The Biology of *Triticum aestivum* L. (Wheat)

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Biology Document BIO1999-01: A companion document to the Assessment Criteria for Determining Environmental Safety of Plant with Novel Traits

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Part A - General Information

A1. Background

The Canadian Food Inspection Agency (CFIA) is 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.

The 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. CFIA's **Directive 94-08** (Dir94-08), entitled "*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**. It is intended to provide background information on the biology of *Triticum aestivum*, its centres of origin, its related species and the potential for gene introgression from *T. aestivum* into relatives, and details of the life forms with which it may interact.

Such species-specific information will serve as a guide for addressing some information requirements of Part D of 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 of natural habitats, or be otherwise harmful to the environment.

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

Part B - The Biology of *T. aestivum*

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

Triticum is a genus of the family *Graminae* (Poaceae) commonly known as the grass family. Of the cultivated wheats, common wheat, *T. aestivum*, is economically by far the most important.

T. aestivum L. as described by Lersten (1987), is a mid-tall annual or winter annual grass with flat leaf blades and a terminal floral spike consisting of perfect flowers. The vegetative state of the plant is characterized by tillers bearing axillary leafy culms. Culms comprise five to seven nodes with three to four foliage leaves. The uppermost, or flag leaf, subtends the inflorescence. Each culm produces an inflorescence or composite spike, the basic unit of which is termed the spikelet. Spikelets are born on a main axis, or rachis, and are separated by short internodes. Each spikelet is a condensed reproductive shoot consisting of two subtending sterile bracts or glumes. The glumes enclose two to five florets which are born on a short axis, or rachilla. Wheat florets contain three stamens with large anthers and the pistil which comprises a single ovary, with a single ovule, two styles, and two branching plumose stigmas at the end of each style.

T. aestivum L. is hexaploid (AABBDD) with a total of 42 chromosomes (2n=42, six times seven chromosomes). Similarly, the different wheat species also contain some multiple of the basic haploid set of seven chromosomes. Modern wheat cultivars are either tetraploid (durum, AABB) or hexaploid (common and club-types, AABBDD).

Wheat probably derived from a wild form of diploid einkorn (*T. monococcum* sensu lato) in an area that bordered the countries of Iran, Iraq, Syria, and Turkey (Feldman, 1976). Tetraploid species evolved first through a combination of hybridization and amphidiploidy between *T. monococcum* and *T. searsii*, where *T. monococcum* is the source of the "A" genome and *T. searsii* the source of the "B" genome. The result was the tetraploid *T. turgidum* (AABB) which later was domesticated as emmer wheat and gave rise to the modern durum wheat cultivars. Hexaploid cultivars originated through a cross between tetraploid *T. turgidum* and *T. tauschii* (source of the "D" genome). Following an amphidiploidy event, a new species, *T. aestivum*, arose with a genome complement of AABBDD.

The cultivation of wheat began with wild einkorn and emmer (Cook and Veseth, 1991). The earliest plant breeding efforts with these wheats probably gave rise to plants with heads that did not shatter to facilitate harvest. Also, hull-less types were selected by early farmers for ease of threshing. In terms of plant adaptation, hexaploid wheat cultivation was adapted to cool climates due to the contribution of winter hardiness traits present on the "D" genome. Wheat plants were further adapted for cultivation in different environments via flowering behaviour. Spring wheat is planted in locations with severe winters and flowers in the same year yielding grain in about 90 days. Winter wheat is grown in locations with less severe winters. Winter wheat will only head after it has received a cold treatment (vernalization) and is therefore planted in the fall and harvested in the spring of the following year. Wheat varieties were adapted for cultivation in dry climates through the introduction of dwarf traits resulting in small plants that required less water yet produced good grain yield. Modern wheat cultivars have been developed to resist various diseases such as rusts and smuts. In addition to disease resistance, wheat breeding also focuses on increasing overall grain yield as well as grain quality (protein and starch).

Wheat is an important cereal grain for export and domestic consumption in many countries throughout the world. In 1995 there were about 11.4 million hectares planted to wheat in Canada. In 1995 over 40 million hectares were planted to the crop in North America. About one third of this area was in Canada. The principal use of wheat grain is the production of flour which, depending on the specific type of wheat, is used in many baked goods. Flour from hard red wheat is used to make bread dough while cakes, pastries, and crackers are made from soft red wheat flour. Flour from hard and soft white wheat is used in the production of oriental noodles. Additionally, hard white wheat flour is desired for making tortillas while soft white wheat flour has many uses including dough for cakes, crackers, cookies, pastries, and muffins. Durum wheat grain is used primarily to make semolina flour which is the basis for pasta production. Wheat is thus categorized into five main market classes. They include the four common wheat classes: hard red winter, hard red spring, soft red winter, and white. Durum is the fifth market class. Additional significant classes include the utility wheats (CPS) and extra strong wheats.

