The Biology of *Triticum turgidum* ssp. *durum* (Durum Wheat)

Share this page

Biology Document BIO2006-07: A companion document to Directive 94-08 (Dir94-08), Assessment Criteria for Determining Environmental Safety of Plant with Novel Traits

Table of Contents

Part A - General Information

A1. Background

The Canadian Food Inspection Agency (CFIA) is responsible for regulating the field testing of crop plants with novel traits (PNTs) in Canada. PNTs are defined as a plant variety/genotype possessing characteristics that demonstrate neither familiarity nor substantial equivalence to those present in a distinct, stable population of a cultivated species of seed in Canada and that have been intentionally selected, created or introduced into a population of that species through a specific genetic change. Familiarity is defined as the knowledge of the characteristics of a plant species and experience with the use of that plant species in Canada. Substantial equivalence is defined as the equivalence of a novel trait within a particular plant species, in terms of its specific use and safety to the environment and human health, to those in that same species, that are in use and generally considered as safe in Canada, based on valid scientific rationale.

PNTs may be developed using traditional plant breeding techniques or other methodologies such as recombinant DNA technologies. Regulated field testing is necessary when PNTs are: (1) considered unfamiliar when compared with products already in the market; (2) not considered substantially equivalent to similar, familiar plant types already in use, and regarded as safe.

Before PNTs may be authorized for unconfined release, they must be assessed for environmental safety. The **Regulatory Directive Dir94-08**: *Assessment Criteria for Determining Environmental Safety of Plants with Novel Traits* describes the criteria and information requirements that must be considered in the environmental assessment of PNTs to ensure environmental safety in the absence of confined conditions.

A2. Scope

The present document is a companion document to the **Dir94-08** *Assessment Criteria for Determining Environmental Safety of Plants with Novel Traits*. It is intended to provide background information on the biology of *Triticum turgidum* spp. *durum*, its centers of origin, its related species and the potential for gene introgression into relatives, and details of the life forms with which it interacts. Such species-specific information will serve as a guide for addressing some of the information requirements found in Dir94-08. Specifically, it will be used to determine if there are significantly different/altered interactions with other life forms resulting from the PNT's novel gene products, which could potentially cause the PNT to become a weed of agriculture, become invasive in natural habitats, or be otherwise harmful to the environment.

The conclusions drawn in this document about the biology of *T. durum* only relate to plants of this species with no novel traits.

Part B - The Biology of *Triticum turgidum* ssp. *durum*

B1. General Description, Cultivation and Use as a Crop Plant

Durum wheat (*Triticum turgidum* ssp. *durum*) is a monocotyledonous plant of the *Gramineae* family, and of the *Triticeae* tribe and belongs to the genus *Triticum*. For commercial production and human consumption, durum wheat is the second most important *Triticum* species, next to common wheat (*Triticum aestivum* L.).

Durum is a mid-tall annual grass with flat leaf blades and a terminal floral spike consisting of perfect flowers (Bozzini, 1998). As with common wheat, there are durum wheat varieties that have a semi-dwarf stature. The root system is composed of seminal roots which are produced by the young plant during germination and adventitious roots, which arise later from the basal nodes of the plant to become the permanent root system. The stem is cylindrical, erect, usually hollow, and subdivided into internodes. Some durum wheats have solid stems (Clarke et al., 2002).

Culms (tillers) arise from auxiliary buds at the basal nodes of the main stem. The number of culms formed depends on the variety, growing conditions, and planting density. Under usual field conditions, a plant may produce a total of three culms in addition to the main shoot, although not all will necessarily produce grain (Bozzini, 1988). As with other grasses, durum wheat leaves are composed of a basal portion (the leaf sheath) which envelops the stem, and a terminal portion, which is linear with parallel veins and an acute apex. At the attachment of the leaf sheath is a thin, transparent membrane (ligule) with two small lateral appendices called auricles. The main stem and each culm produce a terminal inflorescence.

The inflorescence of durum wheat is a spike with a rachis bearing spikelets separated by short internodes (Bozzini, 1988). Each spikelet consists of two glumes (bracts) enclosing two to five florets, all borne distichously on a rachilla. Each floret is enclosed by bract like structures called the lemma and the palea. Each floret is a perfect flower, containing three stamens with bilocular anthers and a pistil bearing two styles with feathery stigmas. Mature pollen is fusiform, normally containing three nuclei. Each floret has the potential to produce a one-seeded fruit called a caryopsis. Each seed contains a large endosperm and a flattened embryo located at the apex of the seed and close to the base of the floret.

