

# About the origin of feral crops and their relatives, their detection in historic records

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## **1. General Introduction**

Agronomists and ecologists use the terms *weed* and *weediness*, *feral crops* and *domestication of crops* in different ways, and this is often a source of misunderstanding, especially in discussions related to modern breeding. For agronomists, the problem of weediness is solved if the aggressive weed can be removed from the agrosystem by means of adapted measures. They most often do not care about feral populations, since they survive in marginal situations not disturbing production and yield. They are generally also not interested in weed behaviour outside of agrosystems, i.e. in (semi-)natural habitats. From the ecologist's perspective, invasions of weeds into (semi-)natural plant communities are potentially risky. Highly competitive invaders are able to disturb the species pattern of plant communities. As a result, rare indigenous species of tropical islands, of regions and even continents with an old flora, only weakly influenced by migrations of the last few millenias are often weak competitors, be eliminated or markedly reduced in coverage. In worst case scenarios, the invader succeeds in occupying the entire surface of certain areas as a near monoculture, this at least for several years or decades to come until new and 'natural' enemies are fighting back. Maybe seemingly less dramatic, but for the eyes of trained field ecologists still worrisome, are dynamic situations where ecological niches are invaded, precisely wiping out rare indigenous species. This can happen (and unfortunately has happened in the past) with ecological dynamics which is triggered off by agriculture and horticulture, not to speak about all the lenient introductions of aggressive species through international traffic of all kinds. (Ammann, 1997)

It should be clear to all readers, that this problematics is not focussed on transgenic plants alone. It is just 'the bad luck' of this new and elegant technique that it offers more clarity to the agro-ecologists, since transgenes can be followed on a long term basis very precisely. It is now emerging through new field research, that the present day transgenes (Bt proteines to create insect resistance etc.) do not have a dramatic impact on ecosystems, although lab studies clearly show some toxic effects. It will be a future chance to follow the transgenes in their fate in agricultural systems, and thus we will learn about crops and their wild relatives and feral populations.

The disease resistance (whether transgenic or not in its origin) may reveal to be a decisive factor for competitiveness enabling the species, which has so far been retained by disease attacks to spread, thus upsetting the pattern of species.

But even crops themselves may cause a weed problem as studies on *oilseed rape* have shown (Schlink, 1994; Schönberger & de Vries, 1991). Nowadays, volunteering oilseed rape

(*Brassica napus*) has to be controlled by means of an adapted crop rotation system and tillage techniques, sometimes combined with herbicide applications. Furthermore, feral populations can often be observed in disturbed habitats outside agrosystems. How long such a population can survive needs to be checked. In addition, its potential for invading natural plant communities has to be analysed.

By means of an appropriate long-term monitor system observing potentially problematic weeds and their potential (natural) habitats, changes in the pattern of wild species have to be detected at an early stage. Also certain crops, such as oilseed rape will have to be included in the future monitoring system (Ammann et al., 2000). It is an illusion that problematical weed types can „easily“ be eradicated, see (Hartmann et al., 1994). Therefore, early detection of such weed types is essential.

Overall the discussion shows that aggressive weeds are not directly related to the new technologies, and also not related to most feral populations, but in worst case scenarios it is imaginable that the transgenes may contribute. It will be of great importance to follow up pertinent cases, and make good use of the new precision the technology offers.

## **2. Definitions**

### **2.1. From weeds and feral crops**

For an extensive review of definitions, concepts and ecological characterisations of weeds and of the anthropogenic flora see (Lambelet-Haueter, 1990, 1991) as well as (Holzner, 1991) and (Oka & Morishima, 1982) . The current literature reflects the fact that various concepts coexist and that there is no such thing as a generally accepted ‘classic approach’. Referring to feral crops we follow the usual definitions: Feral plants are often semi-domesticated, escaped from the field a long time ago, having been domesticated and now growing wild. But growing wild has to be circumscribed properly: Only in exceptional cases a feral crop really grows in the wild, usually such populations stick to ruderal places, to disturbed habitats, in the dense competitive environment of natural habitats such as dry meadows it is very difficult for weeds and feral plants to establish permanently.

