Beta vulgaris, Beet

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1. Taxonomy

Latin   :   Beta vulgaris subspecies vulgaris
French :   Betterave
German   :   Mangold, Krautstiele, Bete, Rote Rübe, Betarübe
English :   Beet

Beet belongs to the genus Beta, the family Chenopodiaceae and the species Beta vulgaris. Beta vulgaris comprises several cultivated forms of B. vulgaris subsp. vulgaris. Cultivars include leaf beet (var. cicla) and root beet (var. esculenta).
Beta sect. Beta encompasses closely related wild, weedy, and cultivated forms of which more than 4350 unique accessions are maintained in seed collections. 250 samples have been classified as leaf beets. Since Beta germplasm is held by various genebanks in the world an internationally accepted classification system should exist, capable to transmit reliable information on Beta genetic resources. Such a consistent classification system for Beta sect. Beta is unfortunately not available, deplored by (Frese, 1991), and still today the situation is not much better. However, the accurate classification of Beta accessions would be a fundamental prerequisite for a purposeful choice of germplasm from collections (Frese, 1991), citing other sources.
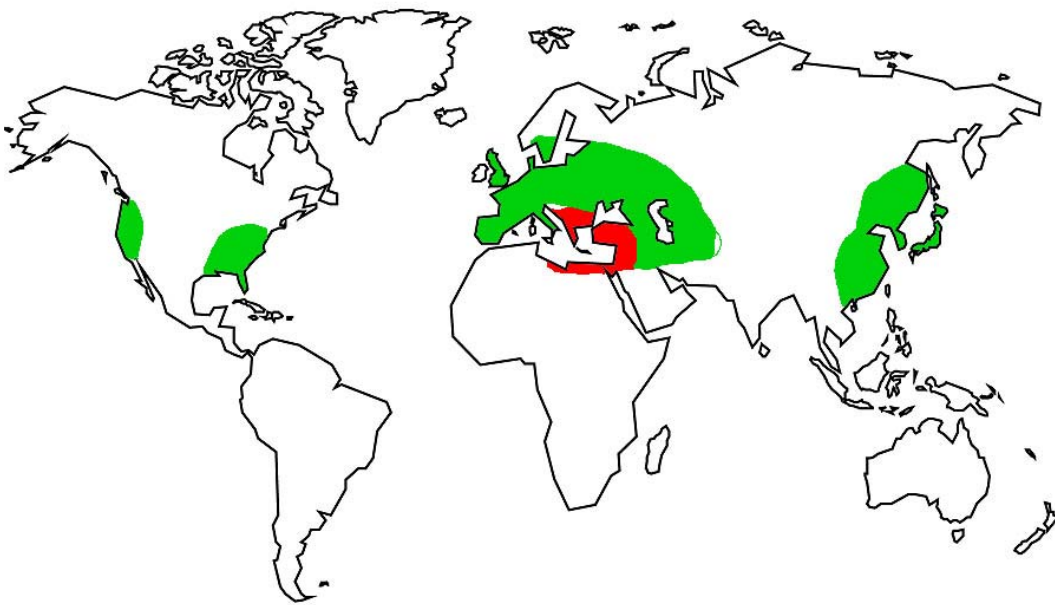
Fig. 1 Biogeography of Beta vulgaris: Green: Area of cultivation, red: area of origin
http://www.mpiz-koeln.mpg.de/oeffentlichkeitsarbeit/kulturpflanzen/Nutzpflanzen/Mangold/index.html

1.1. Classification of beets and problems with cultivars

(Frese, 2003) summarizes the present view on the complex taxonomy of Beta as follows: Though there is a long history of taxonomic research in Beta, no fully consolidated taxonomy of the genus exists. Before 1999, collectors of Beta germplasm had to deal with unsettled taxonomic problems as it is expressed by the 142 synonyms listed by the Mansfeld database (http://ma sfeld.ipk-gatersleben.de/mansfeld/), until two revisions, namely that of Beta section Corollinae (Buttler, 1977) and of Beta section Beta (Letschert, 1993) were published. Both contributions improved our knowledge of the taxonomic structure of the genus. (Buttler, 1977) published the correct names of the four sections as shown in Table 1. Beta section Beta is composed of three species: B. vulgaris, B. macrocarpa and B. patula. B. vulgaris is further divided into two wild subspecies and the cultivated subsp. vulgaris with its four cultivar-groups (Lange et al., 1999; Letschert, 1993). (Lange et al., 1999) argued that none of the morphological or cytological characters are suited to unambiguously delineate taxa within the cultivated beet. All characters used by (Helm, 1957) to distinguish 19 different types of cultivated taxa are subject to continuous variation and will not allow to clearly discern cultivated forms. (Lange et al., 1999), therefore, suggested to apply an open classification system as proposed also by (Hetterscheid et al., 1999; Hetterscheid et al., 1996). The introduction of the "culton" (plural "culta") as taxonomic entity for cultivated beets allowed the formation of large and unambiguous cultivar-groups which can be internationally understood and can be easily handled by users of germplasm who are not familiar with the International Code of Botanical Nomenclature (ICBN) and Latin names. Consequently, the World Beta Network (WBN) recommended the use of the nomenclature as shown in the table below. The introduction of cultivar-groups has simplified the nomenclature and is welcomed as a useful pragmatic approach by beet breeders and other scientists dealing with applied research.

A pictorial summary of the cultonomy view erected by various authors like (Hetterscheid et al., 1999) and (Lange et al., 1999):
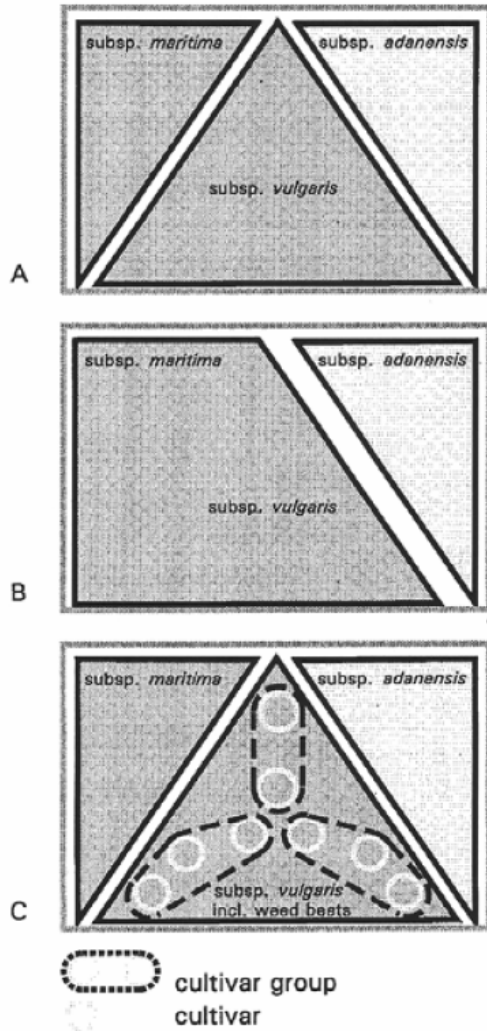
Fig. 2 History of the classification of Beta vulgaris L. A: botanical classification according to (Letschert, 1993). B: another way of botanical classification, without consideration of the nature of wild versus weed populations. C: botanical classification and oben classification with application of the subspecies to distinguish wild and weed pupulations (modified after (De Wet, 1981). From (Lange et al., 1999)

A useful table in beet taxonomy has been summarized by (Frese, 2003)

Primary genepool	**Section *Beta* (syn. *Vulgares* Ulbrich)**
	B. vulgaris L.
	      subsp. *vulgaris* (cultivated beets)
	        Leaf Beet Group
	        Garden Beet Group
	        Fodder Beet Group
	        Sugar Beet Group
	      subsp. *maritima* (L.) Arcang.
	      subsp. *adanensis* (Pamuk.) Ford-Lloyd and Will.
	B. macrocarpa Guss.
	B. patula Ait.

Secondary genepool	**Section *Corollinae* Ulbrich** • Base species *B. corolliflora* Zosimovich *B. macrorhiza* Steven *B. lomatogona* Fisch. and Meyer • Hybrid species *B. intermedia* Bunge *B. trigyna* Waldst. and Kit. **Section *Nanae* Ulbrich** **B. nana Boiss. *and* Heldr.**
Tertiary genepool	**Section *Procumbentes* Ulbrich (syn. *Patellares*)** *B. procumbens* Smith *B. webbiana* Moq. *B. patellaris* Moq.

Fig. 3 Overview of taxonomy of Section Beta (synonymous to Vulgares Ulbrich), from (Frese, 2003) and as described in detail in (Frese et al., 2001b).

However, there are also disadvantages. A taxonomic name like "*Beta* L. *vulgaris* subsp. vulgaris convar. vulgaris provar. flavescens Lam. and DC. f. rhodopleura (Alef.) Helm" readily transfers the information that this germplasm is a red coloured leaf beet with broad petioles. With the replacement of this name by the culton "Leaf Beet Group" this descriptive information linked with the name is lost unless data on petiole width, length, colour etc. have been recorded in an evaluation database. As long as descriptive databases are incomplete it is essential to document the synonyms of accepted names in parallel.
And further on from (Frese, 2003):
(Lange et al., 1999) mentioned another problem. (Letschert, 1993) treated wild species of section Beta, only, and explicitly did not deal with the weedy and cultivated material. As a result, there is no formal link between the wild and cultivated classification system and no possibility to classify weedy types. It is therefore difficult to develop a determination key for the whole genus as noticed by (Frese et al., 2001a). In addition to

taxonomic problems of Beta section Beta, more research is required to consolidate the taxonomy of section Corollinae. (Buttler, 1977) in his thorough revision of section Corollinae could not deal with the hybrid complex in detail nor could he validate the existence of a B. foliosa in Turkey. Section Procumbentes might also need a revision since there are indications that B. webbiana and B. procumbens are closely related if not even identical species (Wagner et al., 1989). Furthermore, there are reasons to assume that the section *Procumbentes* does not at all belong to the genus *Beta* but to a separate genus ((Jung et al., 1993; Williams et al., 1976). Nevertheless, major users of germplasm holdings are satisfied with the taxonomic system presented in Fig. 1 as it transfers all the information they need.

