

Chapter 1

A Taxonomic View on Genetic Resources in the Genus *Linum* L. for Flax Breeding



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1.1 Introduction

The most comprehensive taxonomic review of the genus *Linum* mentioned that there are about 200 botanical species (Winkler 1931). This conspectus is, however, outdated. The lack of a recent review has caused the treatments used for *Linum* taxa in local, national or regional floras to apply scientific names and classifications that are not harmonized. Inconsistencies among floras in assigning a taxonomic rank to a given taxon occur. Many synonyms exist, and they are often used without cross-referencing. A conspectus is needed to compare *Linum* species described from different areas with different names that in fact may be closely related or even identical. A coherent taxonomic review is required to understand and communicate information on the species and infraspecific diversity in the genus *Linum*. Such taxonomic inconsistencies are quite common in many genera and have great implications on managing crop gene pools in genebanks. For example, similar scenarios exist in sunflower (*Helianthus annuus* L.; Atalgić and Teryić 2016) and chickpea (*Cicer arietinum* L.; Diederichsen et al. 2009).

Since 1998, the Canadian national genebank for plant genetic resources for food and agriculture, Plant Gene Resources of Canada, has put major efforts into the conservation and research of flax diversity. Classical taxonomic approaches were

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part of these efforts to group and assess the diversity of the Canadian genebank holdings of 3500 accessions of cultivated flax and more than 100 accessions of 18 other *Linum* species (Diederichsen and Fu 2008; PGRC 2016). This book chapter uses flax as a case study to describe the role of taxonomy and systematics in the conservation and utilization of plant genetic resources. The objective is to review contributions made by taxonomists and crop plant researchers to find a broadly accepted way to describe and communicate the diversity in the genus *Linum* with emphasis on the conservation and utilization of this diversity in the breeding of cultivated flax.

Rational utilization and conservation of genetic diversity, as well as assessing this diversity, requires a tool to communicate unambiguously about such diversity. The taxonomical unit of the species is generally used without much thought. The loss of a species is of great concern and makes the news in public media. Species extinction mobilizes policymakers to take action. However, when we speak of genetic resources, we deal mostly with the diversity within a species, which is the genetic diversity. Loss of such infraspecific diversity is much less spectacular, but to lose such diversity in crop plants and their wild relatives may be of critical importance due to the implications on food security.

It is very much disputed whether systematics and taxonomy, the categorizing and naming of groups of similar elements using scientific methods, are appropriate tools for distinguishing genetic diversity within a species, i.e. on the infraspecific level. Moreover, the relevance of taxonomy for utilization of plant genetic resources is sometimes doubted, as are the concepts of taxonomy in general. Some taxonomists have questioned the Linnaean species concept as such (Bachmann 1998). The main argument is that taxonomy is not considered an objective science, but a subjective view on diversity. Following the path initiated by Linnaeus and well-described in its unfolding over time by Stearn (1986), taxonomy has in particular shied away from applying established taxonomic principles to gene pools of crop plants. Consequently, the rules of the International Code for Botanical Nomenclature of Cultivated Plants (Brickell et al. 2009) are a useful tool for naming modern cultivars, but are not useful for orientation in the wider gene pool of a cultivated species, which is urgently required for genebank management (Diederichsen 2004).

Classical taxonomy was strictly based on morphological features distinguishable with the naked eye. Later, micro-morphological features, chemical features and, more recently, molecular technologies culminating in sequencing the nuclear DNA have become available and are today dominating the debate on biodiversity. Interestingly, research in flax that started in the 1950s has shown that the amount of nuclear DNA within the species varies and can vary from generation to generation (Durrant 1962; Cullis 2005). We may have reached a point in time where we need to acknowledge that the molecular descriptions only represent another approach that contributes to the understanding of a species but do not allow us to capture fully a species as it unfolds in real life. As previously articulated (see

review by Small 1989), the author also feels that each approach to a species will contribute to the understanding of that species. However, we must acknowledge that any definition of a botanical species or other taxon is only an approximation of our thinking to the whole and complex truth and is based on the tools for perception we use for making our observations. Without tools we return to what classical taxonomists relied on: the bare eye, the senses given to us as humans to perceive the world. The highly sophisticated tools used in phenomics applied today are nothing but a major refinement of what our eyes can observe. In addition, molecular methods, including all kind of markers and sequencing of plastome and nuclear DNA, are nothing but observations using other tools and are essentially of a descriptive nature. Slight modifications happen constantly in living organisms. The recently emerging discipline of epigenetics points at genomic plasticity, a phenomenon observed in flax 50 years ago (Durrant 1962; Cullis 2005). It is remarkable that flax has directed research towards epigenetics but at the same time has been the species that guided research to the gene-for-gene interaction between a plant and a pathogen based on very static genetic principles (Flor 1955).