Planting and harvest of a commercial wheat crop depends on the type of wheat grown. Due to the vernalization requirement of winter wheat, it is planted in the early fall (September and October) so that plants can emerge and develop sufficiently prior to onset of winter. During the winter months, winter wheat plants remain in a vegetative, dormant state. Once the temperature begins to rise, the winter wheat plant will resume growth and switch to a reproductive stage resulting in head development. In most areas of North America, a winter wheat crop will be ready for harvest by mid-July. Spring wheat plants do not enter a dormant state, therefore the crop requires approximately 90 days, from planting to harvest. Thus, most North American spring wheat crops are planted in mid-spring (April-May) and harvested in mid to late summer (August-September).

T. aestivum is a cereal for temperate climates. The minimal temperature for germination of *T. aestivum* seeds is between 3 and 4°C. Flowering begins above 14°C. In North America wheat is grown to about 50° latitude. Within Canada, the primary production areas are the prairie provinces of Manitoba, Saskatchewan, and Alberta, although there are some production areas in the eastern provinces. Most wheat grown in the prairies is spring wheat. Winter wheat is produced in eastern provinces. Wheat is the number one food grain consumed directly by humans. A significant amount of wheat is also used for animal feed; mainly of the high-yielding utility wheats and hard red winter types.

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

Bread Wheat

Modern wheat breeding programs focus on the improvement of agronomic and grain quality traits. Agronomic traits include winter hardiness, drought tolerance, disease and insect resistance, straw strength, plant height, resistance to shattering, grain yield, and harvest ability. Grain quality traits include seed shape, colour, test weight, protein concentration and type, starch concentration and type, and flour performance (Knott, 1987).

The majority of wheat varieties grown in North America are pure line, derived from inbreeding. The process of developing a new variety begins with the generation of F1 hybrids. Wheat breeders make many crosses each year in an effort to transfer traits between breeding lines and cultivars. The F2 generation, derived from self-pollinating the F1, exhibits a wide range of genetic differences based upon the genotypes of the parents. Selection of desirable individuals begins in the F2 generation and continues for at least two generations until individuals produce progeny that are genetically uniform. At that point, usually F6, selection for complex traits such as yield and grain quality will commence. Also, once a line is sufficiently uniform, performance data from small plots are generated for use in deciding which lines will be advanced. It should be noted that spring wheat breeding proceeds faster than winter wheat breeding due to the vernalization requirement of winter wheat. Since spring wheat does not require vernalization, breeders can achieve two to three generations per year using nurseries in greenhouses or fields in Southern regions (i.e. California, Arizona) or regions with opposite production seasons (i.e. New Zealand).

Based upon small plot performance data, wheat lines are chosen for pre-registration trials which are comprised of 10 to 20 locations over three years. The data from these trials is used to decide if the line is worthy of registration as a new cultivar. Based on the trial data, administrative groups (i.e. The Prairie Registration Recommending Committee for Grain) will decide whether to support the breeder's application for variety registration. Once a cultivar registration is approved, breeder's 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). Genetic male sterility and fertility restoration systems and/or chemical gametocides are utilized to produce large amounts of F1 hybrid seed for commercial plantings. Several winter wheat hybrids have been commercialized for limited acreage in the United States; no spring wheat hybrids have been commercialized.

In normal agricultural practice, *T. aestivum* is generally used in a crop rotation schedule to prevent the buildup of diseases, insects, and weeds. In western Canada, a number of rotations are possible and may include barley, canola, or flax, depending on the type of soils, culture practices, etc.

B3. The Reproductive Biology of *T. aestivum*

Reproduction of *T. aestivum* is only known in the context of cultivation; dependent on man to harvest and propagate its seed. Wheat is predominantly self-pollinating. In general, outcrossing rates in any species which is primarily selfing may be up to 10% or higher, 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). In wheat, Hucl (1996) found that the frequency of outcrossing for 10 Canadian spring wheat cultivars varied according to the genotype, where the frequency was always lower than 9 per cent. Outcrossing tended to be highest among cultivars with low pollen staining, spikes which tapered at the extremities and with greater spikelet opening at anthesis. Martin (1990) reported outcrossing rates of 0.1-5.6% among winter wheat cultivars and concluded that the semi-dwarf stature of plants did not affect these rates.

