/um/us*; *corsica/um/us*; *flaccidifolia/um/us*		0
pontica/um/us	$2n=70$	28
	$2n=56$	2
Thinopyrum sp.	Likely $2n=70$ and *L. ponticum*	10

[a]In addition to searches with specific epithets alone, the results reflect searches using them with all relevant historical genera in Triticeae: *Agryopyron*, *Agropyrum*, *Elymus*, *Elytrigia*, *Lophopyrum*, *Thinopyrum*, and *Triticum*

[b]While in several treatments, this taxon is treated as a subspecies of a species with the epithet of *caespitosa/um/us*, it should likely be raised to the specific level, using the binomial *L. nodosum* for it. In the GRIN database, the distinctiveness of this subspecies (see Jarvie 1992) has been buried since 2012 when all instances of *Thinopyrum caespitosum* ssp. *nodosum* were changed to simply *Th. caespitosum*, with no subspecific distinctions recognized

[c]The count of accessions for this taxon is likely overestimated since several of the accessions were collected in the Crimean peninsula and are possibly accessions of *L. nodosum*, which is endemic to that region

[d]In the GRIN database for US NPGS, this tetraploid accession was listed erroneously as a *Th. intermedium* accession

[e]The Genesys platform also searches all US NPGS genebanks, but these collections were excluded from the results since the US NPGS was searched directly

Table 3 Chromosome numbers of tall wheatgrass accessions, maintained as taxa of genus *Thinopyrum*, available from the US National Plant Germplasm System (NPGS) determined by author for cases where chromosome numbers either were not reported by the USDA Genetic Resources Information Network (GRIN) or where GRIN-reported numbers differed

Accession designation	Chromosome number	
	Reported here or previously	Reported by GRIN
Received as *Th. elongatum:*		
PI 179162[a]	$2n=56$; 1 plant, 22 Apr. 1980[b] $2n=70$; 2 plants, 21 Jun. 2013[c]	$2n=56$[d], 58[e]
PI 368850	$2n=\sim 70$, 6 plants, 22 Apr. 1980[b]	
PI 502358	$2n=70$; 5 plants, 21 Jun. 2013[c]	
PI 502359	$2n=70$; 4 plants, 21 Jun. 2013[c]	
PI 547326[a]	$2n=28$; 2 plants, 21 Jun. 2013[c] & 27 Oct. 2014[c]	
Received as *Th. caespitosum:*		
PI 229914	$2n=28$; 2 plants, 22 Apr. 1980[b]	$2n=42$[d]

[a]Seed received from the US NPGS on two different occasions; [b]McGuire & Dvořák 1981; [c]This paper; [d]Citing Asay 1989; [e]Citing Zheng et al. 2014

Annex I, FAO 2009) and promoted gap analysis techniques to identify CWRs which are missing in ex situ collections, threatened in their natural habitat, and likely to be of use for crop climate change adaptation. *Lophopyrum elongatum* and *L. scirpeum* fit these criteria, yet they have not been identified and targeted by this process (for example, in Italy specifically (Landucci et al. 2014; Magrini et al. 2016; Perrino and Wagensommer 2021) and more generally (Castañeda-Álvarez et al. 2016)).

Gap analyses (efforts to identify geographic areas from which units of genetic diversity are missing in ex situ and in situ conservation programs) typically begin with efforts to avoid excluding any possible CWR taxon, using a broad net including synonyms across regional and national checklists of threatened taxa. When these analyses are used in service to CWR conservation, a subsequent step characterizes the entries in the working list by their 'crop relatedness' status. An important criterion for crop relatedness can be the gene pool concept of Harlan and de Wet (1971), which emphasizes genetic relatedness and crossability of a potential CWR to the crop itself. However, such detailed information is missing for the majority of CWRs and crops. In lieu of this, a proxy measure had been proposed (taxon group, Maxted et al. 2006). The taxon group concept posits that the genetic distance between a crop and a potential CWR is reflected by the accepted taxonomic relationship between them. Maxted et al. acknowledged that taxonomic inconsistencies may render the application of the taxon group concept inadequate and stressed that its primary utility was for situations when nothing else was otherwise known about genetic affinities between a crop and a wild species. Despite this warning, the database manipulations involved in gap analyses at a country or regional scale make a criterion that can be applied broadly very attractive, so in practice, detailed genetic and crossability relationships of specific CWR-crop situations get overlooked if the taxa are in different genera.

Diploid tall wheatgrass has been in a different genus from wheats since its first taxonomic transfer to genus *Agropyron* (Palisot de Beauvois 1812), therefore it becomes readily excluded as a wheat CWR when the taxon group proxy for gene pool is applied. This is doubly ironic, since in the initial definition of gene pools, the diploid tall wheatgrass (as a species of *Agropyron*) was specifically used as an example for a member of the secondary gene pool of wheat (Fig. 2 in Harlen and de Wet 1971) and secondly, because it ignores documented evidence for diploid tall wheatgrass crossability with wheat and alien chromosome transfer and recombination (with the potential for gene transfer) to wheat (e.g., Jenkins and Mochizuki 1957; Rommel and Jenkins 1959; Dvořák 1980; Dvořák and Knott 1974; Hart and Tuleen 1983; Dvořák and Chen 1984; Tuleen and Hart 1988; Xu et al. 2020), which are the distinctive criteria of the

Harlan and de Wet definition of the secondary gene pool (1971).