It may be impossible to capture the idea of a biological entity with terms that suggest a static and unchangeable state because a living being will always change while alive and even more so over generations. Mansfeld (1962) clearly described this dilemma or pseudo-problem (he used the term *Scheinproblem*) of systematics. We need to find a convention for communication that comes closest to this ever-changing biological entity and, at the same time, enhances our ability to work with it in plant breeding, in agriculture, in trade, in conservation efforts or in research.

Classical concepts may be currently falling out of favour, but to overview trends over time, it is important to understand the earlier publications that were built on the classical concepts for assessing the diversity of crop gene pools. This method was essential to the Vavilov school in crop plant research, which shaped genetic resources exploration in the former Soviet Union and influenced in particular the eastern European countries and Japan (Vavilov 1931; Loskutov 1999). The phenotype of a plant is immediately accessible to our senses, and many phenotypic characters are very relevant for the utilization of that plant. The functionality of many morphological features allows interpretations in the larger ecological or evolutionary context of a species. For efficient communication, the species name is relevant. It is for good reason that common names for plant groups, which are congruent with what later was recognized by cartesian science as a botanical species, have been developed in all cultures. In addition, many infraspecific groups for particular usages based on distinct differences in phenotype have received common names for distinguishing such types within a cultivated plant species (Diederichsen 2004). For farmers and trade, and for interaction among humans, such naming and language have been instrumental for thousands of years. Scientific conventions, such as the taxonomy used in the genebank database

system GRIN-Global, maintained by the United States Department of Agriculture to communicate the content of the National Plant Germplasm System, show how relevant this still is (Wiersema and Leon 2016). The International Seed Testing Association (ISTA) also relies on consistent taxonomy for supporting trade and standardization of testing methods (Wiersema 2013). Small (1993) emphasized the great economic impact plant systematics have on agriculture. Other crop plant researchers such as Hanelt (1988) stressed the relevance of taxonomy for managing genebanks. Unfortunately, most modern genebanks lack a close association with taxonomists. As a result, material is sometimes stored and passed on to genebank clients without stringent protocols for botanical identification. This is of great concern and negatively affects our ability to conserve and utilize this diversity. Concerns regarding the lack of taxonomic expertise for effective conservation of biodiversity have been expressed elsewhere (Small et al. 1995), but how this impacts the operations of genebanks preserving plant genetic resources for food and agriculture is rarely articulated.

1.2 The Primary Genepool of Genetic Resources for Flax Breeding

The only agricultural crop in the genus *Linum* is the species *Linum usitatissimum* L., and it has two distinct usages: linseed is used for seed oil and fibre flax is used for extracting the long stem fibre for textile production. In many languages, distinct names exist for flax plant types used for seed oil extraction and for types used for fibre (Diederichsen and Richards 2003). Obviously, common sense guided people in various language families in creating these distinct names to facilitate efficient communication of genetic diversity below the species rank. Taxonomists, concerned about the correct scientific naming of plants, have become reluctant over the years to be as precise as common language in assigning scientific names to these distinct usage groups in flax. Diederichsen and Richards (2003) supported the grouping of cultivated flax into four major groups and using the scientific names for them proposed by Kulpa and Danert (1962). A wide range of diversity in agronomically important characters exists in cultivated flax (Diederichsen et al. 2013). Research has relied on identifying infraspecific groups in flax to interpret archaeological findings and make conclusions on its evolution under domestication (Herbig and Maier 2011). Even flax workers reluctant to apply a detailed infraspecific classification may see the practical evidence in the grouping of cultivated flax into these four principal groups (convarieties).

1.3 Key for Determination of the Four Convarieties of Cultivated Flax, *L. usitatissimum*

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| <p>A Capsules open completely septicidally and loculicidally during ripening (Fig. 1.1). Seeds are shattered. Later, empty capsules are dropped.</p> <p>A* Capsules not opening during ripening or only slightly septicidally separating from each other (Fig. 1.1). Seeds are not easily shattered. Empty capsules are not dropped.</p> <p>B Plant height more than 70 cm and only the upper 1/3 or less of the entire stem length with side branches; if less than 70 cm, then stem branches only in the upper 1/5 of the entire stem length.</p> <p>B* Plant height usually less than 70 cm; more than 1/5 of the entire stem length with side branches.</p> <p>C Weight of 1000 seeds more than 9 g; plants usually without basal branches.</p> <p>C* Weight of 1000 seeds less than 9 g; plants often with basal branches.</p> | <p>1. convar. <i>crepitans</i></p> <p>B</p> <p>2. convar. <i>elongatum</i></p> <p>C</p> <p>3. convar. <i>mediterraneum</i></p> <p>4. convar. <i>usitatissimum</i></p> |
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1. *L. usitatissimum* convar. *crepitans* (Boenningh.) Kulpa et Danert, Kulturpflanze, Beih. 3, (1962) 374.