Durum wheat is best adapted to regions having a relatively dry climate, with hot days and cool nights during the growing season, typical of Mediterranean and temperate climates. Seed germination will occur as low as 2°C, but the optimal temperature is 15°C (Bozzini, 1988). Most durum wheat produced in the world is of spring growth habit; however, durum wheat lines with winter habit (requires vernalization to initiate the transition from vegetative growth to reproductive growth) have been evaluated for production in the southern USA (Domnez et al., 2000; Schilling et al., 2003).

Worldwide, the average area planted annually to durum wheat is approximately 18 million hectares, with production averaging about 30 million metric tonnes annually (International Grains Council, 2002). The European Union (mainly Italy, Spain, and Greece) is the largest durum wheat producer, averaging eight million metric tonnes yearly. Canada is the second largest producer at 4.6 million metric tonnes per year followed by Turkey (4 million metric tonnes) and the USA (3.5 million metric tonnes) (International Grains Council, 2002).

In Canada, durum wheat production occurs in the drier, south central regions of the prairie provinces of Manitoba (2% of Canadian production), Saskatchewan (84% of Canadian production), and Alberta (14% of Canadian production).

Durum wheat is a separate species from the other commercially grown wheat classes grown in Canada (which are almost entirely *T. aestivum* L.), and possesses unique quality characteristics that differentiates durum wheat from other classes of wheat. The principal use of durum wheat grain is the production of semolina for use in pasta products. However, in North Africa, durum is preferred for the production of couscous and bulgur. Traditional breads are also made with durum flour, particularly in Morocco. Durum (derived from the Latin word for hard) has the hardest kernel of all wheats. Durum wheat with high protein content and gluten strength is the preferred choice of processors for producing pasta products. Durum kernels are amber-colored and larger than those of other wheat classes. Also unique to durum is its yellow endosperm, which gives pasta its golden color. Durum wheat with strong gluten characteristics forms strong, non-sticky dough ideal for pasta production. Semolina with strong gluten properties also results in pasta products with superior cooking characteristics. In Canada, two sub-classes of durum wheat are recognized: conventional varieties with moderate gluten strength, and extra-strong varieties with extra-strong gluten properties similar to the USA desert durum (Clarke et al., 2005).

B2. Brief Outlook at Breeding, Seed Production and Agronomic Practices for *Durum Wheat*

In Canada, durum wheat crops are planted in early spring (April-May) and harvested in mid to late summer (August-September). In normal agricultural practice, *T. durum* is generally grown in an integrated crop rotation schedule to prevent the buildup of diseases, insects, and weeds. In western Canada, a number of rotations are possible and may include summer fallow, where fields are not planted to crops and weed growth is limited either through tillage, non-selective herbicide application, or a combination of both. Depending on cultural practices, cropping history, soil texture, available moisture and potential economic return, other crops are grown in rotation with durum wheat in Western Canada and can include barley, oat, canola, mustard, flax, pea, lentil, and chickpea.

B2.1 Breeding of Durum Wheat

The full range of genetic variation of traits related to grain composition and biotic/abiotic stress resistance has not been surveyed in Canadian germplasm, and there is undoubtedly considerable variation that is currently not being exploited. Durum wheat breeders focus on the simultaneous improvement of agronomic performance, disease resistance and grain quality traits. Agronomic traits include grain yield, drought tolerance, disease and insect resistance, straw strength, plant height, resistance to shattering, and harvest ability. Grain quality traits include physical quality traits such as test weight, seed size, and percentage hard vitreous kernels. Processing quality traits include, protein concentration, yellow pigment concentration, grain cadmium concentration, gluten strength, semolina milling properties, and pasta cooking quality and color. There is considerable variation in concentration of metal ions in the grain, which is currently being exploited to breed cultivars with low grain cadmium concentration (J. Clarke et al., 2002). Durum breeders are also breeding to maintain resistance to the wheat rusts, and continue efforts to incorporate stable resistance to the leaf-spotting diseases, seed borne diseases, and fusarium head blight. Resistance to pests such as the orange blossom wheat midge (*Sitodiplosis mosellana*) and the wheat stem sawfly (*Cephus cinctus*) and Hessian Fly (*Mayetiola destructor*) is available (Lamb et al., 2000; Lamb et al., 2002; Clarke et al., 2002) in Canadian durum wheat germplasm and is currently being utilized by Canadian durum wheat breeders in their breeding programs.

