

Linum, flax

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1. Taxonomy

1.1. General taxonomy

(Muravenko et al., 2003) undertook genome comparisons with chromosomal and molecular markers for three closely related flax species and their hybrids.

The genus *Linum* L. comprises more than 200 species, including commercially valuable cultivated *Linum usitatissimum* L.

Taxonomy of the genus is complex and questionable (Flora USSR, 1949; Tsvelev, 1996; Tutin et al., 1978). Karyotypic analysis of *Linum* L. species started more than half century ago and allowed several flax species to be recognized (Chennaveeraiah & Joshi, 1983; Harris, 1968; Lewis, 1964; Ray, 1944). It has been observed that chromosome number ranges from 12 to 72 in the genus, and that chromosomes are small (1–4 μ m) and morphologically similar. Although monochrome staining reveals only general karyotypic differences, the results obtained with this method have made it possible to construct a putative phylogenetic tree both for the Old World and for New World species of the genus *Linum* (Chennaveeraiah & Joshi, 1983; Harris, 1968). In addition, intra- and interspecific genetic diversity has been characterized with molecular (RAPD) (Fu, 2005; Fu et al., 2002a; Fu et al., 2003a; Fu et al., 2002b; Fu et al., 2003b; Lemesh et al., 2001; Lemesh et al., 1999a; Lemesh et al., 1999b) and protein (Kutuzova et al., 1999; Mansby et al., 2000) markers, allowing certain taxonomic relationships to be assumed for several flax species. Notwithstanding, there are still numerous questionable issues in taxonomy and phylogeny of the genus *Linum*.

First and foremost, this is true for cultivated *L. usitatissimum* and its close or distant wild relatives, which are commonly assigned to the section *Linum* (Davis, 1967; Flora USSR, 1949; Tutin et al., 1978).

1.2. Taxonomy of *Linum usitatissimum* and related species

Taxonomy of cultivated *L. usitatissimum* and closely related species is rather complex and equivocal. It is believed that *L. usitatissimum* L. was domesticated approximately 6000 years ago (Lay & Dybing, 1989; Zohary & Hopf, 1988), and yet this species is still able to cross with its putative wild ancestor, *Linum angustifolium* Huds. (Gill & Yermanos, 1967a, b; Seetharam, 1972; Seetharam & Srinivas, 1972). The two species

each have 30 chromosomes in the karyotype. The same chromosome number is characteristic of *Linum bienne* Mill., which is also thought to have contributed to the origin of *L. usitatissimum* L. (Lay & Dybing, 1989). However, some authors consider *L. bienne* as a subspecies of *L. angustifolium* Huds., and some others even equate these two species (Flora USSR, 1949; Tutin et al., 1978). On the other hand, there is an opinion that *L. bienne* Mill. is a subspecies of *L. usitatissimum* L. (Chernomorskaya & Ctankevich, 1987). Hence, to eliminate this disagreement, it is necessary to employ modern molecular and cytogenetic techniques. Genetic polymorphism of the above three species has been assessed preliminarily by RAPD analysis [10]. Yet complex genome comparisons with the use of chromosome and molecular markers have not been carried out so far in order to clarify the taxonomic status and phylogenetic relationships of the three closely related flax species.