But it would be illusionary to think, that the cultonomy will be an easy approach, the culton diversity and variety is enormous, and with more modern breeding attempts the 'evolution' of such culta will show increasing pace. Already with the classic cultons the attempt to discriminate the different traits is not easy, as shown by a figure from (Helm, 1957):
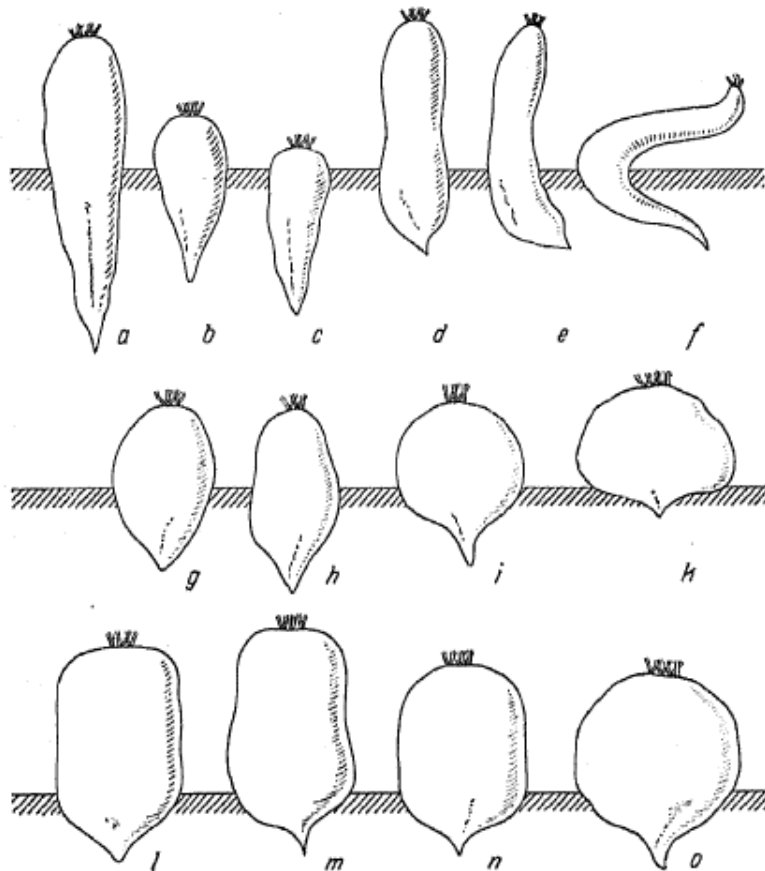
Fig. 4 Scheme of the best known pro-varieties crassa and altissima Döll. a – c: pile-shaped 'Veni-Vidi-Vici', 'Halbzuckerrübe', 'Kleinwanzlebener Zuckerrübe'; d – e: bottle-shaped 'Frankes Rekord', f: shaped like a cows horn 'Weisse Kuhhorn', g – h: olive-shaped 'Ovana', 'Barres', i – k: spheric 'Umstätter' 'Oberdörfer', l – n: barrel-shaped 'Eckendorfer' 'Criewener' 'Kirsches Ideal', o: cask-shaped 'Altenburger Tonne'. An extensive table see p. 215, From (Helm, 1957).

This figure manifests the difficulty to distinguish the traits i: 'Umstätter' from o: 'Altenburger Tonne' with means of shape characters.

The real complexity of shape based genetics has been revealed by (Baranski et al., 2001), one figure from his paper reveals this clearly:
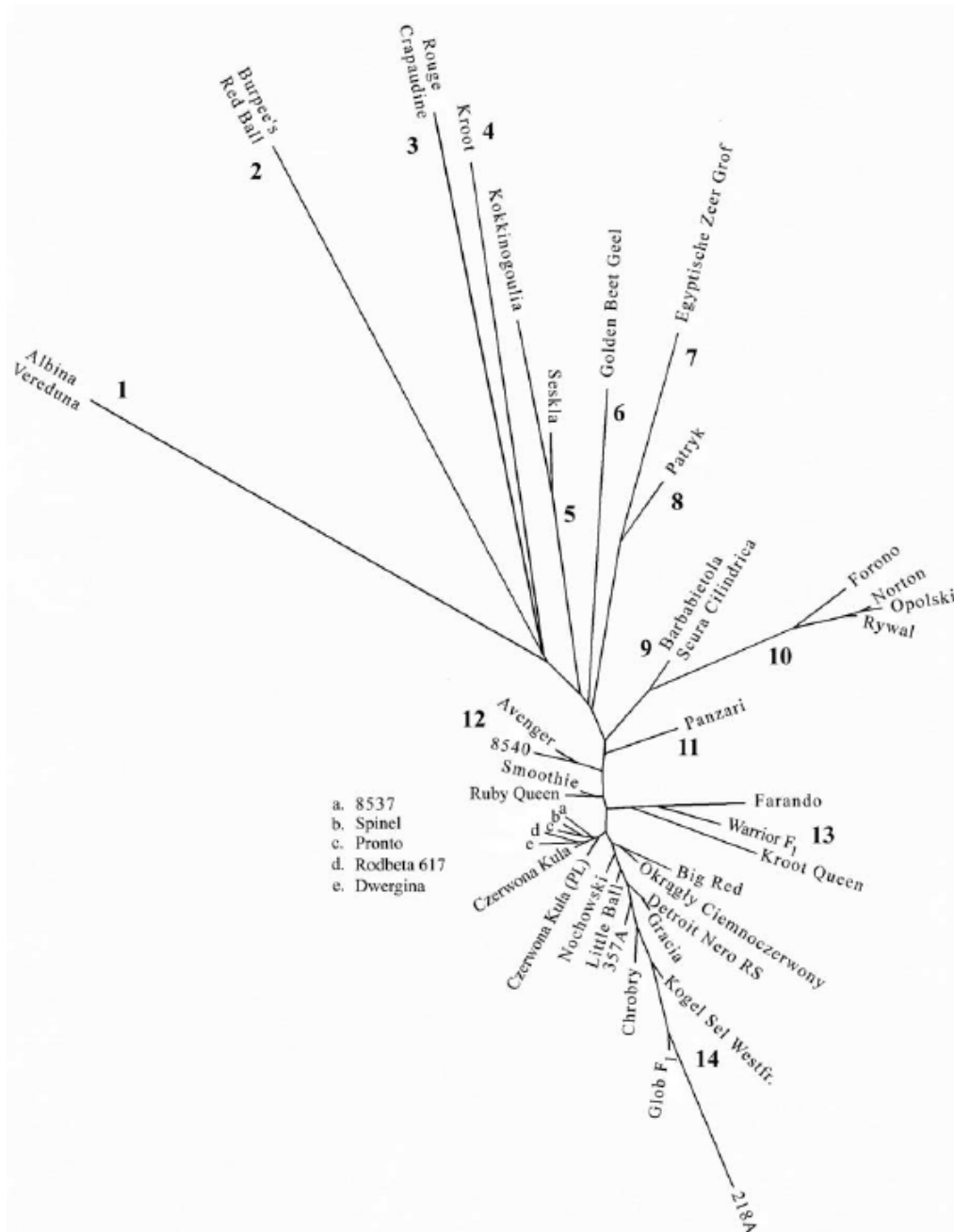
Fig. 5 Diversity with regard to root morphology of 40 accessions of *Beta vulgaris* subsp. *vulgaris* (Garden Beet Group). From (Baranski et al., 2001), who calculated a similar diagram for the chemical components with different branches,

Often the roots within a particular accession were divided into different classes with regard to a given trait. In some extreme cases, roots in one accession belonged to all 9 classes, e.g. skin roughness of cultivar 'Warrior F1'. Assessment of the complex data table using correspondence analysis allowed to reduce the 39 root morphological trait classes evaluated to a few principal components. The first three components accounted for 62% of variation. They were mainly correlated to skin and flesh colour, and in some extend to root shape. These three components allowed to distinguish singular accessions like 'Albina Vereduna', 'Golden Beet Geel', 'Burpee's Red Ball', and Rouge Crapaudine with regard to pigmentation, as well as three groups of cultivars with a narrow elliptic, circular and narrow oblong root shape. All of the accessions were well represented in a 10-dimensional space, where the axes accounted for 97% of the observed variation.

The calculated distances between accessions enabled to visualise the structure of their diversity in an unrooted tree (Figure 1). The core of the tree contained 17 accessions, which were similar in root morphology.

They were characterised by circular root shape, dark red skin with a low level of roughness, dark red flesh, and dark red or non-visible rings. The most distinct accessions were classified to 14 separate groups named by numbers. Nine of these groups contained only a single accession, while the other five consisted of 2 to 4 accessions.

The conclusion: Modern classification must be based on the methods combined of numerical taxonomy and thorough genetic molecular analysis.