The convar. *crepitans* (Fig. 1.2) refers to dehiscent flax. It has been used in Central and Southeast Europe as a fibre plant (Hegi 1925). Seed shattering makes it difficult to harvest the seeds. This type of flax is no longer cultivated, and only the germplasm collections conducted early in the twentieth century facilitated conservation of this type in genebanks. Its range of variation is limited. With the exception of the dehiscence of the capsules, the plants are phenotypically similar to those of the convar. *usitatissimum*.



Fig. 1.1 Different degrees of dehiscence in mature flax capsules. The complete dehiscence characterizes the primitive type of cultivated flax, *L. usitatissimum* convar. *crepitans*. (Photo: R. Underwood, Agriculture and Agri-Food Canada)

Fig. 1.2 Flowering/maturing plant of *L. usitatissimum* convar. *crepitans*. This type of flax has only been conserved in genebanks. PGRC accession CN 100852, landrace from Portugal. (Photograph: Z. Baines, Agriculture and Agri-Food Canada)



2. *L. usitatissimum* convar. *elongatum* Vav. et Ell. in Kul't. Fl. SSSR 5, 1 (1940) 153, pro prole sub *L. indehiscens* Vav. et Ell. subsp. *eurasiaticum* Vav. ex Ell.

The convar. *elongatum* (Fig. 1.3) refers to typical fibre flax. It has long stems, which are only branched at the top. This type of flax has been of great importance in the temperate and northern areas of Europe and in particular Eastern Europe (Vavilov 1926). China is also a centre of diversity for fibre flax. Fibre flax has a shorter vegetative period than the large-seeded flax. This group is identical with the fibre flax as defined by Dillman (1953).

3. *L. usitatissimum* convar. *mediterraneum* (Vav. ex Ell.) Kulpa et Danert, Kulturpflanze, Beih. 3, (1962) 376.

The convar. *mediterraneum* (Fig. 1.4) refers to large-seeded flax with large flowers and capsules and branched stems. It is only used for seed production. Flax of this type originates from the Mediterranean area and has a long vegetative period. This group is identical with the Mediterranean seed flax defined by Dillman (1953).

4. *L. usitatissimum* convar. *usitatissimum*.

The convar. *usitatissimum* (Fig. 1.5) refers to the intermediate flax, or dual purpose flax. This is the most common type of flax in the world. Within this convariety, further segregation into several different morphotypes is possible. This group covers the spring-type seed flax, winter-type seed flax and Indian and Ethiopian (Abyssinian) flax, as

Fig. 1.3 Flowering/maturing plant of *L. usitatissimum* convar. *elongatum*, the typical plant type for using the long stem fibre that was common in Europe. PGRC accession CN 18991, cultivar Nike from Poland. (Photograph: Z. Bainas, Agriculture and Agri-Food Canada)



Fig. 1.4 Flowering/maturing plant of *L. usitatissimum* convar. *mediterraneum*. This type is only used for seed production and most flax from India and the Mediterranean area belongs to this group. PGRC accession CN 98566, landrace Neelum (3/2) from India. (Photograph: Z. Bainas, Agriculture and Agri-Food Canada)



Fig. 1.5 Flowering/maturing plant of *L. usitatissimum* convar. *usitatissimum*. This intermediate flax covers the majority of flax types and is common in all regions. PGRC accession CN 19017, cultivar CDC Normandy from Canada. (Photograph: Z. Baines, Agriculture and Agri-Food Canada)



defined by Dillman (1953). All Canadian oilseed cultivars belong to this group because their weight of 1000 seeds does not reach the size of the large-seeded flax types.

On the next lower taxonomic level, Kulpa and Danert (1962) proposed the distinction of 28 botanical varieties within these 4 convarieties of cultivated flax. This classification system was used to compare the genebank holdings of the national genebanks of Germany (1606 accessions) and Canada (2748 accessions) (Diederichsen 2009). The results showed a similar concentration towards certain phenotypes in both genebanks. This grouping was also instrumental when assembling a core collection of the Canadian flax collection (Diederichsen et al. 2012). However, the utilization of formal taxonomic names for describing genetic diversity within a species is not widely accepted, and it will probably remain a tool only used by genebank curators specializing in particular crops.