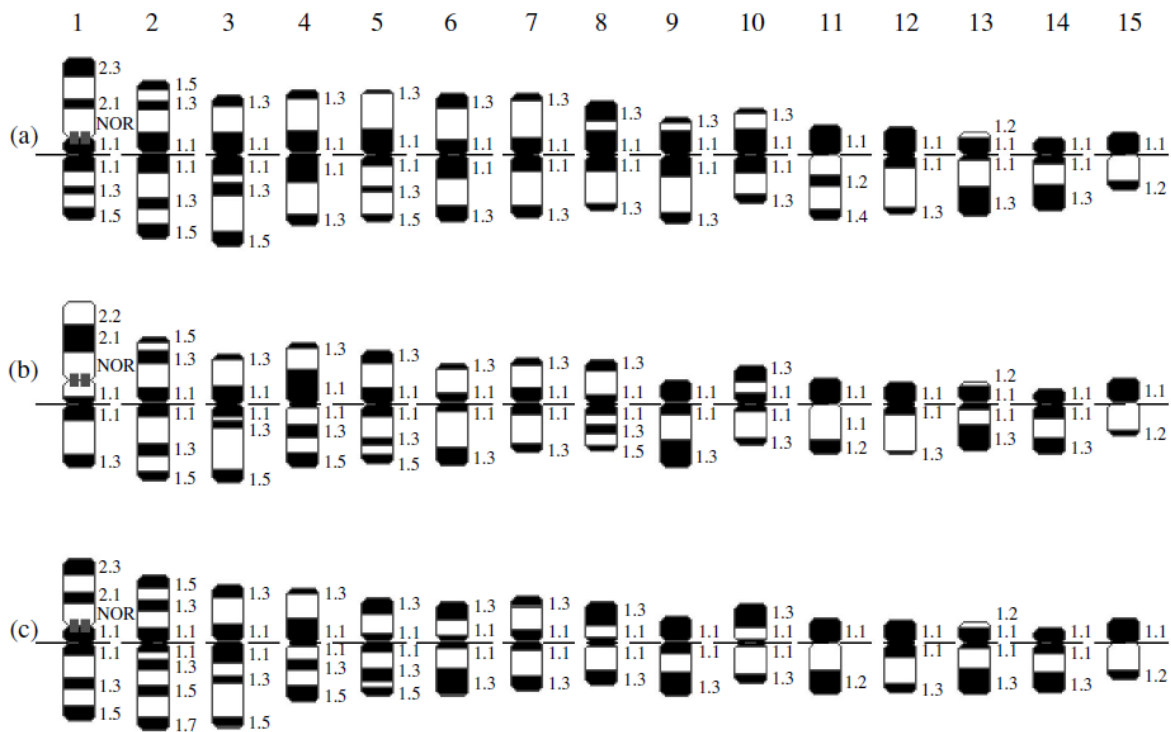


Fig. 1 Ideograms of C-banded chromosomes of (a) *L. angustifolium*, (b) *L. bienne*, and (c) *L. usitatissimum* cultivar Orshanskii 2. From (Muravenko et al., 2003)