1.2. Origin of beets

The cultivated form originates from the Mediterranean area, in the Near East. All cultivated beets may have originated from *B. maritima*, as already (Linnaeus, 1753) knew, but did not admit it officially, and indeed on p. 222 of his classic book he gave a cryptic hint on his own evolutionary view of species origins, which he had to hide at that time of the ruling creationism in order not to provoke the church 'unnecessarily'.

BETA.

maritima.

1. BETA caulibus decumbentibus.

Beta caulibus decumbentibus, foliis triangularibus petiolatis. *Mill. dict.*

Beta fylveftris maritima. *Bauh. pin.* 118. *Raj. angl.* 4. *p.* 127.

Habitat in Angliæ, Belgii *littoribus maris.*

vulgaris.

2. BETA caule erecto.

Beta. *Hort. cliff.* 83. *Hort. upf.* 56. *Mat. med.* 113. *Roy. lugdb.* 220.

rubra.

α. Beta rubra vulgaris. *Bauh. pin.* 118.

β. Beta rubra major. *Bauh. pin.* 118.

γ. Beta rubra, radice rapæ. *Bauh. pin.* 118.

δ. Beta lutea major. *Bauh. pin.* 118.

ε. Beta pallide virens major. *Bauh. pin.* 118.

Cicla.

ζ. Beta alba vel pallefcens, quæ Cicla officinarum. *Bauh. pin.* 118.

η. Beta communis viridis. *Bauh. pin.* 118.
Habitat - - - - -, ♂, forte a maritima, in exoticis, prognata.

Fig. 6 bottom of page 222 of Linaeuss Species Plantarum, with his cryptic hint on the evolution of Beta vulgaris, from (Linnaeus, 1753)

Beta vulgaris L. ssp. maritima, wild sea beet, is regarded as the mother species of the Beta beets (fodder beet, sugar beet, beetroot, yellow beet, Swiss chard). (OECD, 2001). It is indigenous to European coastal regions, particularly the Mediterranean. Beet spinach, convar. cicla, has been cultivated in the Mediterranean region since 2000 B.C. In Europe B. vulgaris species with distinctly swollen roots were cultivated in the Middle Ages. Central European types are presumed to be descended from those used in Arabian horticulture in Spain. These plants were taken to the Netherlands, where they were cultivated beginning in 1500, and then to the Palatinate region, later spreading throughout Germany as "Burgundy beet". During the sixteenth and seventeenth centuries, red and yellow beets became increasingly common as salad vegetables. Fodder beet cultivation only began to increase during the course of the eighteenth century. The crop was introduced into the USA in 1800 where it became known as a garden beet. Sugar beet was introduced to North America around 1830 and to South America circa 1850 (Mansfeld, 1986).

(Bartsch & Ellstrand, 1999) present a dendrogram showing the relationships between cultivated and wild beets:
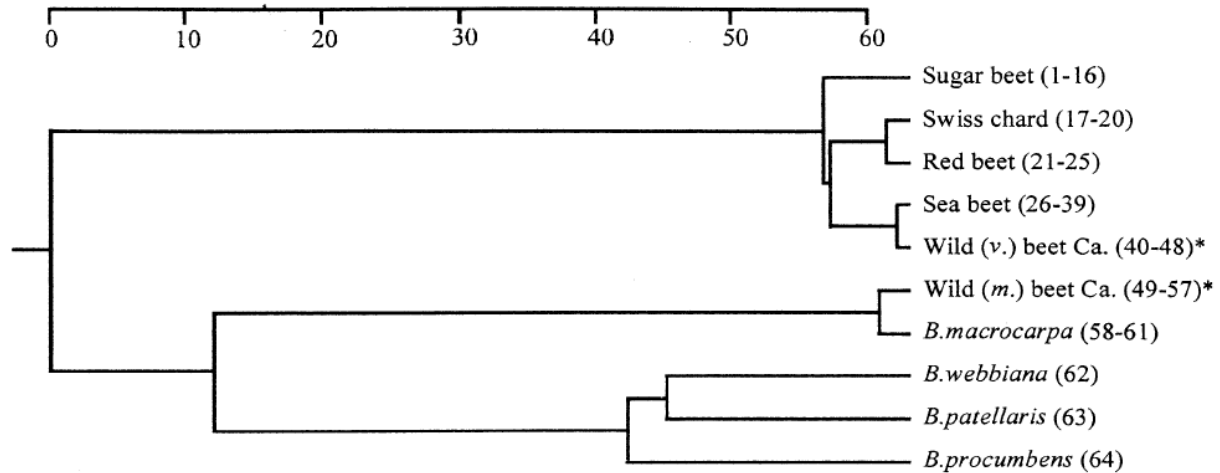
Fig. 7 UPGMA dendrogram of systematic relationships among ten major groups (with accession number) of wild and cultivated beet based on Nei's (1978) genetic distances derived from allele frequencies at 13 polymorphic allozyme loci. From (Bartsch & Ellstrand, 1999)

To evaluate relationships among groups of accessions, we constructed a UPGMA dendrogram based on (Nei, 1978) genetic distances (Fig. 3). According to this pattern, the Californian wild beets have major affinities to both B. vulgaris and B. macrocarpa. In the tree, sea beet clustered with the wild v.-type beet, and the wild m.-type clustered with Old World accessions of B. macrocarpa. By incorporating the three different outgroup species, the unique nature of the two distinct wild Beta species in California is clearly apparent. The genetic distance obtained for B. vulgaris and B. macrocarpa is nearly as great as the distance of each of them to the outgroups of B. procumbens, B. webbiana, and B. patellaris (all of which are cross-incompatible with B. macrocarpa and B.vulgaris). It is remarkable that, despite their substantial distances, hybridization between B. vulgaris and B. macrocarpa is still possible, as both allozyme markers in this study demonstrated and prior literature (Abe et al., 1986; Coons, 1975) has suggested. In summary, we found strong evidence for the classification of B. macrocarpa as a separate species from B. vulgaris. Although the two species are cross-compatible, they are clearly differentiated at the molecular level. In summary, (Bartsch & Ellstrand, 1999) found strong evidence for the classification of *B. macrocarpa* as a separate species from *B.vulgaris.* Although the two species are cross-compatible, they are clearly differentiated at the molecular level.

According to (Boutin et al., 1987) mitochondria1 and chloroplast DNAs from Beta maritima and cultivated Beta vulgaris plants were compared in our study. No variability of chloroplast DNA could be detected between the two taxa. Fertile plants of Beta maritima and Beta vulgaris gave closely similar restriction patterns of mitochondria1 DNA. Beta maritima hermaphrodites from two different provenances present the same pattern and differed from *Beta vulgaris* mtDNA only by three bands. The interesting results of the present study of the Canche population demonstrate a novel cytoplasmic male sterility system which differs from that described by Owen.
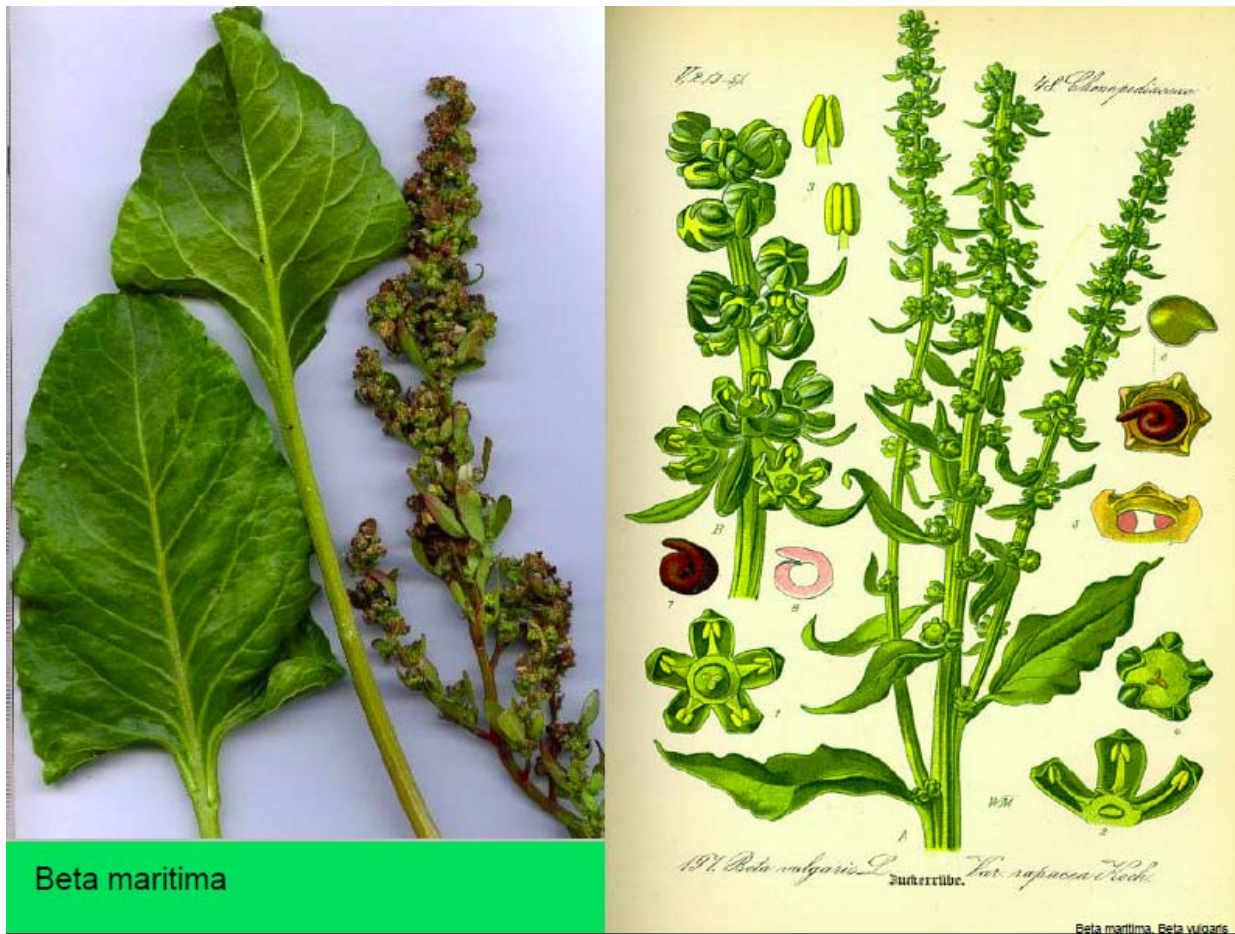
Fig. 8 Beta maritima left: http://perso.orange.fr/argaud/botanique/beta_vulgaris_maritima.html
right: from Prof. Dr. Otto Wilhelm Thomé *Flora von Deutschland, Österreich und der Schweiz* 1885,
Gera, Germany, downloadable from Wikimedia.
http://commons.wikimedia.org/wiki/Image:Illustration_Beta_vulgaris_var._rapacea0.jpg