Isolation of wheat plants for crossing purposes within the context of plant breeding can be done with greaseproof paper, cellophane bags, or dialysis tubing. Modest spatial isolation (3 metres) is required to prevent outcrossing in the production of foundation seeds in Canada (Anonymous, 1994).

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. Following dehiscence, wheat pollen viability was observed to range between 15-30 minutes. After release, wheat pollen attaches to the stigma branches via a brief electrostatic force followed by absorption of water by the pollen grain through gaps in the stigma cuticle (Heslop-Harrison, 1979). This process enables the pollen tube to grow which in turn facilitates fertilization. The duration of wheat stigma receptivity depends on variety and environmental conditions; the general range is 6-13 days. In general, pollen tube growth is initiated 1-2 hours after pollination followed by fertilization after an additional 30-40 hours (deVries, 1971). However, pollen grains can germinate within minutes after landing on the stigmatic surface with fertilization taking place in less than one hour (personal communication, George Fedak, 1999). The first spikelet to flower is generally in the middle third of the spike and usually near the upper part of this section; the flowering progresses rather rapidly upwards, downwards a little slower. The primary florets of a spikelet flower first, then the secondary and so on. The stamens are smaller and produce fewer pollen grains (1000-3800 per anther; 450,000 per plant) compared to other cereal grasses. According to deVries (1971), this compares to 4 million for rye (*Secale cereale* L.) and 18 million for maize (*Zea mays* L.).

B4. The Centres of Origin of the Species

Although, the origins of wheat is complicated by various taxonomic opinions most researchers consider that modern wheat cultivars were derived from einkorn (*T. monococcum* ssp. *urartu*) and emmer wheat (*T. turgidum*) (Feldman, 1976). Wild einkorn wheat originated in southeastern Turkey where it still grows today. Wild emmer wheat has a similar distribution but also extends into the Mediterranean portions of the middle east. Emmer wheat is often found in mixtures with einkorn wheat. Durum wheat cultivars were derived from domesticated emmer, while common hexaploid wheat originated from a combination of emmer and the diploid *T. tauschii* (donor of the "D" genome). *T. tauschii* is believed to have originated in the northern regions of Mesopotamia thus explaining the evolution of the winter hardiness traits residing on the "D" genome.

B5. Cultivated Wheat as a Volunteer Weed

During the domestication of modern wheat, key traits were modified that benefited early farmers but eliminated the ability of the resulting wheat races to survive in the wild. Plants with heads that did not shatter were favoured due to easier harvest. While farmers benefited by harvesting heads full of grain instead of gathering grain from the ground, the trait placed the wheat plants at a competitive disadvantage to plants of other species which could more efficiently distribute seed. In addition, hull-less type-plants were easier to thresh but exposed the developing seed to environmental extremes.

Despite these disadvantages, plants of modern wheat cultivars are occasionally found in uncultivated fields and roadsides. These occurrences are usually associated with 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, wheat plants can also grow as volunteers in a cultivated field following a wheat crop. These plants are usually eliminated from the crop via cultivation or the use of herbicides.

Manipulation of wheat genetics has led to ever increasing gains in yield and grain quality, while decreasing the ability of wheat to survive in the wild. In fact, after hundreds of years of cultivation in North America and throughout the world, there have been no reports of wheat becoming an invasive pest.

Part C - The Close Relatives of *Triticum aestivum*

C1. Inter-Species / Genus Hybridization

Important in considering the potential environmental impact following the unconfined release of genetically modified *T. aestivum*, is an understanding of the possible development of hybrids through interspecific and intergeneric crosses between the crop and related species. The development of hybrids could result in the introgression of the novel traits into related species resulting in:

- the related species becoming more weedy;
- the introduction of a novel trait into a related species with potential for ecosystem disruption.

Wheat is primarily a self-pollinated crop and therefore there are only a few reports concerning natural cross hybridization with related species and genera. Hybridization within the genus *Triticum* was reviewed by Kimber and Sears (1987). While hybridization between cultivated wheat and related species can occur, no known wild *Triticum* species exist in North America.