The majority of durum wheat varieties grown in North America are pure lines, derived either from repeated cycles of inbreeding, or through the use of double haploid technology (Knox et al., 2002). The process of developing a new variety begins with the generation of F1 hybrids by crossing two or more parents. Breeders must ensure that all parents used in a cross collectively possess the majority of desirable traits wanted in a new variety. In the case of inbreeding populations, the F2 generation is derived from self-pollinating the F1 and exhibits a wide range of genetic differences. Selection of desirable individuals can begin in the F2 generation and continues for a minimum of two generations until individuals produce progeny that are genetically uniform. Some plant breeders may chose not to make selections in the F2, and delay selection until the F3 or F4 generations. Selection at these early stages of the breeding program is usually for those traits with little environmental influence on the level of expression. Selection for complex traits such as grain yield and grain quality will usually commence in the F6 generation when a breeding line is sufficiently uniform. In the cases of doubled haploid technology, either the ovary or developing pollen grains from F1 plants are subjected to tissue culture techniques to develop many haploid plantlets. Following a chromosome doubling treatment with mitotic inhibitors like colchicine, breeding lines are developed that are 100% homozygous. After one or two cycles of seed increase and visual selection, doubled haploid lines are advanced to replicated field trials for assessment of yield and grain quality traits. Regardless of breeding method, performance data from small plots are generated for use in deciding which lines will be advanced. Many breeders use contra-season nurseries or greenhouses to achieve two generations per year to decrease the amount of time required to release a durum wheat variety. The use of molecular markers to assist in selection for "difficult to measure" traits is becoming a routine tool used by durum wheat breeders to increase the efficiency of selection.

Based upon small plot performance data in the F6 generation, wheat lines are chosen for pre-registration trials which are conducted, usually for two years, at 4-6 locations each year. Lines that perform equal to or better then current check varieties are then advanced to registration trials, which are conducted at 10-20 sites over three years. Based on registration trial data, administrative groups such as The Prairie Recommending Committee for Wheat, Rye and Triticale (PRCWRT) will decide whether to support the breeder's application for variety registration. Once a cultivar registration is approved, breeder seed is distributed to seed growers for increase. Breeder seed is increased to foundation seed from which commercial production registered and/or certified seed will be derived (Anonymous, 1994).

B3. Reproductive Biology of *Triticum turgidum* ssp. *durum*

Durum wheat is predominantly a self-pollinating species. During flowering, flowers generally remain closed (cleistogamous flowers), and the three anthers burst and release pollen (anthesis). Flowers may also open prior to pollen release. deVries (1971) reported the duration of time that wheat florets remain open ranged from 8-60 minutes depending on genotype and environmental conditions. Once the anthers dehisce, 5-7% of the pollen is shed on the stigma, 9-12% remains in the anther, and the remainder is dispersed. Wheat pollen generally remains viable for 15-30 minutes. Flowering of the spike can last for three to six days, depending on weather conditions. Flowering generally begins in the basal florets just above the centre of the spike and proceeds towards the apex and base of the spike. Unfertilized florets usually open, exposing the receptive stigma to foreign pollen. The duration of wheat stigma receptivity depends on variety and environmental conditions, but ranges from 6 to 13 days (deVries, 1971). Once, fertilized, the ovary rapidly increases in size. Two to three weeks after fertilization, the embryo is physiologically functional, and able to generate a new seedling (Bozzini, 1988).

There are very few reports measuring outcrossing rates in durum wheat. Outcrossing rates in primarily self-pollinating species can be up as high as 10%, where the rate varies between populations, genotypes and with different environmental conditions (Jain, 1975). Grass populations that normally have outcrossing rates of less than 1% have shown rates of 6.7% in some years (Adams and Allard, 1982). Harrington (1932) measured outcrossing in durum wheat, and reported outcrossing rates no higher than 1.1%, but rates of 5% have been reported (Bozzini, 1988). In hexaploid wheat, average outcrossing range from 0-6.7%, depending on the cultivar (Martin, 1990; Hucl, 1996; Hucl and Matus-Cadiz, 2001). In hexaploid spring wheat, Hucl (1996) has shown that cultivars with higher outcrossing rates tended to have a greater degree of spikelet opening at anthesis. This is likely applicable to durum wheat as well. In durum wheat, outcrossing rates are also dependent on the environment. Humid conditions are favorable to self-pollination whereas outcrossing rates can increase during periods of drought (Bozzini, 1988).