Beet is an annual, biennial or perennial plant. Crops are essentially biennial and are grown for the swollen root that it develops at the end of the first growing season.

A study by (Desplanque et al., 1999) demonstrated the intermediate position of weed beets between the cultivated and south-western ruderal inland gene pools of beets. Weed beets clearly appeared to be produced by accidental hybridization of cultivated lines and ruderal-beet pollen donors in the seed-production area. This result con"rms the previous study (Boudry et al., 1993; Boudry et al., 1994) which identified their maternal origin. Indeed, the genetic distances used by (Desplanque et al., 1999) are based on nuclear markers with a biparental transmission. This, in turn, makes it possible to infer the paternal contribution, which had been previously determined on the sole basis of the transmission of the bolting gene's B allele. Another interesting result that emerges from the present study is the high genetic diversity of weed beets despite their recent evolutionary history. Their high nuclear genetic diversity contrasts with the previously

found uniformity of mtDNA (Boudry et al., 1993; Boudry et al., 1994). This suggests that: (1) pollen flow from inland to cultivated beets is likely to be both frequent and recurrent, and (2) the transportation of crop-wild hybrids from the seed-production area to the sugar-beet fields in Northern France is also likely to be a recurrent phenomenon rather than the result of a single introgressive event followed by local expansion in sugar-beet fields. By using greenhouse studies on life-history traits, (Bartsch & Schmidt, 1997) suggested that a similar scenario occurs in northern Italy, the other important European seed-production area. Introgression between cultivated and wild beets could therefore be a general trend but one which has to be ascertained more accurately by fine-scale genetic analyses in crop-wild sympatric areas.
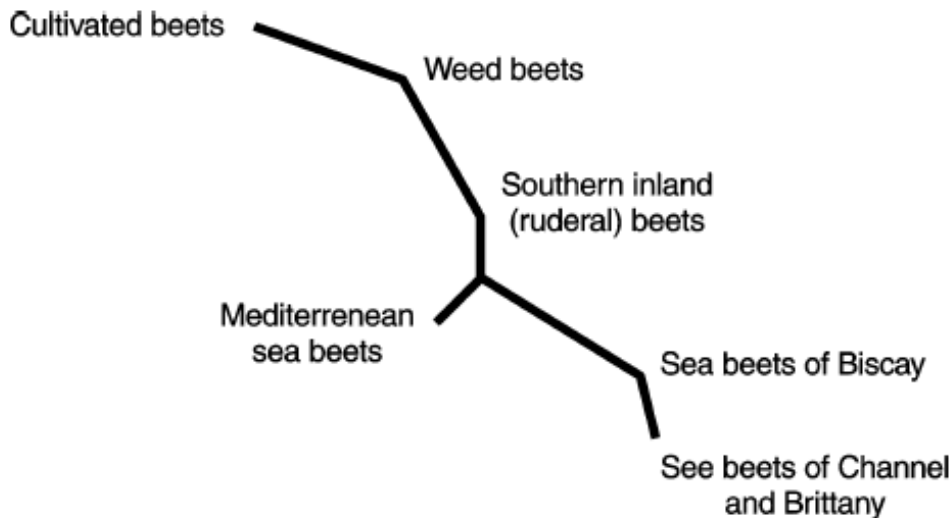
Fig. 9 Unrooted dendrogram inferred from Reynolds' genetic distance matrix between the di!erent forms of beet, based on six nuclear loci (Neighbor-Joining method). From (Desplanque et al., 1999)

The origin of south-western rural inland beets is less obvious. Their genetic diversity appears to be high, since one can find as many alleles in this group as among coastal forms. In addition, their closest relatives appeare to be the coastal beets, in particular those of the Mediterranean, but not the Atlantic beets despite the latter's closer geographic proximity. Genetic proximity is corroborated by the fact that many ruderal populations occur all along a geographic continuum, linking up the south-western seed-production area to the Mediterranean coastlines, while no populations were observed when moving towards the Atlantic coasts. Although these ruderal populations seem to be of wild origin, their position in the tree (Fig. 3) indicates an introgression with cultivated forms.

2. Reproduction biology

2.1. Flowering

Flowers of Beta vulgaris sspp vulgaris are located on the terminal portions of the main axis and on lateral branches subtended from this. Flowers are sessile and occur singly or in clusters of two to eight (Smith, 1980). Flowers are perfect and consists of a tricarpellate pistil surrounded by five stamens and a perianth of five narrow sepals (Smith, 1980). The flowers, solitary or in clusters of 2-8, are rarely selfpollinating (Free, 1970). The flower has a raised ovary with three or four secure stigmata. Three leaves are fused together into a single gynoecium to form the ovary. The seed arrangement is campylotropous.

Beets need a vernalisation in order to flower. However, a small proportion of plant flowers in their first year ("bolters") and may set seeds that persist in the soil. It is probably from this source and from volunteer or "groundkeeper" beets remaining after the harvest, that the population of annual beets that constitute the "weed beet" population arose (Hornsey, 1973a, b, 1975; Hornsey & Arnold, 1979). A second possible source of annual beets is the contamination of seed crops by pollination from annual wild beets (Evans & Weir, 1981; Hornsey & Arnold, 1979; Longden et al., 1974). This may have happened especially in southern Europe during the production of seed of triploid monogerm varieties, where the male-sterile diploids used as mother plants could have been especially susceptible to pollination by diploid plants rather than the intended tetraploids (Scott & Longden, 1970).

Flowering weed beets in sugar production areas have rapidly emerged as a serious problem since the early 1970's in Europe. This weed beet appears to be phenotypically different from volunteer sugar beet in that it produces more seed and in France this seed has been shown to usually not need a vernalization (Harding & Harris, 1994). The weedy form theoretically may have entirely evolved in parallel from bolters *in situ* in sugar producing areas - but more plausibly, molecular evidences suggest that weed beet originated from crosses in seed producing areas along the Mediterranean following by introgression from wild diploid species (Boudry et al., 1993).

Beet is basically a self-incompatible plant (Bruun et al., 1995; Lundqvist et al., 1973; Smith, 1980; Valdeyron, 1884) (the stigma is not fully mature when the flower opens). It is an allogamous species, pollinated by wind and occasionally by insects, the former being the most important. Some cross-pollinations are also done by thrips and syrphids (Free et al., 1975; Valdeyron, 1884) Wind-borne pollen can be distributed horizontally at least 4,500 m and has been observed at vertical distance of 5,000 m (Archimowitsch, 1949). But Gliddon (Harding & Harris, 1994) assumed that the pollen movement takes place to around 8 km. In commercial practice, plantings of related seed types are separate by distances of 1.6 km or more. Fields of unrelated seed types usually are separated by 3.2 km or more, depending on terrain and prevailing winds (Campbell & Mast, 1971).

2.2. Seed dispersal

Sugar beet possesses long-lived dormant seeds that can become a volunteer weeds in sugar beet fields (Hojland & Pedersen, 1994). They tend to germinate in the field 1-3 days later than planted sugar beet seeds (Hojland & Pedersen, 1994). Sugar beet seeds may remain in the soil for ten years or more and still retain some germination capacity (Brouwer et al., 1976; Lysgaard, 1991; OECD, 1993). It is generally accepted that six year-old multigerm and four year-old monogerm sugar beet seed exhibit the same germination level of 70%. Eight-year-old sugar beet seeds have been shown to germinate at a level of 59% in laboratory conditions. These germination percentages depend of the quality of the seeds and of the conditions of germination. Thus Beta vulgaris has the ability to generate a viable seed bank (Hojland & Pedersen, 1994). The seed-balls of Beta are resistant to salt water, and ocean currents can move propagules over relatively long distances. Above the high water line, strong winds distribute them over the shoreline, and sometimes even inland (Smart, 1992).
Since commercial sugar producing sugar beet is biennial and is harvested during the first year whilst still in the vegetative phase, sexual reproductive organs (floral parts) never develop. Varieties that tend to bolt in the first year of growth pose some problems and much effort has gone into developing currently cultivated varieties that limit bolting. When Beta vulgaris is planted for seed production, some seeds may remain on the field after harvesting the seed crop. Agricultural practices tend to limit those shoots.