(Lambelet-Haueter, 1990, 1991) divide weed definitions up into popular, economical and ecological concepts whereas (Holzner, 1991) groups them similarly into subjective and ecological ones.

*Popular* as well as *subjective concepts* define weeds as plants growing in the wrong place, causing damage, being of no benefit and suppressing cultivated plant species.

*Economical concepts* reflect the view of agronomists who concentrate on the phenomena in agrosystems. Competition between crops and weeds, which reduce yield production is central to the definition. Thereby, the damage aspect is stressed. A weed problem is solved as soon as the plant no longer creates considerable damage in the fields, a state which is reached by means of adjusted weed control (crop rotation, tillage, herbicide application).

In contrast to the previous concept, *ecological definitions* include habitats outside agrosystems colonized by weeds. The usual preference of weeds for anthropogenically disturbed habitats is emphasized. They include cultivated fields and gardens which are artificially kept open as well as disturbed areas on road sides, recently built artificial slopes and other similar habitats. An aggressive weed can cause damage not only in agrosystems but also in (semi-)natural plant communities by outcompeting weak species.

Following , it is sometimes difficult to call a plant a weed because one and the same species may be considered in some parts of its area as a harmless component of natural vegetation, in others as a weed and again in others, even as a useful plant species.

(Williamson, 1988) pays attention to the fact that 17 out of 18 most feared „World’s Worst Weeds“ (Holm et al., 1997; Holm LG. et al., 1977) are also cultivated. The list was integrated

into the German technology assessment by (Sukopp & Sukopp, 1994) : *Cyperus rotundus*, *Cynodon dactylon*, *Echinochloa crus-galli*, *Echinochloa colonum*, *Eleusine indica*, *Sorghum halepense*, *Imperata cylindrica*, *Portulaca oleracea*, *Chenopodium album*, *Digitaria sanguinalis*, *Convolvulus arvensis*, *Avena fatua*, *Amaranthus hybridus*, *Amaranthus spinosus*, *Cyperus esculentus*, *Paspalum conjugatum*, *Rottboellia exaltata*.

Except for *Portulaca oleracea*, the above mentioned species are not cultivated in Europe.

## 2.2. Characteristics of weeds and feral plants and weediness

Weeds and feral crops are perfectly adapted to life conditions in anthropogenically disturbed areas. Thus, surviving strategies of weeds and feral crops are so diverse that any list of weedy and feral characteristics remains incomplete, even the well known one of (Baker, 1967, 1974). He lists the following characteristics of an ideal weed:

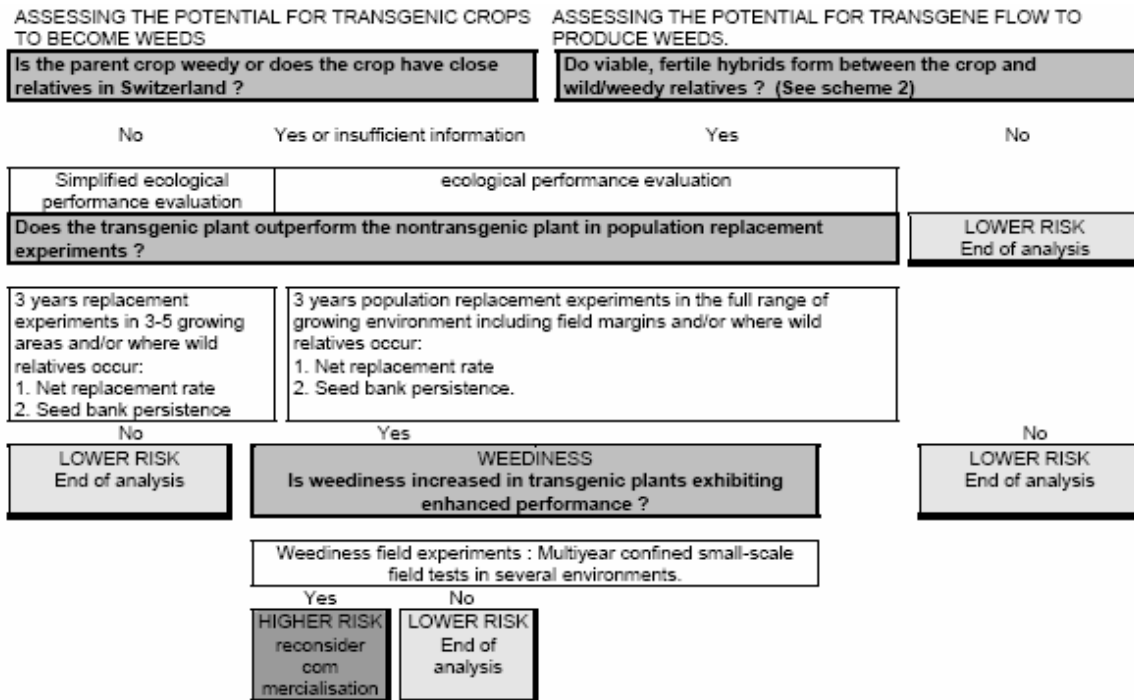
Ideal weed characteristics:

1. Germination requirements fulfilled in a broad range of habitats
2. Discontinuous germination (internally controlled) and great longevity of seeds
3. Rapid growth through vegetative phase to flowering
4. Continuous seed production for as long as growing conditions permit
5. Self-compatible but not completely autogamous or apomictic
6. When cross-pollinated, unspecialized visitors or wind-pollinated
7. Very high seed output under favourable environmental circumstances
8. Produces some seed in wide range of environmental conditions; tolerant and plastic
9. Adaptations for short- and long-distance dispersal
10. If a perennial, vigorous vegetative reproduction or regeneration from fragments
11. If a perennial, brittleness, so not easily drawn from ground
12. Ability to compete interspecifically by special means (rosette, choking growth, allelochemicals)

When applying Baker's concept of the ideal weed, we have to consider that in reality, a weed never embraces all the characteristics of the list, consequently we have to speak about a *weed-syndrome* with even additional characteristics not mentioned here.

For a discussion of Baker's characters by means of statistical analysis see (Williamson, 1993)

Closely related species may show dissimilar behaviour. According to (Williamson, 1993), in Britain there are native, invasive and pest-like *Impatiens* species. In a detailed study of their biology, he shows that they have a range of ecological behaviour parallel to relatively small morphological differences. To predict and detect pest status, a well-defined monitoring system is needed. (for details see 4.6.4. in (Ammann et al., 1996), it follows a scheme published by (Rissler & Mellon, 1993)).



**Fig 1 Risk assessment decision making scheme embedded into a monitoring system. Summarized by (Ammann et al., 1996) drawn from Concepts of (Rissler & Mellon, 1993)**

The only attribute which all weeds might have in common is a marked plasticity enabling quick adaptation to continuous environmental changes.  
So, then what is a cultivated plant: Just about the opposite of all the characters of a weed enumerated by Baker:

1. Germination requirements fulfilled in a small range of habitats
2. Continuous germination and shortlived seeds
3. Normal growth through vegetative phase to flowering
4. Ontime seed production after flowering period.
5. Cross pollinated to autogamous.
6. When cross-pollinated, unspecialized or specialized visitors or wind-pollinated
7. Small to high seed output under favourable environmental circumstances
8. Produces seed in selected range of environmental conditions
9. No specific adaptations for short- and long-distance dispersal, or often seed dispersal disabled
10. If a perennial, weak vegetative reproduction and no regeneration from fragments
11. If a perennial easily drawn from ground
12. Ability to compete interspecifically by special means are weak or not existent (rosette, choking growth, allelochemicals)

### **3. The origin of weeds and feral populations**

For summaries of the origin of weeds see (Zoldan, 1993) and (Rauber, 1977). Rauber lists the following pathways through which weeds evolve even today:

1. wild plants evolve into weeds
2. hybrids between crop and wild relatives evolve into weeds
3. crops evolve into weeds