B4. Centers of Origin of Durum Wheat

Wild tetraploid wheats were largely distributed in the Near East when humans started harvesting them in nature (Bozzini, 1988). The large spike and seed size compared to diploid wheats made them much more attractive for domestication. Durum wheat is thought to have originated in present day Turkey, Syria, Iraq, and Iran (Feldman, 2001). Durum wheat is an allotetraploid (two genomes: AABB) with a total of 28 chromosomes (2n=4x=28), containing the full diploid complement of chromosomes from each of its progenitor species. As such, each chromosome pair in the A genome has a homoeologous chromosome pair in the B genome to which it is closely related. However, during meiosis, chromosome pairing is limited to homologous chromosomes by the genetic activity of inhibitor genes. A number of inhibitor genes have been identified, but the *Ph1* gene located on the long arm of chromosome 5B is considered the critical inhibitor gene (Wall et al., 1971).

Based on cytological and molecular analysis, *T. turgidum* subspecies are believed to have originated from the natural hybridization of *Triticum monococcum* L. subsp. *boeoticum* (Boiss.) (synonym: *Triticum urartu*: AA) and an unknown diploid wheat species containing the B genome (Feldman, 1976). Kimber and Sears (1987) suggested that one or more of five diploid species in section *Sitopsis* of *Triticum* may have donated the B genome to the polyploid wheats. Molecular evidence suggests that the genome from *T. speltoides* is most related to the durum and common wheat B genome (Talbert et al., 1995; Khlestkina and Salina 2001). Furthermore, analysis of chloroplast DNA suggests that *T. speltoides* is likely the maternal donor of durum wheat (Wang et al. 1997). The result of this natural hybridization was wild emmer wheat (*Triticum turgidum* ssp. *dicoccoides* (Korn.) Thell) which was later domesticated as emmer wheat (*Triticum turgidum* ssp. *dicoccum* (Schrank) Thell). Emmer wheat spread from the Near East to large areas of the Mediterranean and Middle East, including Egypt and Ethiopia (Bozzini, 1988). Thousands of years of cultivation and selection have resulted in tremendous variability in the tetraploid wheats derived from wild emmer. As a result, a number of subspecies have been characterized, primarily based on morphological features (van Slageren, 1994): *T. turgidum* ssp. *paleocolchicum*, *T. turgidum* ssp. *polonicum*, *T. turgidum* ssp. *turanicum*, *T. turgidum* subsp. *carthlicum*, and *T. turgidum* ssp. *turgidum*, and *T. turgidum* ssp. *durum*. Among all cultivated tetraploid wheats, *T. turgidum* ssp. *durum* is by far the most important.

B5. Cultivated Durum Wheat as a Volunteer Weed

A weed may be defined as any plant growing where it is not wanted. Commercialized durum wheat cultivars are occasionally found in uncultivated fields and roadsides (Thomas et al., 1996). These occurrences usually result from grain dropped during harvest or transport. Plants growing in these environments do not persist and are usually eliminated by mowing, cultivation, and/or herbicide application. Similarly, durum wheat plants can also grow as volunteers in a cultivated field following durum wheat production. These plants are usually eliminated from the subsequent crop via cultivation or the use of grassy-weed herbicides. There are no reports of durum wheat becoming an invasive pest.

Part C - The Close Relatives of *Triticum turgidum* ssp. *durum*

C1. Inter-Species / Genus Hybridization

An understanding of the possible development of hybrids through interspecific and intergeneric crosses between the crop and related species is important in considering the potential environmental impact following the unconfined release of genetically modified *T. turgidum* ssp. *durum*. The development of hybrids could result in the introgression of the novel traits into related species resulting in ecosystem disruption and the related species becoming more weedy.

Durum wheat and *T. turgidum* ssp. *paleocolchicum*, *T. turgidum* subsp. *polonicum*, *T. turgidum* subsp. *turanicum*, *T. turgidum* subsp. *carthlicum*, and *T. turgidum* subsp. *turgidum* are sexually compatible and produce fertile hybrids. While hybridization between durum wheat and related species can occur, no known wild *Triticum* species exist in North America. Hybridization within the genus *Triticum* was reviewed by Kimber and Sears (1987).

C2. Potential for Introgression of Genes from *Triticum turgidum* ssp. *durum* into Relatives

The closest known North American relatives of durum wheat are species within the *Aegilops* genus. Jointed goat grass (*Aegilops cylindrica* Host) is a problem weed in hexaploid winter wheat production, and ranges as far north as Washington, Montana, and Idaho, U.S.A. Other *Aegilops* species that are known weeds in California include: *Ae. crassa*; *Ae. geniculata*; *Ae. ovata*; and *Ae. triuncialis*. *Ae. cylindrica* is more closely related to *T. aestivum* (common bread wheat) than to *T. turgidum* spp. *durum* since it contains the D genome present in *T. aestivum*. Durum wheat does not contain the D genome of *Triticum*. Prazak (2001) reported hybridization between *Ae. cylindrica* and *T. turgidum* ssp. *durum*, but the resulting progeny were sterile. Natural hybridization between *Ae. triuncialis* and *T. turgidum* spp. *durum* has also been reported in Turkey (Mamedov et al., 1996), but these results have not been confirmed.