2.3. Fertility, in- and outbreeding

Most of the sugarbeet grown since 1960s has been triploid. Triploids are produced by crossing tetraploid parents with diploid male sterile and are usually doubly sterile because of chromosome imbalance and cytoplasmically inherited male sterility. However, a small proportion of plants does produce aneuploid pollen some of which will give fertile progeny on crossing with diploids. Diploid varieties (2n=18) are now used more frequently, as they allow the production of true F1 and 3- and 4-way cross in breeding programs.

Certain inbred sugarbeet lines are reported to have developed apomixis and are thus able to reproduce without fertilisation (Bruun et al., 1995; Fang et al., 2004; Gao & Jung, 2002; Jassem, 1976; Jassem & Jassem, 1971; ReamonButtner et al., 1996).

A summary of breeding systems and seed yield of Beta vulgaris and relatives is given by (Frese, 2003)

Botanical name	Seed type	Prevailing breeding system*	Days from sowing to flowering	Average single plant seed yield in gr. (min–max)
B. vulgaris Leaf Beet Group	Normal	Outcrossing	up to 180	70 (15-170)
B. vulgaris Garden Beet Group	Normal	Outcrossing	up to 180	40 (15-70)
B. vulgaris Fodder Beet Group	Normal	Outcrossing	180	50 (15-70)
B. vulgaris Sugar Beet Group	Normal	Outcrossing	180	50 (15-70)
B. vulgaris subsp. maritima	Varying degrees of dormancy	Outcrossing	40-260	30 (4-110)
B. vulgaris subsp. adanensis	Varying degrees of dormancy	Inbreeding	40-60	20 (13-75)
B. macrocarpa	Varying degrees of dormancy	Inbreeding	40-60	20 (8-57)
B. patula	Normal	No records	40-60	12
B. corolliflora	Hard pericarp	Outcrossing	430	30 (25-50)
B. macrorhiza	Hard pericarp	Outcrossing	420	10 (1-21)
B. lomatogona	Hard pericarp	Outcrossing	450	5 (1-26)
B. intermedia	Hard pericarp	Apomictic	450	20 (15-25)
B. trigyna	Hard pericarp	Apomictic	430	30 (25-50)
B. nana	Hard pericarp	No records	No records	No records
B. procumbens	Hard pericarp	Outcrossing	60	20 (2-80)
B. webbiana	Hard pericarp	Outcrossing	60	20 (2-80)
B. patellaris	Hard pericarp	Inbreeding	60	20 (2-80)

*according to JASSEM (1992) and own observations

Fig. 10 Overview on breeding systems and seed yield of Beta vulgaris and its relatives, * according to (Jassem, 1992), from (Frese, 2003)

Beta vulgaris belongs to the section Vulgare with B. maritima, B. macrocarpa, B. patula and B. atriplicifolia that are the wild species of the cultivated beet (Valdeyron, 1884). All these species are cross-compatible (Smith, 1980). No evidence of interfertility has been found between the cultivated beet and the Caucasian beet (Beta trigyna), an introduced ornamental species.

The Beta vulgaris subspecies are relatively interfertile ; they are pollinated by both wind and insects, while being self-incompatible.

2.4. Resulting hybridisation

It is an old and persistent problem in assessing outcrossing impact that many studies do not distinguish between *potential* and *realized* outcrossing (gene flow, bolting and seed dispersal).
Sugar beet is normally triploid, produced by crossing tetraploid pollen parents with diploid male sterile genotypes. Such hybridisation cause chromosome imbalance and instability in hybrids that often results in both male and female sterility. However, it is assumed that bolters will hybridise with weed beets to some degree.

Sugar beet and sea beet (Beta maritima) are both protandrous, self-incompatible and gynodioecious. Male sterility is under the control of the cytoplasm with nuclear genes restoring male fertility (although cultivated and wild beet may have different nuclear and cytoplasmic components (Boutin et al., 1988; Boutin et al., 1987; Owen, 1945). They can hybridise freely and hybrids are spontaneously formed in the wild and in seed-production fields.
There is extensive evidence of hybridisation in the wild between, and introgression from wild beet to sugar beet.
Sugarbeet can hybridise with other wild beet species (B. procumbens, B. webbiana and B. patellaris) (Hojland & Pedersen, 1994). Strong hybridisation barriers exist between sugarbeet and *B.* vulgaris subsp. Macrocarpa (but still records exist) or subsp. patula. More references to hybridization dynamics of Beta vulgaris in (Bartsch et al., 1999; Desplanque et al., 2002; Driessen et al., 2001; Lorenz et al., 1994; ReamonButtner et al., 1996; Schmidt et al., 1997; Viard et al., 2004; Viard et al., 2002)

2.5. Bolting

A special problem for beet cultivation is bolting. (Boudry et al., 1994) demonstrated, that annual habit which results in bolting is due to complete or partial absence of the vernalization requirement and can cause severe problems in the beet crop. The absolute vernalization requirement in beet is controlled by a major gene B (bolting), known to be linked to the gene R (red hypocotyl color), in linkage group I. (Boudry et al., 1994) studied segregation for the B and R genes in several beet progenies. Penetrance of the annual habit in Bb genotypes was affected by both environmental and genetic factors. The precise location in linkage group I of the major gene B was found by restriction fragment length polymorphism (RFLP) analysis in a back-cross progeny exhibiting partial penetrance of the annual habit. Evidence of pseudo-compatibility was found in the wild coastal beet (Beta vulgaris ssp maritima) used as the mother plant of the back-cross: the selfing rate was estimated as 7%. See more on bolting in chapters on hybridization and risk assessment.

4. Biosafety considerations

4.1. General remarks

Sugarbeet may itself become a weed through the remaining roots or crowns left in the field after harvest. These sources of flowers need to be eradicated by effective herbicide.

Even without hybridisation, the transgene may be able to persist in weed beets derived from bolters or volunteers and from seeds remaining viable for many years in the soil. Introgression of these plants or of the wild beet with the crop and selection under cultivation could produce annual weed beet, as in the past, containing the construct. Thus the escape of the transgene to a crop weed, and perhaps to a lesser extent to a weed of disturbed habitats, is entirely plausible. It is a realistic scenario to deal in risk assessment and risk management with transgenic feral populations. This possibly will be made less likely by retention of doubly sterile triploid varieties, decreased frequency of bolting and by producing seed in selected areas away from the coast in southern Europe. It will be made more likely to depend on the method of designing the nature of the finished transgenic variety and the extent to which it can be mixed by diploids.

Cultivated beet may possibly run wild but it is difficult to distinguish between cultivated beets and the wild beet. Beet is often found outside cultivation but there is no indication of such plants establishing in the wild (Frietema, 1996).
Transfer of the transgene from cultivated beet to sea beet is also possible (Bartsch et al., 1999).
The sugarbeet does not generally reproduce asexually, but some varieties have been developed for apomixis (Hojland & Pedersen, 1994). See also: (Fang et al., 2004; Gao & Jung, 2002; Jassem, 1976; Jassem & Jassem, 1971). In conclusion, aware of the difficult gene flow situation, see chapter 4.2., apomictic Beta should be a desirable option.

4.2. Gene flow studies

Gene flow studies have been carried through by (Desplanque et al., 2002)
The figure below demonstrates the complexity of gene flow possibilities.
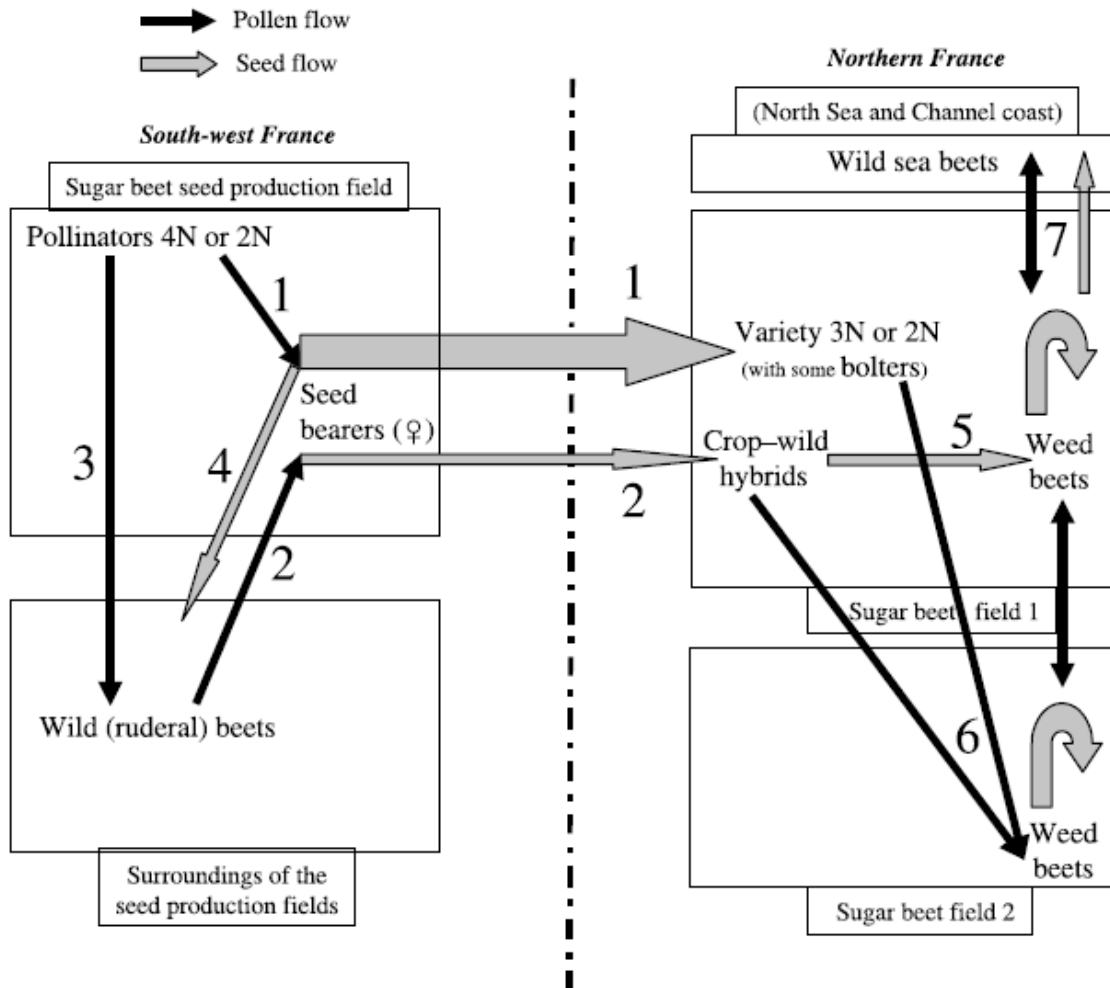
Fig. 11 A schematic presentation of the possibilities of gene flow by seeds and pollen in the sowing seed-production area (left) and in the sugar-production area (right). The seed bearers are male-sterile, the pollinator plants are hermaphrodite; all other plants can be both. The pollinator plants can be tetrapoid (4N) or diploid (2N), leading to triploid (3N) or diploid (2N) varieties, respectively; all other plants are usually diploid. From (Desplanque et al., 2002)