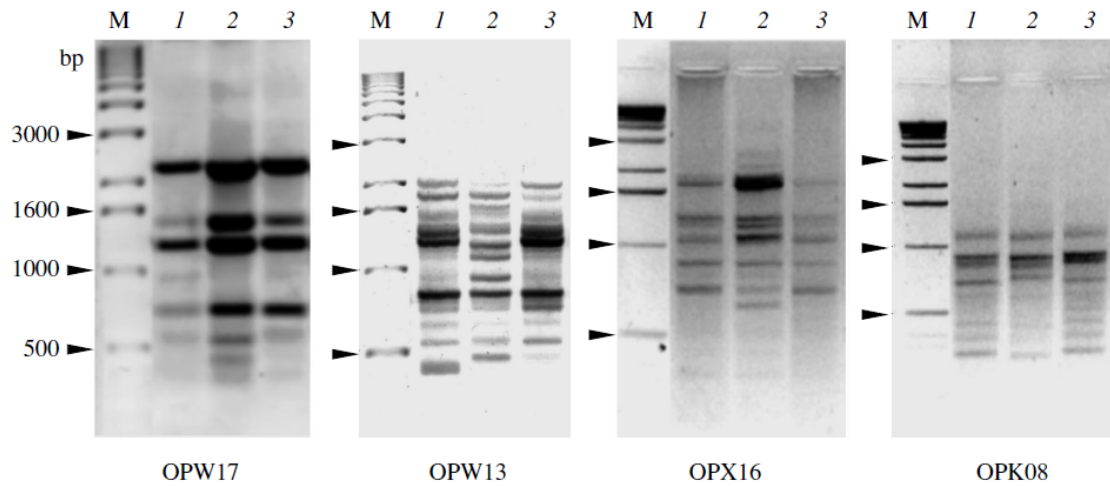


Fig. 2 RAPD patterns obtained with primers OPW17, OPW13, OPX16, and OPK08 for (1) *L. angustifolium*, (2) *L. bienne*, and (3) *L. usitatissimum*. M, molecular weight marker. From (Muravenko et al., 2003)

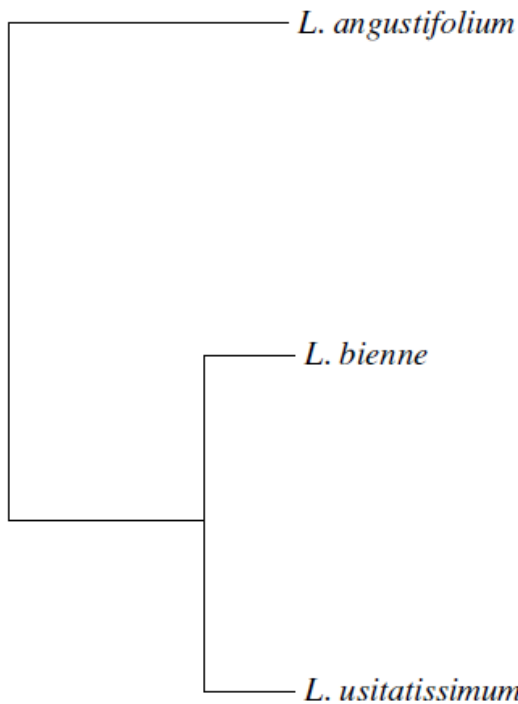


Fig. 3 Dendrogram of phylogenetic relationships of the three flax species, as inferred from analysis of genetic distances. From (Muravenko et al., 2003).

The RAPD patterns were used to construct a dendrogram of genetic similarity between the three flax species (Fig. 5). The genotypes under study formed two clusters, one including *L. usitatissimum* and *L. bienne* and the other combining these species with *L. angustifolium*. Genetic distance was 0.226 between *L. usitatissimum* and *L. bienne* and

0.305 between *L. angustifolium* and *L. usitatissimum* and between *L. angustifolium* and *L. bienne*. Thus, molecular analysis of genomic DNA showed that *L. bienne* clusters with *L. usitatissimum* and, therefore, cannot be considered as a separate species.

The analysis of chromosome numbers of North American taxa led (Harris, 1968) to the following conclusions in the evolution of *Linum*:

Among the North American species of *Linum* there are three basic chromosome numbers representing invasions from the Old World of three distinct evolutionary lines. $N=9$ is found only in the blue-flowered group represented in North America by two species, *L. lewisii* and *L. pratense*, which are closely related to and may be conspecific with the Old World *L. perenne*. The basic number for the yellow-flowered species is $N=18$, which is characteristic of the *Scabrella* and *Virginiana* subgroups. The loss of chromosomes in the *Neomexicana* ($N=13$) and *Sulcata-Rigida* ($N=15$) subgroups suggests that the basic haploid number of 18 might be a polyploid derivative of an Old World ancestor with $n = 9$. The incidence of $n = 9$ among Old World species of *Linum* may indicate that this represents an ancestral condition. *Linum catharticum* has $n = 8$; this number and features of morphology and distribution suggest that it is not directly related to either the blue-flowered or yellow-flowered groups in North America but represents a separate introduction on this continent.