Both hexaploid and tetraploid wheat have been the subject of considerable research involving interspecific and intergeneric crosses (Sharma and Gill, 1983). However, this work has little relevance to the natural environment as only a few species related to wheat are native to Canada. The stability of the durum wheat genome is the result of genes (*Ph1* and other genes) which restricts chromosome pairing to homologous chromosomes. Furthermore, laboratory techniques such as hand pollination, embryo rescue, and artificial chromosome doubling using meiotic inhibitors are necessary to obtain fertile progeny. For example, under laboratory conditions hybrids between *T. turgidum* ssp. *durum* and *Ae. cylindrica*, *Ae. triuncialis*, *Ae. crassa* and *Ae. ovata* have been reported (Knobloch, 1968; Arzani et al., 2000; Benavente et al., 2001; Prazak, 2001).

In Canada, the most common weedy relative is quack grass (*Agropyron repens*), which is present in all provinces and territories of Canada (Crompton et al., 1988). It is a perennial weedy grass common in the agricultural areas especially in grasslands, cultivated fields, gardens, roadsides and waste places (Frankton and Mulligan, 1993; Alex and Switzer, 1976). Tsitsin (1940) reported hybrids between durum wheat and *A. repens*, but this report is questionable. In laboratory settings, tetraploid wheat has been hybridized with other *Agropyron* species including *A. repens*, *A. elongatum*, and *A. intermedium* (Knobloch, 1968; Schulz-Schaeffer, 1969). Schulz-Schaeffer (1969) indicated that the chromosomes of *Triticum* spp. generally do not pair with the chromosomes of *Agropyrum* indicating that natural gene flow between the two genera is unlikely Furthermore, no known naturally-occurring hybrids or species derived from hybridization of *T. turgidum* ssp. *durum* and *Agropyron* spp. have been reported (Knott, 1960). Other weedy relatives native to North America include *A. bakeri* (includes *A. trachycaulum*, Bakers Wheatgrass), *Hordeum californicum*, *Hordeum jubatum* (Squirreltail Grass), *Elymus angustus* (includes *Leymus angustus*, Altai Wild Rye), *E. canadensis* (Canadian Wild Rye) and *E. virginicus* (Virginia Wild Rye). There is a single report of development of a hybrid between *A. trachycaulum* and *Triticum turgidum* spp. *durum* in laboratory settings (Knobloch, 1968). However, there are no reports of natural hybrids in the literature. Furthermore, no reports of natural hybrids between *Triticum turgidum* spp. *durum* and *H. californicum*, *H. jubatum*, *E. angustus*, *E. canadensis* and *E. virginicus* have been reported.

A well known intergeneric combination involving wheat is triticale (Lukaszewski and Gustafson, 1987) derived from crossing and amphidiploidy between wheat and rye (*Secale cereale* L.). Most triticale is synthesized starting with durum wheat, although hexaploid wheat is also used (Bozzini, 1988). There have been no reports of triticale serving as a bridge for hybridization with other wild grass species.

C3. Occurrence of Related Species of *T. turgidum* ssp. *durum* in Canada

There are no wild Triticum species in Canada (Feldman, 1976). Of the genera most closely related to *Triticum*, only *Agropyron repens* is native and widespread in Canada. Knobloch (1968) cited reports of hybrids between *T. turgidum* ssp. *durum* and *A. repens*, *A. elongatum*, and *A. intermedium*. However, such hybrids are difficult to reproduce, and require manual pollination, embryo rescue, and chromosome doubling to survive and produce viable progeny.

Although present in winter wheat crops in the United States, the weedy relative *Aegilops cylindrica*, is not reported in Canada. However, due to the close proximity of *Ae. cylindrica* weed populations to the Canadian border (Washington State and Idaho), it is currently classified as a noxious weed in British Columbia and included in the Noxious Weed List, under the B.C. Weed Control Act. *Ae. cylindrica* is not listed in Weeds of Canada (Frankton and Mulligan, 1993), nor in Weeds of Ontario (Alex and Switzer, 1976).

The following species are relatives of wheat from the *Triticeae* tribe and have been cited by Knobloch (1968) to produce artificial hybrids when crossed with durum.