In a summary, the authors give a comprehensive view of gene flow in the seed production and sugar production areas in France, which are strictly separated:

1. Weed beets pose a serious problem for sugar beet Beta vulgaris crops. Traditionally, the only efficient method of weed control has been manual removal, but the introduction of transgenic herbicide-tolerant sugar beets may provide an alternative solution because non-tolerant weed beets can be destroyed by herbicide. The possibility that new, transgenic, weed beets may arise by gene flow between wild and crop plants was evaluated.

2. In a study area in northern France, weed beets were present in variable densities in sugar beet fields of up to 80 weed beet plants m $^{-2}$. Weed beets arise from a long-lived seed bank, with seeds germinating from depths of 5 cm or less. In addition, diploid F1 crop–wild hybrids and triploid variety bolters (individuals with a low vernalization requirement) were present in low densities in virtually all sugar beet fields. The authors found gene flow to be possible between all forms, illustrated by both overlapping flowering periods in the field and successful controlled cross-pollinations.

3. The F1 crop–wild hybrids result from pollination in the seed-production region by wild plants possessing the dominant bolting allele B for flowering without experiencing a period of cold. In the case of a transgene for herbicide tolerance incorporated into male-sterile seed-bearer plants, such hybrids will contain both the herbicide-tolerance and the bolting allele. Contamination of the fields by transgenic weed beets will be the result *unless bolters are removed manually.* The same will apply in the case of a cytoplasmically inherited transgene.

4. Incorporation of the transgene into the pollinator plants will prevent the immediate formation of transgenic weed beets. However, in sugar beet fields, variety bolters may successfully cross-pollinate with weed beets in neighbouring fields. The use of diploid pollinator plants instead of tetraploids will considerably enhance gene flow towards wild beets, and is not, therefore, an attractive option.

5. In conclusion, the appearance of transgenic weed beets is possible *but can best be* retarded if the transgene for herbicide tolerance is incorporated into the tetraploid pollinator breeding line.

4.3. Competition, fitness as an assessment factor

However, the research team of (Bartsch et al., 2001) demonstrated in field trials with transgenic sugar beet that the competition factor strongly influences the results. Transgenic beets with beet necrotic yellow vein virus (BNYVV) coat protein (*cp*), phosphinothricin-acetyl-transferase (*bar*), and neomycinphospho-transferase (*nptII*) genes were hand-crossed to Swiss chard. The resulting F1 plants and controls were grown at two different BNYVV infestation levels and three different competitive conditions with *Chenopodium album*. Transgenic hybrids had consistently higher biomass than controls under high background BNYVV infestation, ad consistently lower biomass than controls under low background infestation. The transgenic hybrids had a significantly lower rate of bolting than controls at all sites. Competition with Chenopodium album always had a strong negative influence on the performance of all genotypes. The authors conclude that ecological implications due to the introduction and spread of virus-resistant transgenic hybrids will be observed only in those feral Swiss chard and wild beet populations where
fitness is significantly influenced by high infestations of BNYVV.

Weed competition always had a strong negative influence on all genotypes (Fig. 5), but there was no statistically significant interaction between competition and genotype as well as between competition and virus infestation. Additionally, no three-way interaction was observed for genotype x competition x virus infestation.
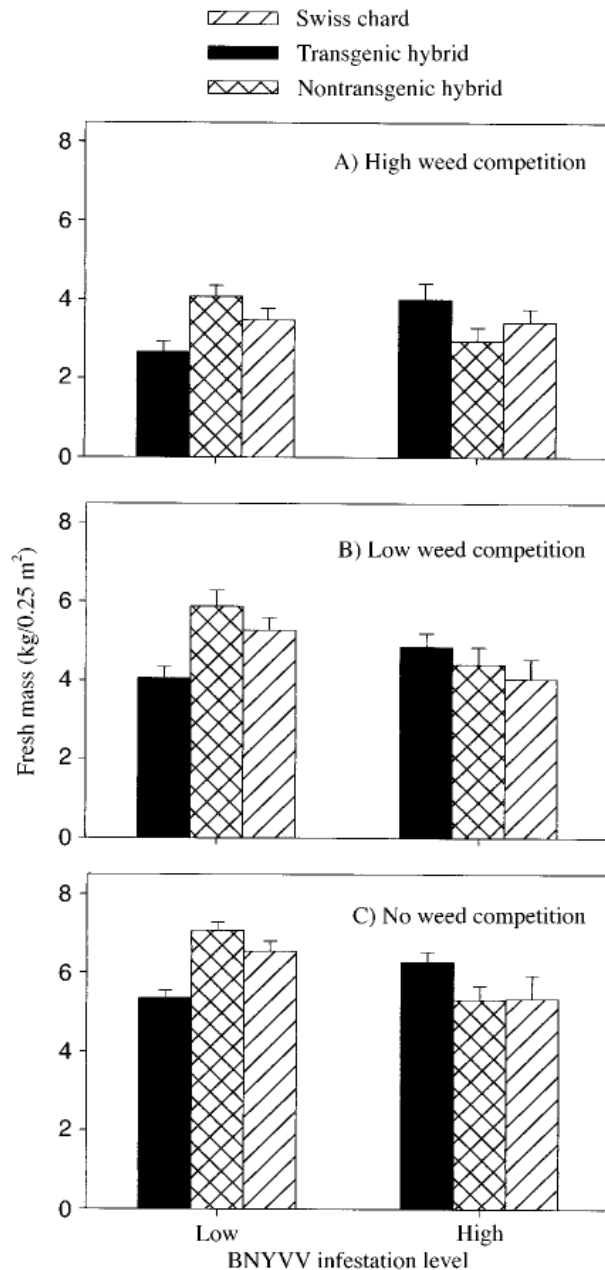
Fig. 12   Performance of transgenic and nontransgenic Beta vulgaris. The biomass production (1 1 SE) in the field test included a hybrid between transgenic sugar beet and Swiss chard, a nontransgenic hybrid, and the female Swiss chard parent. The plants were grown first in the greenhouse and then planted in three different competition densities with Chenopodium album (Fig. 1A–C) sites with either low or high BNYVV infestation. From (Bartsch et al., 2001)
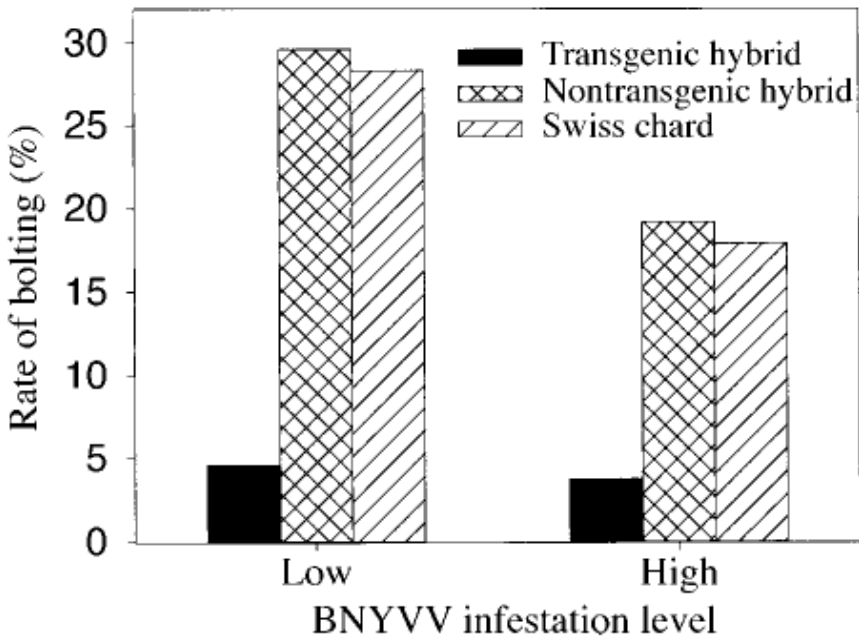
Fig. 13 Bolting rate of experimental plants in the study from (Bartsch et al., 2001)