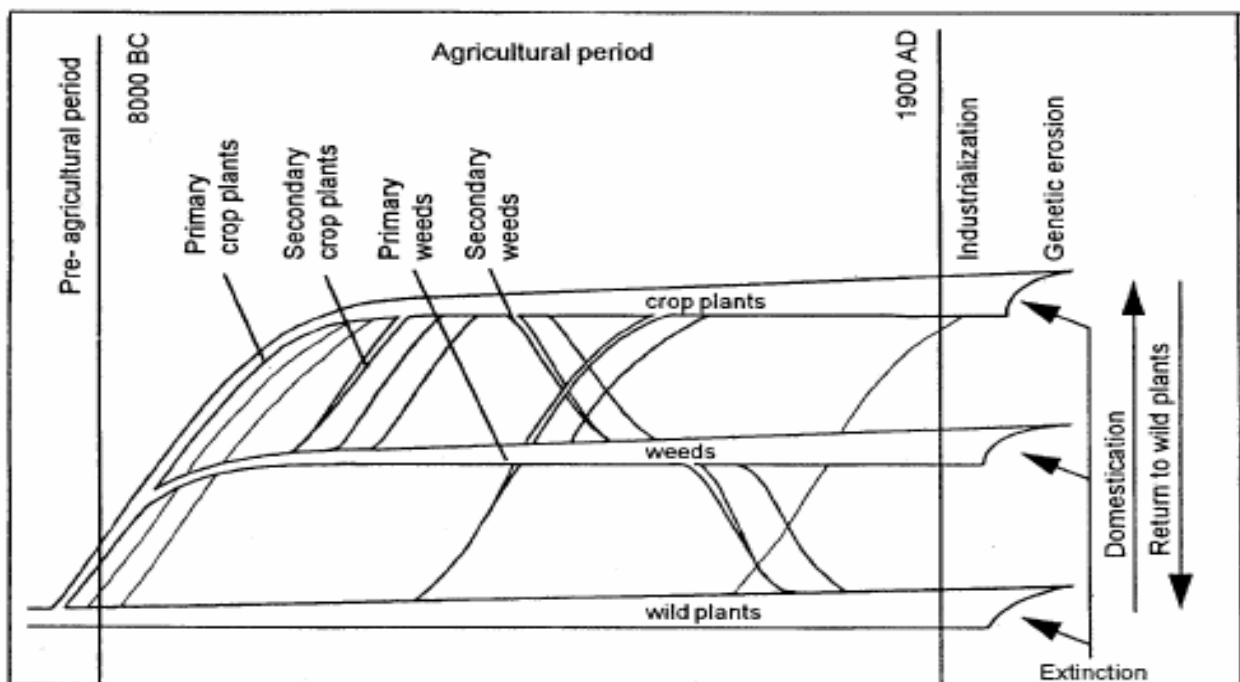
Especially point two and three are important for this study.

For weed evolution, co-evolution of the crop-weed complex is essential. (Pickersgill, 1981) p. 378 shows the following phylogenetical relations in crop-weed complexes:

Three different evolutionary relationships between crops and their weedy relatives are possible.