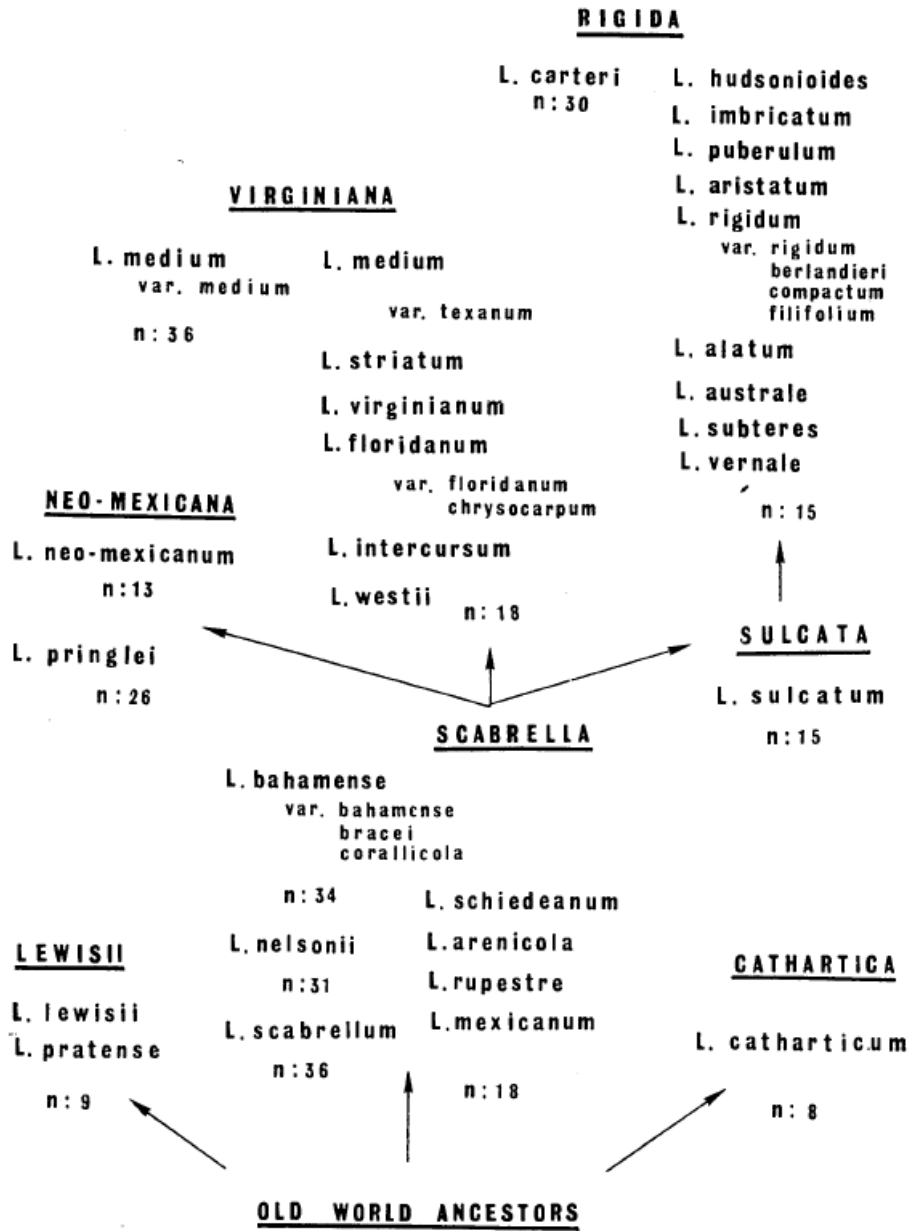


Fig. 4 Diagram of the probable evolution of *Linum* in North America from unknown Old World ancestors. From (Harris, 1968)

1.3. Taxonomy of *Linum usitatissimum*

(Fu et al., 2002a):