In contrast to the hybridization rate not showing significant differences, the bolting rate of the transenic traits is significantly lower, probably due to pleiotropic effects: The transgenes cause a lower competitiveness as (Bergelson & Purrington, 1996) suggested with the term 'cost of resistance'. The unexpected phenotype demonstrates that genetic engineering may alter life histories in unintended ways (Linder and Schmitt 1995, Bergelson et al. 1998). For what ever reason, the bolting depression would probably reduce, but not eliminate, the risk of gene flow to wild relatives of cultivated plants. But as long as we have not more experience, we will have to anticipate that the bolting depression depends also of the nature of

4.4. Seed dispersal

(Arnaud et al., 2003), concluded, that although pollen usually represents a significant vector for the spread of genetically modified traits, the present results suggest: (i) that seed flow may have a deeper and longer impact in connecting wild and crop relatives within the complex *Beta*; and (ii) point out the key role of a long-lived seed bank, a factor often neglected. Sugarbeet seeds aged of 8 years can germinate till 59% in laboratory conditions.
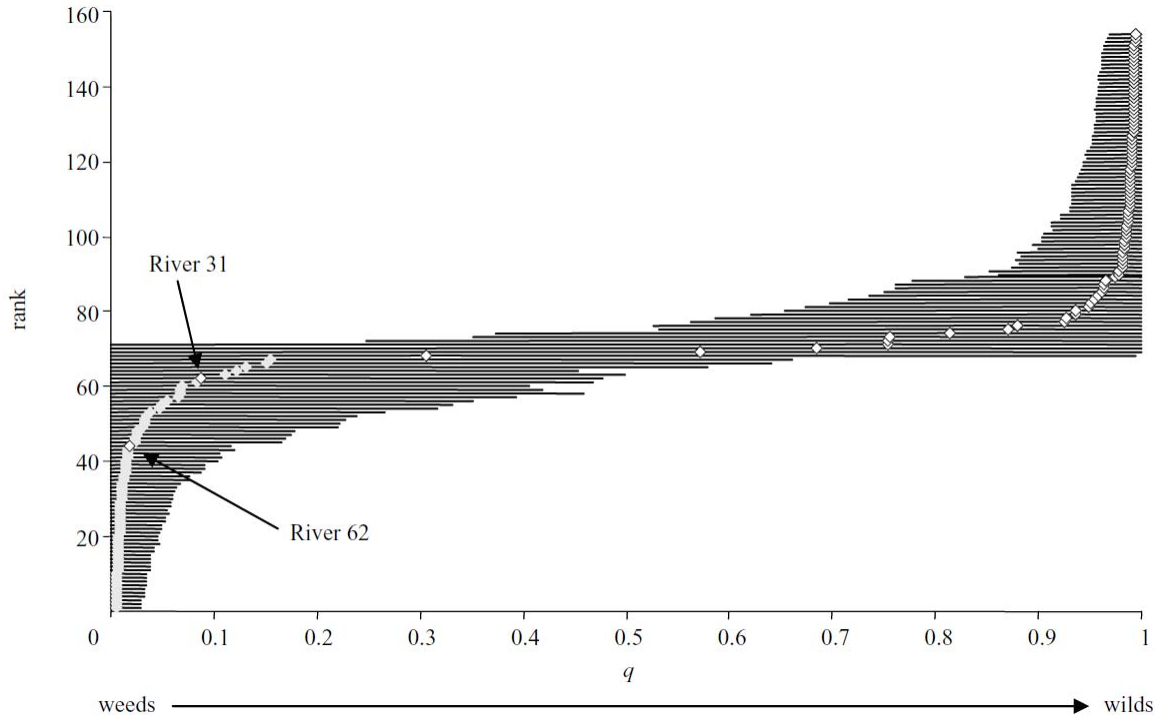
Fig. 14 Distribution of the mean individual admixture coefficients *q* estimated using Structure (Pritchard et al., 2000) without prior population information. In this analysis, *K* (the number of population contributing to the gene pool of all sampled individuals) is assumed to be 2. Individuals were ranked from lowest to highest *q*-values and ranks were plotted against *q*. A *q*-value of 1 denotes a wild individual, whereas 0 denotes weedy individuals. Also displayed are lines giving the 95% posterior probability intervals of *q* for each individual. The cytoplasmic status of individuals is represented by a grey diamond for a OwenCms cytoplasm and a white diamond for a non-OwenCms cytoplasm. From (Arnaud et al., 2003).

4.5. Mitigation of gene flow

4.5.1. Cytoplasmic Male Sterility (CMS)

In an extensive study, (Satoh et al., 2006) demonstrate the complexity of the location and function of the Owen Cytoplasmic Male Sterility (discovered by (Owen, 1945): The mitochondrial genomes of normal fertile and male-sterile (Owen CMS) cytoplasms of sugar beet are highly rearranged relative to each other and dozens of inversional recombinations and other reshuZing events must be postulated to interconvert the two genomes. In this paper, a comparative analysis of the entire nucleotide sequences of the two genomes revealed that most of the inversional recombinations involved short repeats present at their endpoints.

Attention was also focused on the origin of the Owen CMS-unique mtDNA regions, which occupy 13.6% of the Owen genome and are absent from the normal mtDNA. BLAST search was performed to assign the sequences, and as a result, 7.6% of the unique regions showed significant homology to previously determined mitochondrial sequences, 17.9% to nuclear DNA, 4.6% to mitochondrial episomes, and 0.1% to plastid DNA. Southern blot analysis revealed that additional sequences of nuclear origin may be included within the unique regions. We also found that the copies of many short

repeat families are scattered throughout the unique regions. This suggests that, in addition to the incorporation of foreign DNAs, extensive duplication of short repetitive sequences and continued scrambling of mtDNA sequences may be implicated in the generation of the Owen CMS-unique regions.

This is illustrated in the below figure:
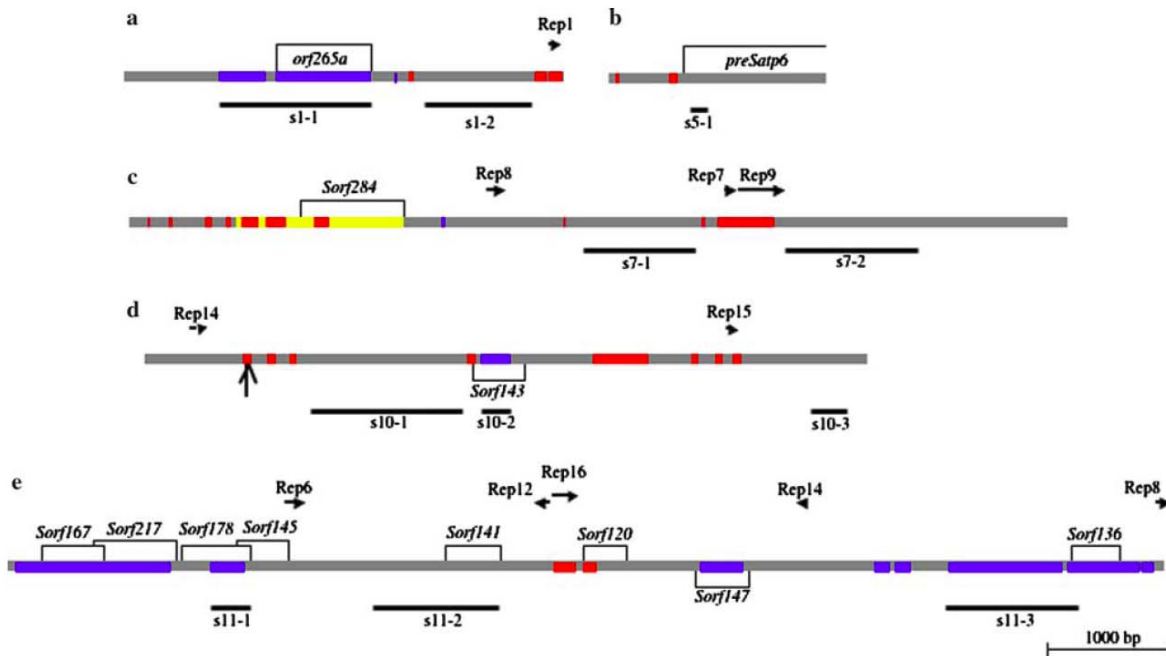
Fig. 15 Organization of Wve Owen CMS unique regions: s1 (a), s5 (b), s7 (c), s10 (d) and s11 (e). *Scale bar* is shown below. BLAST search revealed that the unique regions contain sequence segments homologous to nuclear DNA (shown in *blue*), previously characterized mtDNA sequences (*red*) and mitochondrial episome (*yellow*). The extent of ORFs is indicated by *open boxes*. Their direction is from left to right for those above lines and from right to left for those below lines. Probes for hybridization experiments are shown by *black horizontal bars*. Repeated sequence families are shown by *horizontal arrows*. A *vertical line* in d indicates a sequence segment homologous to *Arabidopsis* and rapeseed mtDNA but not to TK81-O mtDNA