In the process of producing a prioritized inventory for CWRs in Italy by Landucci et al. (2014), the diploid and tetraploid tall wheatgrass taxa (as species of *Elytrigia: E. elongata* and *E. scirpea*, respectively) emerged, but they were each ranked in the 'C category', meaning 'not being in need of protection or monitoring' for two apparent reasons: First, this study used the taxon group concept as a proxy for the Harlan and de Wet (1971) gene pool concept, which meant the diploid and tetraploid tall wheatgrass taxa as species of *Elytrigia* could not be in the primary, secondary, or even tertiary gene pool categories for wheats (genus *Triticum*). Second, there was no apparent concern for genebank representation because the specific epithet '*elongatum/elongata*' is used broadly to encompass the diploid, octoploid, and decaploid taxa (and sometimes the tetraploid) and the overwhelming presence of decaploid entries under that epithet in tall wheatgrass records in genebanks masked the dearth of diploid and tetraploid taxa.

A later effort to quantify the extent of Italian CWR representation in genebanks began with lists of taxa endemic to Italy, species listed in Annexes of the Habitats Directive 92/43/EEC, and threatened and near threatened taxa from International Union for the Conservation of Nature analyses for Italy and Europe in general (Magrini et al. 2016). The only tall wheatgrass taxon that emerged from these lists was *L. corsicum* (*Elytrigia corsica*, as Magrini et al. designated it). This species, initially described as endemic to Corsica (see above), is apparently also found in Sardinia. By virtue of that 'endemism' and the fact that there is only one accession of it in the Sardinian Germplasm Bank, BiodiversitaSardegna, Cagliari, the species was assigned the lower of the two possible collection priorities of this analysis (Magrini et al. 2016). The diploid and other tetraploid tall wheatgrass taxa were not flagged by this analysis and received no priority for collection.

Finally, the most recent study to assign priority for CWR conservation in Italy did not flag any tall wheatgrass taxa for conservation attention (Perrino and Wagensommer 2021). Following the lead of Landucci et al. (2014) and Magrini et al. (2016), the use of the taxon group proxy for the gene pool concept was employed, eliminating the tall wheatgrasses from further consideration. Thus, three consecutive efforts of gap analysis over seven years failed to capture at least two CWR species able to be crossed with wheat and serve as genetic resources, both of which are underrepresented in genebanks and are threatened in the wild by habitat loss, conversion, or fragmentation.

An exception to the sequential narrowing of the CWR possibilities that resulted from the above gap analyses was the effort to produce an inventory of CWR important for the United States (Khoury et al. 2013). While they followed a path to defining CWRs using the gene pool concept and, when necessary, the taxon group proxy for gene pool, similar to the above-discussed efforts, they recognized an increasing technological ability to make useful gene transfers across wide genetic distances. To accommodate that progress, they broadened their definition of CWR to include the tertiary gene pool, for which the taxon group of differing genera is a proxy. Thus, taxa in genera *Elymus* and *Thinopyrum* were included in their targets of CWR important for wheat. In the end, these wheat CWRs did not end up being listed as 'threatened' CWRs. However, it is a notable precedent that they were not summarily excluded as CWRs by virtue of the taxon group application or perceived tertiary gene pool classification.

Conclusion

None of the current taxonomic treatments for the diploid and tetraploid tall wheatgrasses remedies the concern of their underrepresentation in genebanks and in protected habitats. In fact, lumping them all in genus *Thinopyrum* adds another layer of synonymy, creating more confusion for geneticists and genebank curators. All of the cytogenetic work that supports one or the other of these taxonomic treatments (lumping them into one genus or keeping them separate) was done with a single accession of each of the diploid *Lophopyrum* and *Thinopyrum* taxa in any one publication and no more than three altogether. This underscores the need for a broad study of the within-species genetic and chromosomal diversity of each diploid taxon and the related species with higher chromosome numbers. Key to this is determining the current distributions of these taxa and making genebank collections for use by researchers. The importance of this is exemplified by the work of Margiotta et al. 2020. In a limited portion (Apulian coastal wetlands,

Italy) of the full range of the diploid tall wheatgrass, *L. elongatum* (*Th. elongatum* as used by them) was found in 24 populations (none of which is represented in any of the genebanks surveyed here). The extent of genetic diversity, assessed by biochemical characterization of seed storage proteins, within these populations was high and varied among the populations in positive correlation with the population size. This conclusion argues for greater geographic representation of diploid tall wheatgrass in genebanks.

Gap analyses undertaken to determine the status of representation in ex situ collections and in natural reserves of CWRs have not served to identify these gaps for many taxa of CWRs for wheat. The problem is not with the logic of gap analysis, but with the simplifying assumptions about the targets that define crop wild relatives. Those assumptions (that taxonomy is a proxy for genetic and genomic relationships) should not be relied upon when there is a large body of evidence for the utility of diploid and tetraploid tall wheatgrasses as CWRs for wheat that are dangerously underrepresented in collections or at risk in their native habitats.

The activity most urgently needed is the survey and collection of seed samples of populations of diploid and tetraploid tall wheatgrass taxa throughout their current range with subsequent deposition of seed samples in relevant national, regional, and international genebanks. Concurrently with surveys and seed collection efforts, the status of the habitats themselves should be characterized and monitored. The impacts of development, habitat conversion, habitat fragmentation, and climate change on what are increasingly becoming threatened refuges for native taxa have been documented (Tomaselli et al. 2012; Sciandrello et al. 2019; Margiotta et al. 2020). Many of the habitats in which the diploid and tetraploid tall wheatgrass taxa are found are already recognized with designations of conservation importance (e.g., Veronico et al. 2017; Sciandrello et al. 2019; Margiotta et al. 2020). These conservation efforts could be enhanced if it were more widely understood that a native species of a monitored habitat was also a useful CWR of wheat.

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The author has no relevant financial or non-financial competing interests to disclose.

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