Analysis of the extent and distribution of genetic diversity in crop plants is essential for optimizing sampling and breeding strategies. We used random amplified polymorphic DNA (RAPD) markers to assess genetic diversity and relationships in 22 Canadian cultivars, 29 selected world cultivars and 10 landraces of flax (*Linum usitatissimum* L.). RAPD variation was generally low and more variation was detected among, than within, the investigated flax accessions. Based on 53 variable RAPD loci observed for the 61

accessions, the landraces had a lower proportion of fixed recessive RAPD loci (0.427) (i.e., more genetic variation) than all of the flax cultivars examined (0.492). The linseed cultivars had a lower proportion of recessive loci (0.469) than the fiber flax cultivars (0.529). Canadian linseed cultivars had a lower proportion of recessive loci (0.465) than the selected world flax cultivars (0.512). A trend was also observed that the rate of loss in genetic variation in Canadian flax breeding programs over the last fifty years was approximately two variable loci per 100 loci per 10 years. Clustering analyses based on similarity estimates showed that the fiber cultivars were more related (or similar to each other) and were classified as a homogeneous group. All of the linseed cultivars were clustered in diverse groups with the nine landrace accessions. Implications of these findings for flax breeding and germplasm management are discussed.

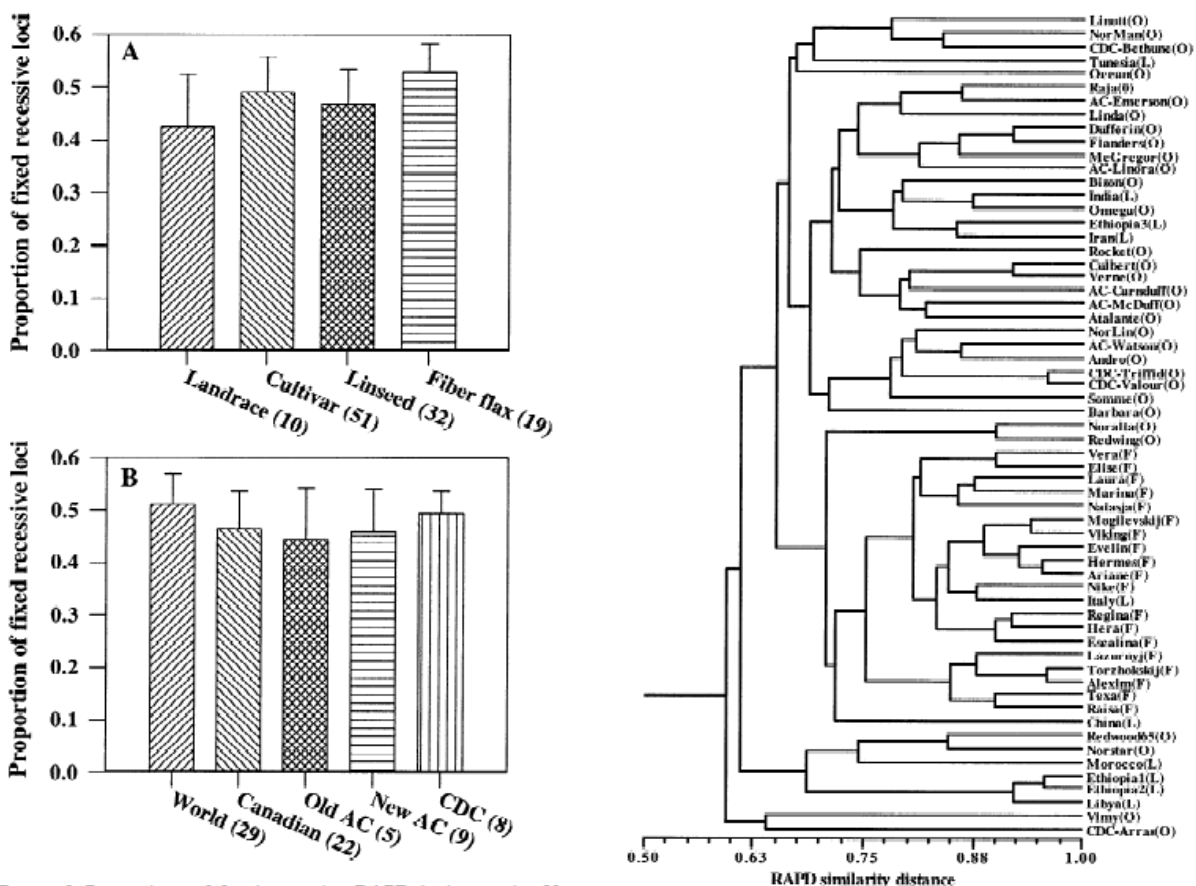


Fig. 5 LEFT: Proportions of fixed recessive RAPD loci over the 53 variable RAPD loci observed for various groups of flax accessions. Their standard errors are shown in bar. The number following the group label is the number of accessions used for the group. RIGHT: Genetic relationships of all the 61 flax accessions reflected in RAPD similarity distance. The letters (O, F, L) following the accession names stand for oil, fiber, landrace flax, respectively. From (Fu et al., 2002a)

2. Biosafety considerations

2.1. Gene flow