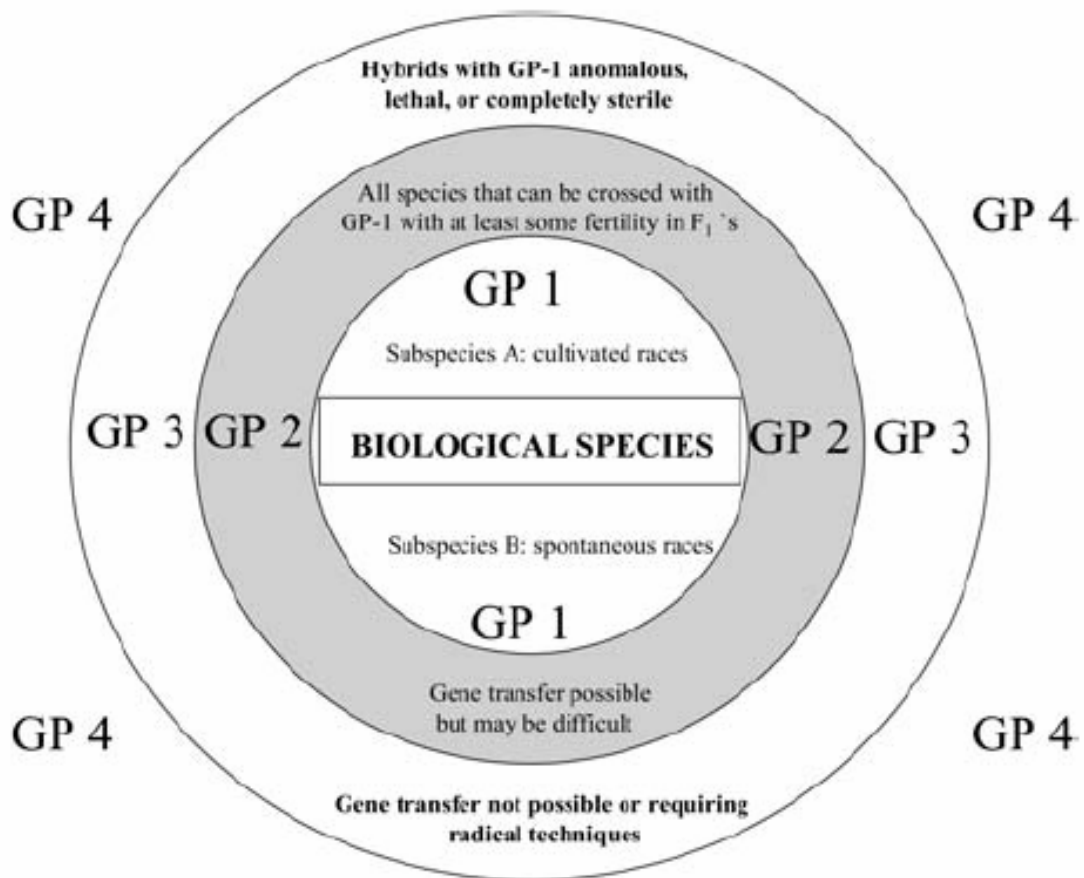
- Firstly, the weed may have been domesticated to be genetically altered to a crop.
- Secondly, the weedy traits may be derived from the crop.
- Thirdly, crop and weed may have diverged simultaneously from a common ancestral wild population.

Rye as an example is a well-known secondary cultivar having evolved from the perennial diploid weed *Secale montanum* Guss.