- *Agropyron intermedium* (Host) Beauv. **Intermediate Wheatgrass** (naturalized/cultivated)
- *Agropyron elongatum* (Host) Beauv. **Tall Wheatgrass** (cultivated/naturalized)
- *Agropyron dasystachyum* (Hook.) Scribn. **Northern Wheat Grass** (cultivated/naturalized)
- *Agropyron trachycaulum* (Link) Malte. **Slender Wheat Grass** (cultivated/naturalized)
- *Agropyron trichophorum* (cultivated/naturalized)
- *Agropyron cristatum* (L.) Gaertn. **Crested Wheatgrass** (cultivated/naturalized)
- *Leymus arenarius* (L.) Hochst (*Elymus arenarius* L.) **Sea Lyme Grass**, **Strand-Wheat** (naturalized)
- *Leymus mollis* Trin (*Elymus mollis* Trin) **Sea Lyme Grass**, **Strand-Wheat** (native)

All of these species occur in Canada as naturalized and cultivated plants and, in some cases, are used as forage crops. They are adapted to Canada and are known to colonize disturbed habitats such as uncultivated fields and roadside areas. Since the chromosomes from *Agropyron* and *Triticum* do not pair easily, if at all (Schulz-Schaeffer, 1969), it is improbable that fertile hybrids between durum wheat and these relatives occur in nature.

C4. Summary of the Ecology of Relatives of *Triticum turgidum* ssp. *durum*

Ae. cylindrica and *A. repens* are weedy relatives of durum wheat. Both are native to North America, but only *A. repens* is a native species in Canada. *Ae. cylindrica* is included in the provincial Noxious Weed List in British Columbia which helps to limit the spread of this weed into Canada. *A. repens* is listed as a primary noxious weed in the *Weed Seeds Order* (1986) and is a troublesome weedy grass of agricultural areas throughout Canada. It is a relatively easy species to control in crops by the use of selective herbicides.

Part D - Potential Interactions of *Triticum turgidum* ssp. *durum* with Other Life Forms During its Life Cycle in a natural environment

Table 1 is intended to be used to guide applicants in their considerations of potential impacts of the release of a PNT on non-target organisms. The intention is not to require comparison data between the PNT and its *T. turgidum* ssp. *durum* counterpart(s) for all interactions. Depending on the novel trait, applicants might decide to submit data for only some of the interactions. Sound scientific rationale will be required to justify the decision that data would be irrelevant for the remaining interactions. For example, the applicant might choose not to provide data on the weediness potential of the PNT if it can be clearly shown that the novel trait will not affect reproductive or survival characteristics of *T. turgidum* ssp. *durum*, either directly or indirectly. Where the impact of the PNT on another life form (target or non-target organism) is significant, secondary effects may need to be considered.

Table 1. Examples of potential interactions of *T. turgidum* ssp. *durum* with other life forms during its life cycle in a natural environment

"X" indicates the type of interaction between the listed organisms and *T. turgidum* ssp. *durum* (information requirements may be waived if valid scientific rationale is provided).

Other Life Forms	Pathogen	Symbiont or Beneficial Organism	Consumer	Gene transfer
Rust (Leaf Rust: *Puccinia recondita* f. sp. *tritici*)	X			
Stem Rust: *Puccinia graminis* f. sp. *tritici*)	X			
Loose Smut (*Ustilago tritici*)	X			
Fusarium Head Blight (*Fusarium graminearum*)	X			
Fusarium culmorum	X			
Fusarium avenaceum	X			
Leaf Spots (*Pyrenophora tritici-repentis*)	X			
Septoria tritici	X			
Septoria nodorum [also causes Glume Blotch]	X			
Cochliobolus sativus [also causes black point]	X			
Root Rot (Common Root Rot: *Cochliobolus sativus*)	X			
Take-All Root Rot: *Gaeumannomyces graminis*	X			
Fusarium Root Rot: *Fusarium* spp.	X			
Powdery Mildew (*Erysiphe graminis*)	X			
Black Chaff (*Xanthomonas translucens* f. sp. *undulosa*)	X			
Ergot (*Claviceps purpurea*)	X			
[illegible]	[illegible]			

Common Bunt (*Tilletia caries*)	X			
Hessian Fly (*Mayetiola destructor*)			X	
Russian Wheat Aphid (*Diuraphis noxia*)			X	
Orange Blossom Wheat Midge (*Sitodiplosis mosellana*)			X	
Grasshoppers (*Melanoplus sanguinipes*)			X	
Melanoplus bivittatus			X	
Melanoplus packardii			X	
Wheat Stem SawFly (*Cephus cinctus*)			X	
Beneficial Soil Microorgansims		X		
Beneficial Insects/Earthworms		X		
Other *Triticum turgidum* ssp. *durum* plants				X

Part E - Bibliography

Adams WT, RW Allard. 1982. Mating system variation in *Festuca microstachys*. Evolution, 35:591-595.