L. usitatissimum and *L. bienne* can freely produce fertile F1 hybrids (Green, 1983). However, *L. usitatissimum* × *L. catharticum* are strongly isolated (Green, 1983). (Seetharam, 1972; Seetharam & Srinivas, 1972) examined crossing relationships between wild *Linum* taxa and cultivated *L. usitatissimum*. Levels of hybrid seed set were typically high and normal meiotic pairing was observed in most F1 hybrid combinations. Interfertility of cultivated flax with the native *L. monogynum* (New Zealand) is unknown.

This view is differentiated by (Seetharam, 1972; Seetharam & Srinivas, 1972): Twelve interspecific hybrids obtained by crossing 9 different 30-chromosome species of the genus *Linum* were studied in detail for important morphological characters like, tillering, height, secondary branching, oil content, rust resistance, pollen and seed Sterility in the hybrids. *L. strictum* appeared to be important from the viewpoint of improvement of the cultivated linseeds with regard to number of tillers. The oil content in different species ranged from 24.6 % in *L. palliscence* to 37.1 % in *L. angustifolium*. The fact that *L. angustifolium* tops the list of the wild species in oil content seems to lend support to the view that it is one of the progenitors of *L. usitatissimum*. All the species under study were found resistant to all the locally prevalent seven Indian races of rust. They can be sources of rust-resistant genes to the cultivated linseeds. The hybrids showed varying degrees of pollen and seed sterility in spite of their chromosomes pairing and separating regularly, Studies are needed in order to understand the real potential of hybridization in the field. *On the other hand one has to understand that Linum usitatissimum is grown in most cases in the absent of interfertile close relatives.*

The collection and study of wild relatives is an integral part of any sound breeding programme. such investigations throw some light on the usefulness of these materials as gene sources for breeding. The first report of successful interspecific hybridization was of (Tammes, 1923). She obtained fertile hybrids between *L. usitatissimum* and *L. angustifolium* and the hybrid was intermediate between the parents. (Rogach, 1941) crossed *L. Sibericum* with *L. alpinurn*, *L. narbonense* with *L. austriacum* and the hybrids obtained were highly sterile. (Ray, 1944) also attempted interspecific hybridization between 10 species and only hybridization between *L. usitatissimum* and *L. angustifolium* was successful.