Other formal infraspecific groupings of cultivated flax into several botanical varieties exist. Alefeld (1866) described 11 botanical varieties. Howard (1924) suggested a grouping of Indian flax into 26 botanical varieties based on flower and seed colour. Elladi (1940) expanded the classification to 119 botanical varieties. The most recent formal classification of cultivated flax was proposed by Černomorskaja and Stankevič (1987) and distinguished five subspecies (Diederichsen and Richards 2003). None of these classifications has been applied to a genebank collection. In this context, it is also important to note Dillman's (1953) very comprehensive description and categorization of diversity of cultivated flax. This is not a formal taxonomic grouping, but a grouping into cultivar groups. In contrast to the formal taxonomic groupings,

it considered agronomically relevant traits such as the need for vernalization as a distinguishing feature. Dillman's system was applied to the world flax collection of the United States Department of Agriculture (USDA) by grouping the genepool into six plant types: (1) fibre flax; (2) spring-type seed flax; (3) winter-type seed flax; (4) short, large-seeded, Indian seed flax; (5) Ethiopian forage-type flax; and (6) Mediterranean or Argentine seed flax.

1.4 The Wild Progenitor of Cultivated Flax Belonging to the Primary Genepool

Linum bienne Mill., Gard. dict. ed. 8 (1768) n. 8 – *L. usitatissimum* subsp. *angustifolium* (Huds.) Thell., Fl. adv. Montp. (1912) 361; other synonyms are *L. ambiguum* Jord., *L. hohenackeri* Boiss., *L. usitatissimum* subsp. *hispanicum* Thell., *L. dehiscens* Vav. et Ell. subsp. *angustifolium* (Huds.) Vav. et Ell. and *L. angustifolium* Huds. (Hammer 2001). The English common name of the wild progenitor is pale flax.

Pale flax (Fig. 1.6) has a biennial or perennial growth habit, i.e. it needs a vernalization to induce flowering. Heer (1872) was the first to identify pale flax as the wild

Fig. 1.6 The middle row are plants of *L. bienne* Mill., the wild progenitor of cultivated flax. The many basal branches, bushy growth habit and the dehiscence and shattering of capsules are typical for this species. (Photograph: A. Diederichsen, Agriculture and Agri-Food Canada)



progenitor of cultivated flax. The flowers are homostylous and self-pollinated. The capsules open spontaneously and the seeds shatter. The species occurs in the Mediterranean area and in Western Europe. Tammes (1928) demonstrated that this species is interfertile with cultivated flax. However, no reports exist about its usage in flax breeding.

A significant contribution towards the conservation and understanding of *L. bienne* was made by scientists collecting germplasm of this species in Turkey and depositing it in a genebank (Uysal et al. 2012). This germplasm originated from areas of flax domestication that were until recently not represented in world genebanks, and it is in particular useful for domestication research in flax. Investigation of the morphology of pale flax showed that some characters have a wider range of variation in this taxon than in cultivated flax (Diederichsen and Hammer 1995). Recent molecular studies have confirmed the relationship with the cultivated species (Fu and Allaby 2010; Soto-Cerda et al. 2014). Additional germplasm of this species from the Balkans has recently been deposited in genebanks (Gutaker 2014).

From the biological point of view, pale flax should be placed in the same botanical species as cultivated flax since the two types can freely intercross. Harlan and de Wet (1971) proposed the genepool concept as a basis for rational classification of crop genepools and strongly suggested that formal taxonomy reflected such biological and evolutionary relationships. Based on this principle, the correct name for pale flax is *L. usitatissimum* subsp. *angustifolium* (Huds.) Thell., and all cultivated flax would fall in the other subspecies, *L. usitatissimum* subsp. *usitatissimum*. Hammer (2001) followed this principle. However, lengthy names are often cumbersome to use. Even worse, if someone is lax and omits the subspecies name, the cultivated form and wild progenitor can be easily confused. For that reason, and for convenience, it seems the species rank is mostly still applied to distinguish pale flax, and the correct name for pale flax at the botanical species rank is *L. bienne* Mill. All other *Linum* species will not produce fertile offspring when crossed with cultivated flax and, therefore, belong to the tertiary genepool from the perspective of plant breeding. Various reports about crossing cultivated flax with taxa other than its wild progenitor are very questionable, as the taxonomic identification of the material was not presented convincingly (Diederichsen 2007). This exemplifies how important it is to verify the botanical identity of material based on solid taxonomy. When scientists specializing in physiology or genomics use misidentified material, errors in communication occur.