The origin of Owen CMS is an interesting and open question. Bonavent et al. (1989) speculated that in the past, a cross occurred between a CMS plant of the old garden-beet cultivar 'Crapaudine' and a sugar-beet plant, and some individuals of the progeny were collected by Owen. The Owen cytoplasm was also reported to be rarely found in wild beet populations growing along the French coasts (Laporte et al., 2001). This raises the possibility that a fertile progenitor to the Owen cytoplasm and/or the derived sister cytoplasms may be discovered in garden-beet landraces or wild beet accessions. Such cytoplasms, if any, would be valuable materials to gain a better understanding of how and when the Owen mitochondrial genome was created. A lot has been published about CMS, some links are given in the bibliography: (Boutin et al., 1987; Fenart et al., 2006; Ferrant & Bouharmont, 1994; Hallden et al., 1991; Hornsey, 1973a; Ivanov et al., 2004; Ivanov et al., 2005; Khvorostov et al., 2001; Kubo et al., 1999; Laporte et al., 2001; Lorenz et al., 1994, 1997; Majewska-Sawka et al., 1993; Owen, 1945; Ran & Michaelis,

1995; Sadoch et al., 2003; Saeglitz et al., 2000; Satoh et al., 2006; Saumitoulaprade et al., 1993; Smith & Ruppel, 1980; Weihe et al., 1991)

4.5.2. Apomixis

(Fang et al., 2004) constructed a plant-transformation-competent binary BAC library for the B. corolliflora chromosome 9 monosomic addition line in sugar beet (M14). This library was estimated to have an average insert size of 127 kb and to be equivalent to 7.5 haploid genomes of the addition line, which contains not only the entire genome of sugar beet, but also the B. corolliflora chromosome 9 carrying the genes responsible for apomixis. Therefore, this library will be useful for isolation of the genes for apomixis in M14, as well as for genome research in sugar beet in general. Furthermore, because the library was cloned into an Agrobacterium-mediated, plant-transformation-competent binary vector pCLD04541 (Jones et al., 1992; Tao & Zhang, 1998), it can be directly transformed into plants via Agrobacterium. Therefore, this library will streamline the identification of apomixis genes and large-scale functional analysis of sugar beet genome sequences by transformation. The authors identified the BACs that originated from the B.corolliflora chromosome 9 and developed a sublibrary (bcBAC-IX) of clones specific for this chromosome. The sublibrary contains a total of 2,365 clones, providing genome coverage of approximately 3.8 equivalents of the alien chromosome (80 Mb). The genome coverage of the sublibrary is highly consistent with that which was expected. This sublibrary represents an important resource for the molecular characterization of the alien chromosome and the final isolation of the genes for apomixis. However, it is possible that this sublibrary may not completely cover the whole alien chromosome.

(Fang et al., 2004) give furthermore some final remarks about results: Successful transformation of large DNA fragment via binary BAC or TAC has been reported by (Hamilton et al., 1996; Hamilton et al., 1999; Liu et al., 1999). This system would make it feasible to study the expression of plant genes or gene clusters in their native genomic context and might eliminate genomic site-dependent gene expression. Therefore, it would be applicable for the isolation of genes that encode complex quantitative traits as well as genes within complex loci located in a chromosomal region of low recombination frequency (Hamilton et al., 1996; Liu et al., 1999). Combined with the physical map and genetic delimitation of the chromosomal region in which the apomixis locus resides, the genes for apomixis could be identified by genetic transformation of successive binary BAC clones in the contigs, or selective transformation of candidate binary BAC clones containing ESTs of interest within the delimited chromosomal region. Thus, the practically impossible long distance chromosome walking and precisely positioning of the apomixis gene(s) in the conventional positional cloning could be avoided. Further literature on apomixis: (Bruun et al., 1995; Gao & Jung, 2002; Jassem, 1976; Jassem & Jassem, 1971; ReamonButtner et al., 1996)

4.5.3. Monitoring schemes
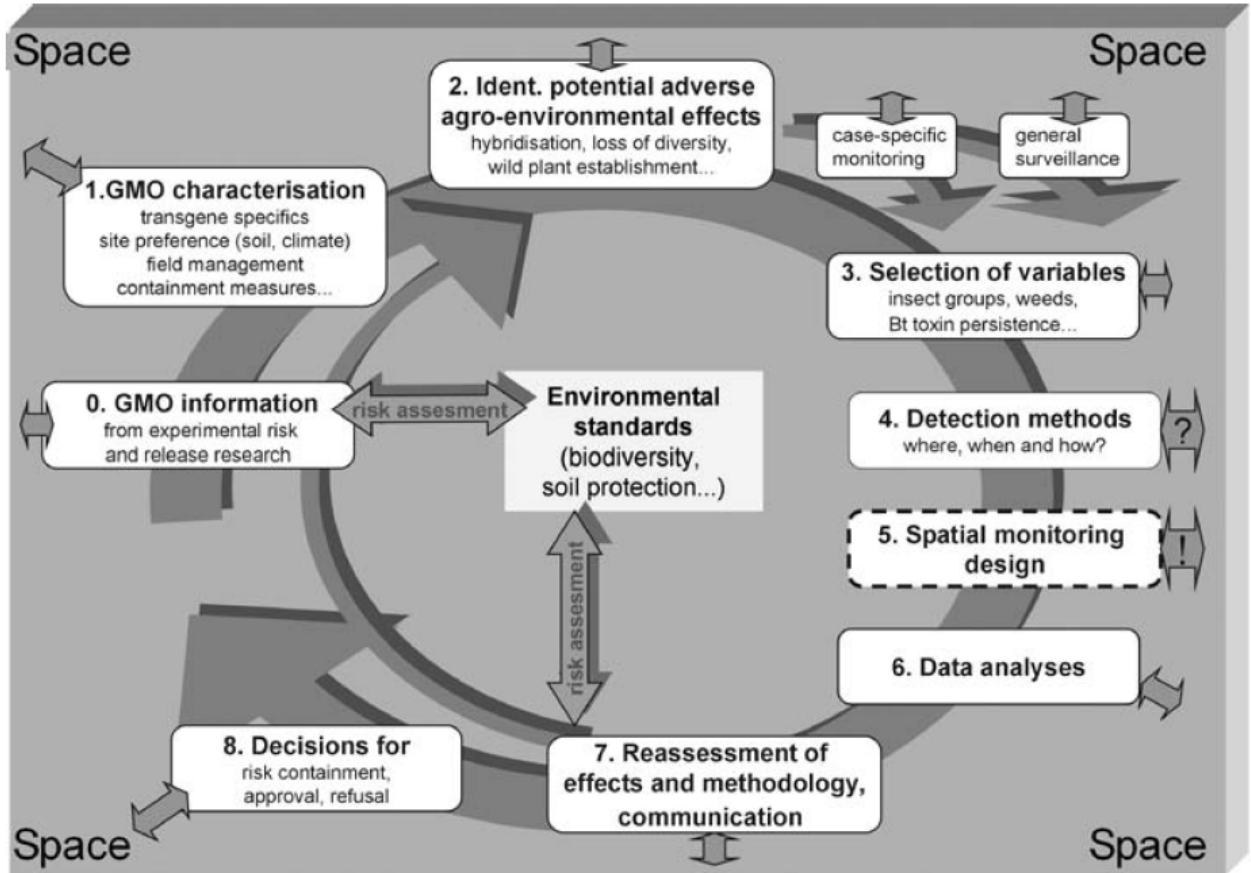
Fig. 16 StepwiseGMOmonitoring and assessment approach (Umweltbundesamt, 2001, modified), from (Graef et al., 2005).

(Graef et al., 2005) propose a monitoring system as shown in fig. 18 with the following steps: (1) characterisation of the market-ready GM crop from release-related risk research information; (2) information on potential adverse environmental effects. Both (1) and (2) are part of the environmental risk assessments prior to environmental release; (3) selection of indicators for anticipated adverse effects, in the following referred to as variables. The choice of variables to be monitored should be scientifically based, in particular depending on their exposure and on their indicator value. Various research groups, e.g. (Firbank et al., 2003; Romeis et al., 2006; Saeglitz et al., 2006; Zueghart & Breckling, 2003) have proposed concepts for selecting monitoring variables for potential agro-environmental effects of GMplants; (4) analytical methods by which these can be measured and evaluated; (5) adapted spatial design of a GMcrop monitoring network. Once GM crop monitoring is carried out, (6) measurement data are produced and analysed. From the results (7) subsequent risk (re)assessments are carried out to derive (8) decisions on risk containment, approval or refusal of the GM plant and to possibly adapt the monitoring methodology.

Strand	Question	Score
CPW	***Propensity for successful pollen-mediated gene flow between the crop and wild relatives***	
CPW1	Do interfertile wild relatives of this crop exist ? (0/1) southern Europe yes, northern Europe no	1
CPW2	Is there a probability that the crop will flower and produce viable pollen during its cultivation? (0/1)	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)	6
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)	1

Strand	Question	Score
CPC	***Propensity for successful pollen-mediated gene flow between the crop and related commercial varieties***	
CPC1	Probability that crop flowers and produce viable pollen during its cultivation? (0/1)	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)	6
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)	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)**   **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)**   **1**

CGC3   **Does crop produce volunteers and/or seed deposits and pose an environmental threat ? (0/1)**   **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)   **3 (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,**

Fig. 17 Beta vulgaris, var. Rapa Dum. 55   common beet Missouri Botanical Gardens, Rare Books: From Köhlers Medizinalpflanzen in naturgetreuen Abbildungen mit kurz erläuternden Texten, 1883-1914
http://www.illustratedgarden.org/mobot/rarebooks/page.asp?relation=QK99A1K6318831914B1&identifier=0344

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