In the study o 12 (Seethara.A, 1972) interspecific hybrids involving 9 species were studied in detail for the important morphological characters of diagnostic value. Considerable diversity was observed between different species for different morphological characters like plant height, number of primary tillers, position and number of secondary branches, 1000-grain weight and oil content in the seed. Regarding oil content in the wild species, it was generally lower than in the cultivated types. Amongst the wild species the maximum oil content was in *L. angustifoliunz* with 37.1 %. Incidentally this species has maximum 1000-grain weight also amongst the wild species. According to (De Candolle, 1904; Heer, 1865, 1872) the cultivated linseeds are said to have arisen from *L. angustifolium* presumably by human selection. The

occurrence of genes for oil production in *L. angustifolium* provides some additional evidence of its ancestry for this school of thought. In view of the low oil content of the wild species they do not seem to be an important source of genic material. But their utility in improving oil quality may prove to be of value as (Plessers, 1966) observed variation in the fatty acid composition of the oil of different species. The wild species seem to be also important as gene sources for rust resistance since they possess resistance for all the prevailing races of India.

The interspecific hybrids were generally intermediate for most of the morphological characters studied. However some of them exhibited hybrid vigour for characters like height, number of tillers etc. All the hybrids expressed partial pollen sterility, which was reflected in reduced seed fertility. An attempt was also made to cross the species with varying chromosome numbers with the cultivated species but without any success. (Sizova, 1958, 1961) studied the process of fertilization in some interspecific crosses with varying chromosomes. She observed partially developed embryos and attributed the incompatibility to somatoplastic sterility. It may be possible by embryo culture to overcome this difficulty, and secure fertile hybrids which may be useful not only in transferring some of its useful genes into the cultivated species but also in establishing interrelationships.

2.2. Field experiments with transgenic Linum

(McHughen & Holm, 1991) reports from a first field experiment with transgenic Linum: Two linseed flax (*Linum usitatissimum*) lines transformed with a mutant *Arabidopsis* ALS gene conferring resistance to sulfonylurea herbicides were tested in a replicated, randomized field test against its non-transformed commercial cultivar parent (cv. NorLin) in normal soil and in soil containing the commonly used sulfonylurea herbicides chlorsulfuron (Glean®) or metsulfuron methyl (Ally®). There were no significant differences between the transgenic lines and the parent for any agronomic trait measured in untreated soil, indicating that there is no detrimental effect of T-DNA or foreign gene expression. Similarly, there were no significant differences for performance of the transgenic lines between the untreated and the herbicide treated soils, indicating that the transferred gene does confer a field level of tolerance to the flax. The control NorLin was devastated by the presence of the herbicides in the soil.

In later experiments (McHughen & Holm, 1995a, b) and his team demonstrate, that transgenic Linum has its merits regarding sustainability:

Among the major concerns raised about the commercialization of transgenic herbicide-resistant crop cultivars are the fear that such lines will increase chemical usage and non-sustainable agronomic practices, that the transgenes will not be efficacious under field conditions, or that there will be an agronomic penalty, such as reduced seed yield, in exchange for the new trait. To address these concerns, transgenic sulfonylurea-resistant flax (*Linum usitatissimum* L.) lines were tested in replicated, randomized field trials over three years. The results show that at least one transgenic line is fully resistant to the field doses of the herbicides, shows no agronomic penalties regardless of the presence or absence of the herbicides, and will lead to less chemical usage and more sustainable agronomic practices in commercial production.

More literature references related to taxonomy and biosafety:

(Blaringhem, 1921; BretagneSagnard et al., 1996; Burdon et al., 1999; Chaudhuri & Sen, 1976; Chen & Dribnenki, 2002; Cross et al., 2003; Diederichsen, 2001; Dubey & Singh, 1966; Ferguson et al., 1997; Foster et al., 1998; Friedt et al., 1995; Gill & Yermanos, 1967a, b; Gorshkova et al., 1998; Gorshkova et al., 2003; Gorshkova et al., 2000; Himmelsbach et al., 1998; Jarosz & Burdon, 1991; Jeanmonod & Schlusser, 2003; Kearns & Inouye, 1994; Lei et al., 2003; Lisson & Mendham, 2000; McDougall et al., 1992; Muravenko et al., 2003; Murray, 1980; Ockendon, 1968, 1971; Oostdam & vanderPlas, 1996; Roberts & Pryor, 1995; Rogers, 1982; Salonen & Lammi, 2001; Salonen & Suhonen, 1995; Seethara.A, 1971; Seethara.A & Srinivas.D, 1972; Srinivas.D et al., 1972; Stegnii et al., 2000; Sundback et al., 2003; Sylven, 1925; Webb, 1964; Yermanos & Gill, 1969; Yilmaz & Kaynak, 2006a, b)