There are many examples of successful classical cross-breeding within the genome lineage of *T. aestivum*. Hybridization is possible between all members of the hexaploid lineage (*T. aestivum* ssp. *vulgare*, *T. compactum*, *T. sphaerococcum*, *T. vavilovii*, *T. macha*, and *T. spelta*), as the genomes are identical (Körber-Grohne, 1988). The stability of the hexaploid genome of *T. aestivum* is a result of genes (i.e., Ph1 locus and other genes) which suppress homoeologous pairing. Consequently, the deactivation of the Ph1 locus is an important tool for plant breeders performing interspecific and intergeneric crosses. This can be achieved by using mutants such as Ph3a, Ph3b etc.

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.). There have been no reports of triticale serving as a bridge for hybridization with other wild grass species.

Wheat has been the subject of considerable work involving wide crossing (Sharma and Gill, 1983). However, much of these works will have little relevance to the natural environment as only a few species related to wheat are native to Canada and techniques such as embryo rescue, hand pollination, and use of male sterile plants may be necessary to obtain viable progeny.

C2. Potential for Introgression of Genes from *T. aestivum* into Relatives

The closest known relative to wheat, with species in North America, is *Aegilops*. Jointed goat grass, *Ae. cylindrica*, ranges as far as the north of Washington, Montana, and Idaho, U.S.A. As a weed, *Ae. cylindrica* is only a problem in winter wheat crops. Zemetra *et al.* (1996) reviewed the hybridization between *Ae. cylindrica* and cultivated wheat and concluded that there is little chance of a new weed species emerging due to high levels of sterility. In the case of fertile progeny, plants were phenotypically very similar to wheat, due to substantial chromosomal deletions to the "C" genome of *Ae. cylindrica*. Other *Aegilops* species that are known weeds in California include: *Ae. crassa*; *Ae. geniculata*; *Ae. ovata*; and *Ae. triuncialis*. There are no reports of wheat outcrossing to these species.

In Canada, the most common weedy relative is *Agropyron repens*, quack grass 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). Although Knobloch (1968) cited reports of hybrids between wheat and *A. repens*, these reports are old and questionable.

Cultivated wheat is known to hybridize with other *Agropyron* species (Mujeeb-Kazi, 1995). Hybrids between *T. aestivum* and Intermediate Wheatgrass, *Agropyron intermedium* have been reported in Russia where fertile plants were successfully produced (Tsvelev, 1984). Similarly, Smith (1942) repeatedly obtained fertile progeny from hand pollinations between wheat and *A. intermedium*. These hybrids are of interest, as Intermediate Wheatgrass occurs in Western Canada for use as a range improvement forage grass and as an adventive weedy grass.

Additionally, complex hybrids have been made between wheat and several species of *Agropyron* including *A. curvifolium*, *A. distichum*, and *A. junceum*. All involved deliberate cross-pollinations in greenhouse settings. No known naturally-occurring hybrids have been reported (Knott, 1960). In addition to the above-mentioned *A. intermedium*, Smith (1942) performed artificial pollinations with wheat and many grass species and obtaining fertile hybrids with *A. cristatum*, *A. elongatum*, and *A. trichophorum*.

Other weedy relatives native to North America include *A. bakeri* (includes *A. trachycaulum*, Bakers Wheatgrass), *Hordeum californicum*, *H. jubatum* (Squirrel- tail grass), *Elymus angustus* (includes

Leymus angustus, Altai Wild Rye), *E. canadensis* (Canadian Wild Rye) and *E. virginicus* (Virginia Wild Rye). These native species have formed hybrids with wheat using artificial methods (personal communication, George Fedak, 1999). There are no reports of natural hybrids.

The potential for interspecific and intergeneric gene flow between wheat and other *Triticeae* species under natural conditions is very unlikely in Canada. However, the numerous reports of hybridizations with wheat should be considered when evaluating the potential for the introgression of 'novel traits' from transgenic wheat into wild relatives.

C3. Occurrence of Related Species of *T. aestivum* in Canada

There are no wild *Triticum* species in Canada (Feldman, 1976). Of the genera most closely related to *Triticum*, only one species of the genus *Agropyron* is native and widespread in Canada. Knobloch (1968) cited reports of hybrids between wheat and *A. repens*, however, such hybrids have been found to be difficult to reproduce by manual pollination.

Although present in winter wheat crops in the United States, the weedy relative *Ae. cylindrica*, is not reported in Canada. However, due to the close proximity of *Ae. cylindrica* weed populations to the Canadian border with Washington State and Idaho, it is currently classified as a noxious weed in British Columbia, included in the Noxious Weed List, under the B.C. *Weed Control Act*. *Ae. cylindrica* is not listed in Weeds of Canada, nor in Weeds of Ontario (Frankton and Mulligan, 1993; 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 wheat. They occur in Canada as naturalized and cultivated plants and are used as specialized forage crops or for soil stabilization purposes. These grass species are adapted to Canada and are known to colonize disturbed habitats such as uncultivated fields and roadside areas. It is improbable that hybrids between wheat and these relatives would occur in nature.