Alex JF, CM Switzer. 1976. Ontario Weeds. Ontario Ministry of Agriculture and Food Publication 505. 200 pp.

Anonymous. 1994. Regulation and Procedures for Pedigreed Seed Crop Production. Canadian Seed Growers Association Circular 6-94. Ottawa, ON, 97 pp.

Anonymous, Weed Seed Order 1986. Canadian Federal Seeds Act.

Arzani A, MM Poursiahbidi, A Rezai. 2000. Influences of durum wheat and Aegilops genotypes on production of amphihaploid plants. Iran Agric Res., 19: 49-62.

Benavente E, K Alix, JC Dusautoir, J Orellana, JL David. 2001. Early evolution of the chromosomal structure of *Triticum turgidum - Aegilops ovata* amphiploids carrying and lacking the Ph1 gene. Theor Appl Genet., 103 : 1123-1128.

Bozzini A. 1988. Origin, distribution, and production of durum wheat in the world. In Fabriani G and Lintas C (ed). Durum: Chemistry and Technology. AACC, Minnesota, USA. pp 1-16.

Clarke, F.R., Clarke, J.M., and Knox, R.E. 2002. Inheritance of stem solidness in eight durum wheat crosses. Can. J. Plant Sci., 82: 661-664.

Clarke, J.M., Norvell, W.A., Clarke, F.R. and Buckley, W.T. 2002. Concentration of cadmium and other elements in the grain of near-isogenic durum lines. Can. J. Plant Sci. 82:27-33.

Clarke, J.M.; McCaig, T.N; DePauw, R.M.; Knox, R.E.; Ames, N.P.;Clarke, F.R.; Fernandez, M.R.; Marchylo, B.A.; and Dexter, J.E. 2005. Commander Durum Wheat. Can. J. Plant Sci., 85: 901-904.

Crompton CW, J. McNeill, AE Stahevitch, WA Wojtas. 1988. Preliminary Inventory of Canadian Weeds, Technical Bulletin 1988-9E, Agriculture and Agri-Food Canada.

deVries AP. 1971. Flowering Biology of Wheat, Particularly in View of Hybrid Seed Production - A Review. Euphytica, 20:152-170.

Donmez E, RG Sears, JP Shroyer, GM Paulsen. 2000. Evaluation of Winter Durum Wheat for Kansas. Kansas State University Agricultural Experiment Station and Cooperative Extension Service. Publication No. 00-172-S.

Feldman M. 2001. Origin of Cultivated Wheat. In Bonjean AP and Angus WJ (eds) The World Wheat Book: a history of wheat breeding. Intercept Limited, Andover, England, pp 3-58.

Feldman M. 1976. Taxonomic Classification and Names of Wild, Primitive, Cultivated, and Modern Cultivated Wheats. Wheats. In: Simmonds, N.W. (ed)., Evolution of Crop Plants. Longman, London. pp 120-128.

Frankton C, GA Mulligan. 1993. Weeds of Canada. Agriculture Canada Publication. pp 948-217.

Harrington JB. 1932. Natural outcrossing in wheat, oats, and barley at Saskatoon, Saskatchewan. Scientific Agric., 12: 470-483.

Hucl P, M Matus-Cadiz. 2001. Isolation distances for minimizing outcrossing in spring wheat. Crop Sci., 41:1348-1351.

Hucl P. 1996. Out-crossing Rates for Ten Canadian Spring Wheat Cultivars. Can. J. Plant Sci., 76:423-427.

International Grains Council. 2002. World Grains Statistics. pp. 13-17.

Jain SK. 1975. Population structure and the effects of breeding system. In: Frankel, O.H. & Hawkes, J.G. (eds.) Crop Genetic Resources for Today and Tomorrow. Cambridge Univ. Press. pp. 15-36.

Khlestkina EK, EA Salina. 2001. Genome-specific markers of tetraploid wheats and their putative diploid progenitor species. Plant Breeding, 120: 227-232.

Kimber G, ER Sears. 1987. Evolution in the Genus *Triticum* and the Origin of Cultivated Wheat. In: Heyne, E.G. (ed). Wheat and Wheat Improvement. American Society of Agronomy, Madison, WI. pp.-31.