The keyword *Linum* yields some 1507 references in the Web of Sciences and some other sources:

<http://www.botanischergarten.ch/EPOBIO-Linum/Bibliography-Linum-WOS-20070210.pdf>

Linum, flax

<i>Strand Question</i>	<i>Score</i>
CPW <i>Propensity for successful pollen-mediated gene flow between the crop and wild relatives</i>	
CPW1 Do interfertile wild relatives of this crop exist ? (0/1)	1
CPW2 Is there a probability that the crop will flower and produce viable pollen during its cultivation? (0/1)	0,1
CPW3 Upon flowering, is 95% of the crop pollen deposited within 1 m (1), 10 m (2), 50 m (3), 100 m (4), 250 m (5) or 500 m (6)? (1-6)	2
CPW4 If flowering does occur is the wild relative in question rated as an obligate inbreeder (0), a partial inbreeder/outbreeder (1) or an obligate outbreeder (2)? (0-2)	1
CPW5 If fertilization is achieved by the deposited pollen, will a viable F ₁ hybrid individual establish itself? (0/1)	0,1

<i>Strand Question</i>	<i>Score</i>
CPC <i>Propensity for successful pollen-mediated gene flow between the crop and related commercial varieties</i>	
CPC1 Probability that crop flowers and produce viable pollen during its cultivation? (0/1)	0,1
CPC2 Upon flowering, is 95% of the crop pollen deposited within 1 m (1), 10 m (2), 50 m (3), 100 m (4), 250 m (5) or 500 m (6)? (1-6)	2
CPC3 If flowering occurs is receptive crop rated as an obligate inbreeder (0), a partial inbreeder/outbreeder (1) or an obligate outbreeder (2)? (0-2)	0,1
CPC4 If fertilization happens, will a viable F ₁ individual be established itself from hybrid seed in absence of mechanical/chemical control? (0/1)	1

CSV Propensity for successful seed- and tiller mediated gene flow from commercial crop to volunteer

CSV1	Does the crop produce seed during its cultivation? (0/1)	1
CSV2	Post-harvest, will the seed survive and germinate within the confines of a managed field? (0/1)	1
CSV3	Will the volunteer develop into a viable individual? (0/1)	?

CSF Propensity for successful seed- and tiller mediated gene flow from commercial crop to feral

CSF1	Does the crop produce seed during its cultivation? (0/1)	1
CSF2	Following transfer from cultivation site: will wayward seed survive and germinate? (0/1)	1
CSF3	Will the resulting individuals establish into a viable feral population? (0/1)	1

CGC Consequences of Gene Flow

CGC1	Does crop mix with related crop traits and jeopardize harvest value ? (0/1)	1
CGC2	Does crop mix with wild relatives or feral traits and pose an biodiversity threat ? (0/1)	0,1
CGC3	Does crop produce volunteers and/or seed deposits and pose an environmental threat ? (0/1)	?

CMG Mitigation Gene Flow crop to crop, crop to wild relative and crop to feral

CMG1	Mitigation with safety distances possible (J/N) 1 m (1), 10 m (2), 50 m (3), 100 m (4), 250 m (5) or 500 m (6)? (J/N) (1-6)	2 (J)
CMG2	Mitigation with molecular safety measures apomixis AP, cytoplasmatic sterility CS, tandem construc TA, gene switching GS AP, TA, GS, (0/1)	AP, CS, TA, GS, 1

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