- *E. dahuricus* Turcz. ex Griseb. in Ledeb **Dahurian Wild Rye** (introduced/ cultivated)
- *E. junceus* Fisch. **Russian Wild Rye** (cultivated/ naturalized)
- *L. arenarius* (L.) Hochst (*E. arenarius* L.) **Sea Lyme Grass**, **Strand-Wheat** (naturalized)
- *L. mollis* Trin (*E. mollis* Trin) **Sea Lyme Grass**, **Strand-Wheat** (native)
- *A. intermedium* (Host) Beauv. **Intermediate Wheatgrass** (naturalized/ cultivated)
- *A. trichophorum* (cultivated/ naturalized)
- *A. elongatum* (Host) Beauv. **Tall Wheatgrass** (cultivated/ naturalized)
- *A. cristatum* **Crested Wheatgrass** (cultivated/ naturalized)

C4. Summary of the Ecology of Relatives of *T. aestivum*

Ae. cylindrica and *A. repens* are weedy relatives of *T. aestivum*, both native species in North America, where only *A. repens* is a native species in Canada.

In the case of *Ae. cylindrica*, although it is a noxious weed in winter wheat crops in the United States, it is not considered to be a problem in spring wheat which is the main type grown in Canada (Briggle and Curtis, 1987). *Ae. cylindrica* is included in the provincial Noxious Weed List in British Columbia serving to deter the spread of this weed into Canada.

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Part D - Potential Interactions of *Triticum aestivum* with Other Life Forms During its Life Cycle.

Table 1 is intended to guide applicants in their considerations of potential impacts the release of the

PNT in question may have on non-target organisms, but **should not be considered as exhaustive**. Where the impact of the PNT on another life form (target or non-target organism) is significant, secondary effects may also need to be considered.

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

Other Life Forms	Interaction with T. aestivum (Pathogen; Symbiont or Beneficial Organism; Consumer; Gene transfer)
Pseudomonas syringae pv. *atrofaciens* (Basal Glume Rot)	Pathogen
Xanthamonas campestris pv. *translucens* (Black Chaff)	Pathogen
Erwinia rhapontici (Pink Seed)	Pathogen
Corynebacterium tritici (Spike Blight)	Pathogen
Colletotrichum graminicola (Anthracnose)	Pathogen
Ascochyta tritici (includes *A. sorghi*) Ascochyta Leaf Spot	Pathogen
Cephalosporium gramineum (Cephalosporium Stripe)	Pathogen
Tilletia caries (Common Bunt)	Pathogen
Bipolaris sorokinia (includes *Helminthosporium sativum*) Common Root Rot	Pathogen
Scleropthora macrospora Downy Mildew	Pathogen
Tilletia controversa Dwarf Bunt	Pathogen
Claviceps purpurea Ergot	Pathogen
Pseudocerosporella herpotrichoides Eyespot, foot rot	Pathogen
Puccinia spp. Rust	Pathogen
Monographella nivalis (includes *Calonectria nivalis*) Pink Snow Mold	Pathogen
Leptosphaeria herpotrichoides Leptosphaeria Leaf Spot	Pathogen
Sclerotinia borealis	Pathogen

Sclerotinia Snow Mold	
Erysiphe graminis Powdery Mildew	Pathogen
Septoria spp. Speckled Leaf Blotch	Pathogen
Typhula spp. Speckled Snow Mold (Typhula blight)	Pathogen
Gaeumannomyces graminis Take All	Pathogen
Pyrenophora trichostoma Yellow Leaf Spot	Pathogen
Heterodera avenae Cereal Oat Cyst	Consumer
Subanguina radicicola Root Gall	Consumer
Meloidogyne spp. Root Knot	Consumer
Paratrichodorus spp. Stubby Root	Consumer
Pratylenchus spp. Root Lesion	Consumer
Mayetiola destructor Hessian fly	Consumer
Midge	Consumer
Diuraphis noxia Russian Wheat Aphid	Consumer
Beneficial Insects	Symbiont or Beneficial Organism
Soil microbes	Symbiont or Beneficial Organism
Earthworms	Symbiont or Beneficial Organism
Soil Insects	Symbiont or Beneficial Organism
Other *T. aestivum*	Gene Transfer

Part E - Acknowledgments

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Part F - Bibliography

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