Knobloch IW. 1968. A Checklist of Crosses in The Graminae. Department of Botany and Plant Pathology, Michigan State University, East Lansing, Michigan, U.S.A. pp. 47-52.

Knott DR. 1960. The Inheritance of Rust Resistance. VI. The Transfer of Stem Rust Resistance from Agropyron elongatum to Common Wheat. Can. J. Plant Sci., 41:109-123.

Knox, R.E., Clarke, J.M. and DePauw, R.M. 2000. Dicamba and growth condition effects on doubled haploid production in durum wheat crossed with maize. Plant Breeding 119: 289-298.

Lamb R, McKenzie R, Wise I, Barker P, Smith M, Olfert O. 2000. Resistance to wheat midge, *Sitodiplosis mosellana* (Diptera: *Cecidomyiidae*), in spring wheat (*Gramineae*). Can. Entomol. 132:591-95.

Lamb R, Smith M, Wise I, Clarke P, Clarke J. 2001. Oviposition deterrence to *Sitodiplosis mosellana* (Diptera: *Cecidomyiidae*):a source of resistance for durum wheat (*Gramineae*). Can. Entomol. 133:579-91.

Lersten NR. 1987. Morphology and Anatomy of the Wheat Plant. In: Heyne, E.G. (ed). Wheat and Wheat Improvement. American Society of Agronomy, Madison, WI. pp 33-75.

Lukaszewski, A.J. and Gustafson, J.P. 1987. Cytogenetics of Triticale. In: Janick, J. (ed). Plant Breeding Reviews, Vol. 5., AVI Publishing, New York. pp 41-94.

Mamedov J, N Zencirci, Z Kaya, Y Anikster, WT Adams. 1996. Diversity of *Aegilops* in Azerbaijan. Proceedings of international symposium on in situ conservation of plant genetic diversity, Antalya, Turkey, 4-8 November 1996. pp 189-193.

Martin TJ. 1990. Out-crossing in Twelve Hard Red Winter Wheat Cultivars. Crop Sci, 30:59-62.

Prazak R. 2001. Cross direction for successful production of F1 hybrids between *Triticum* and *Aegilops* species. Plant Breeding Seed Sci., 45: 83-86.

Schilling AS, AO Abaye, CA Griffeya, DE Branna, MM Alleya, TH Pridgena. 2003. Adaptation and Performance of Winter Durum Wheat in Virginia. Agron J., 95: 642-651.

Schulz-Schaeffer J. 1969. The *Triticum* x *Agropyron* hybridization project at Montana State University, Wheat Information Service, No. 30. pp. 26-29.

Schulz-Schaeffer J. 1972. An approach toward the development of hybrid intermediate wheatgrass, Agropyron intermedium (Host) Beauv. J Plant Breed., 67: 202-220.

Schulz-Schaeffer J, B Friebe. 1992. Karyological characterization of a partial amphiploid, *Triticum turgidum* L. var. *durum* x *Agropyron* intermedium (Host) P.B. Euphytica, 62: 83-88.

Sharma H, BS Gill. 1983. Current status of wide hybridization in wheat. Euphytica, 32: 17- 31.

Talbert LE, NK Blake, EW Storlie, M Lavin. 1995. Variability in wheat based on low-copy DNA sequence comparisons. Genome, 38: 951-957.

Thomas AG, RF Wise, BL Frick, L Juras. 1996. Saskatchewan weed survey of cereal, oilseed and pulse crops in 1995. Weed survey series, publication 96-1. Agriculture and Agri-Food Canada, Saskatoon Research Centre, Saskatoon, Canada.

Tsitsin NV. 1940. Distant hybridization-the chief method of breeding. Breeding and Seed Growing 10: 4-7.

van Slageren MW. 1994. Wild wheats: a monograph of Aegilops L. and Amblyopyrum (Jaub. & Spach) Eig (Poaceae). Wageningen Agriculture University Papers 1994(7).

Wall AM, R Ripley, MD Gale. 1971. The position of a locus on chromosome 5B of *Triticum aestivum* affecting homoeologous meiotic pairing. Genet Res., 18: 329-339.

Wang GZ, NT Miyashita, K Tsunewaki. 1997. Plasmon analyses of *Triticum* (wheat) and *Aegilops*: PCR-single-strand conformational polymorphism (PCR-SSCP) analyses of organellar DNA. PNAS., 94: 14570-14577.

Zorunko VI, VM Pylnev, AV Ageeva. 1996. Spontaneous hybridization and its relation to the nature of flowering in winter durum wheat. Nauchnoe obespechenie agropromyshlennogo kompleksa. pp. 57-61.

Date modified: 2014-07-02