1.5 The Secondary and Tertiary Genepools of Species in the Genus *Linum*

Studies of the relationships among *Linum* taxa have not changed the views that were based on the earlier morphological and cytological results (Fu and Allaby 2010). The review of Winkler (1931) is still the baseline. In recent years, descriptions of new wild species in the genus *Linum* have been provided for Southern Italy (Peruzzi 2011), Turkey (Tugay et al. 2010; Yılmaz 2010; Yılmaz and Kaynak 2008), Greece (Iatrou, 1989; Christodoulakis 1999) and Mexico (Rogers 1982). The species composition in the genus *Linum* has not been subject to many studies.

Diederichsen (2007) reported that 33 world genebanks preserved about 600 accessions of 52 *Linum* species belonging to the secondary and tertiary gene-pools for breeding of cultivated flax. A recent inspection of the database at the World Information and Early Warning System (WIEWS) on Plant Genetic Resources for Food and Agriculture of the Food and Agricultural Organization of the United Nations (FAO 2016) showed that 82 institutions around the world maintain a total of 685 *Linum* accessions that are not listed as *L. usitatissimum*, *L. bienne*, *L. angustifolium* or *L. usitatissimum* subsp. *angustifolium*. Assuming all these botanical identifications are correct, these 685 accessions would belong to *Linum* taxa that are neither cultivated flax nor its wild progenitor, pale flax. At the same time, the WIEWS database lists 3479 accessions as *Linum* sp., i.e. the botanical identification has not been conducted or at least not been reported to the database. Thus, the situation of *Linum* germplasm conservation has not changed much since Diederichsen's (2007) review. It is obvious, however, that the botanical identification of material even to the species level is a bottleneck in many genebank collections.

The described situation highlights the wide margin of error we must accept when considering the global status of both in situ and ex situ conservation of plant genetic resources in the genus *Linum*, especially when decisions are made that directly affect the conservation of these genetic resources. Without a consistent taxonomy and lacking reliable species identification, we can only make very approximate estimates of the diversity and conservation status of *Linum* germplasm. Databases that are meant to support decision making for conservation and utilization of genetic resources suffer tremendously due to taxonomic insecurity. For example, the Global Biodiversity Information Facility lists only 26 accepted species names in the genus *Linum* (GBIF 2016). This list does not include cultivated flax or the wild progenitor species of the primary gene pool. However, older, well-reputed floras for Turkey (Davis 1967) and Europe (Ockendon and Walters 1968) list more species than that. The database "Plant List" (Royal Botanic Gardens Kew and Missouri Botanical Garden 2016) lists scientific names of species and infraspecific taxa and includes 169 accepted names and 220 names that are unresolved in the genus *Linum*. The species delimitations remain vague for many species, in particular in the *L. flavum* and *L. perenne* groups (Ockendon and Walters 1968). Ornamental plants have been selected in these two groups. These examples show that a great deal of taxonomic confusion continues to exist in the genus *Linum* and that even on the species level we have not improved our ability to communicate *Linum* diversity using taxonomy since Winkler (1931) despite enormous advances in technology. For field botanists, it is essential to have botanical keys that allow identification of plants at least to the species level in the field. In Fig. 1.7, a situation encountered by the author on the Crimean Peninsula south of Sevastopol with three *Linum* species growing on the same meadow in close proximity to each other illustrates this need (Diederichsen et al. 2012). This illustrates the usefulness of species delimitations based on morphological characters that can be recognized by the field botanist, germplasm collector, genebank curator or plant breeder.



Fig. 1.7 Three *Linum* species encountered at the same location in close proximity on the Crimean peninsula south of Sevastopol in 2009. Left to right: *Linum tenuifolium* L., *L. corymbulosum* Reichenb. and *L. austriacum* L. (Photograph: A. Diederichsen, see also Diederichsen et al. 2012).

1.6 Conclusions

A taxonomic revision of the genus *Linum* is urgently required to allow progress in understanding the diversity in this genus and provide an essential tool for conservation and utilization of this diversity. In flax, classical taxonomic concepts can be used to communicate distinct intraspecific diversity. The classical approaches of systematics and taxonomy remain useful tools for those encountering diversity during collecting missions or when dealing with phenotypic diversity during regeneration of diverse ex situ collections of cultivated plants. Results from additional observations using modern molecular methods can be interpreted based on the classical phenotypic groupings and add considerably to our understanding of crops and crop wild relatives.

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