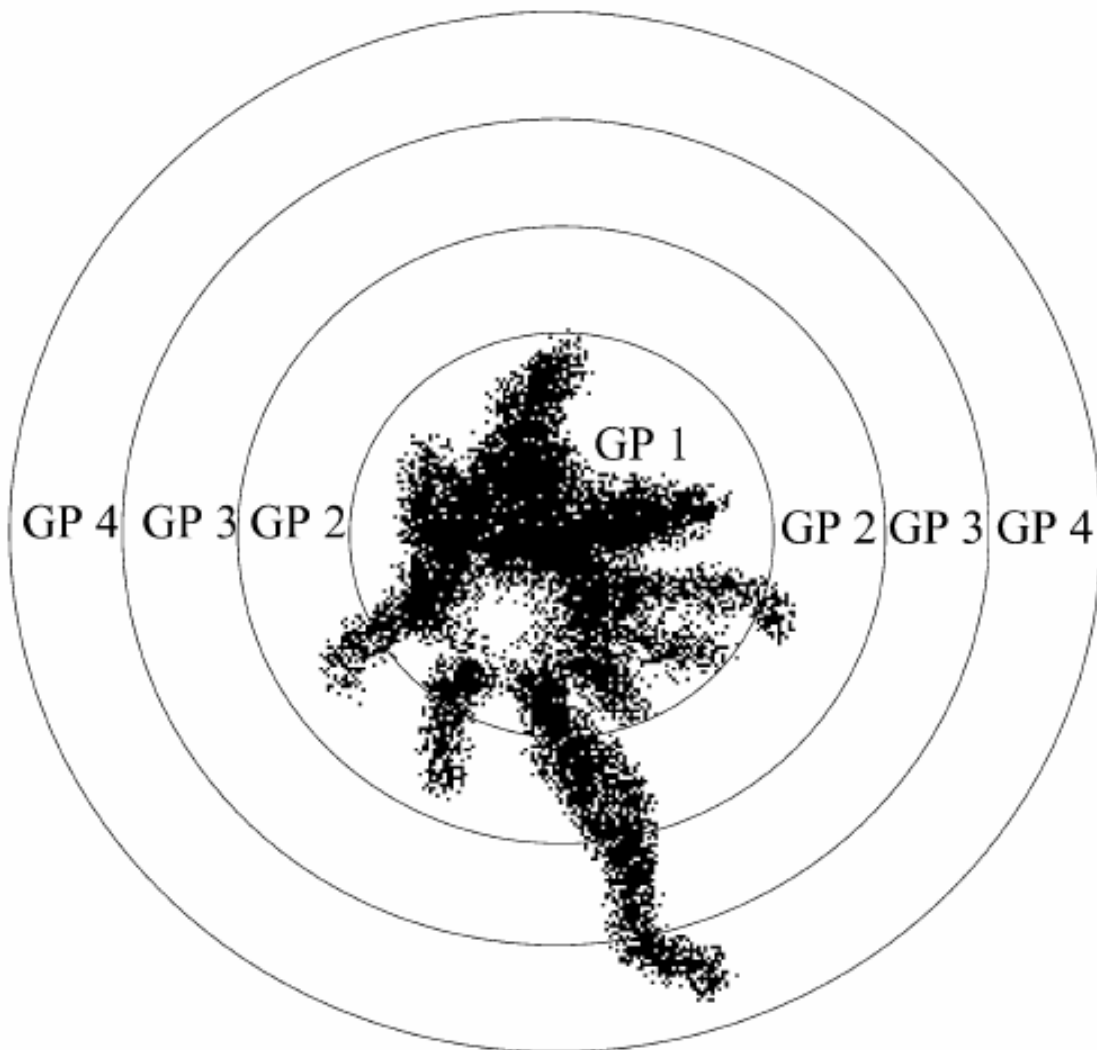


**Fig 2 Multiple origin of feral crops:** The situation is very complex, if we follow fully the time axis, as has been shown by (Gladis, 1966; Hammer et al., 2003), it is demonstrated in a single graph with all details: Feral crops are (or can be) of multiple origin.

It becomes clear from this Figure that ferality is of multiple origins. The pathways between crop plants, weeds and wild plants are manyfold, and for sure in many cases it is almost impossible to trace the origin of ferality.



**Fig 3** The gene pool concept, established by Harlan and de Wet (1971), modified by (Hammer et al., 2003). GP 1 The biological species, including wild, weedy and cultivated races. GP 2 All species that can be crossed with GP 1, with some fertility in individuals of the F<sub>1</sub> generation; gene transfer is possible but may be difficult. GP 3 Hybrids with GP 1 do not occur in nature; they are anomalous, lethal, or completely sterile; gene transfer is not possible without applying radical techniques. GP 4 Any synthetic strains with nucleic acid, i.e., DNA or RNA, frequencies that do not occur in nature. (Hammer et al., 2003)



**Fig 4** Example of an organismoid or a hypothetically designed crop with a genome composed of different gene pools and synthetic genes [for the explanation of this complicated matter, see (Gladiš & Hammer, 2000)]. As complex as this situation is depicted, it might well come close to reality.

#### **4. Crops running wild**

According to (Sukopp & Sukopp, 1994) p. 5 who follow the definition of naturalisation by (Thellung, 1912), a crop, usually showing domestication characteristics, has successfully run wild if it develops a range of characteristics of a wild indigenous species, i.e., if it grows and reproduces naturally without the care of man, if it appears more or less frequently and continuously in suitable habitats and if it has succeeded in surviving for a number of years (even years with extraordinary climatic conditions). For details see chapter 4.3. (Ammann et al., 1996)

Having occupied an ecological niche, a plant may develop poorly and may be eliminated after a short time, it may be integrated inconspicuously in the existing species pattern or it may turn out to be an aggressive, competitive weed (often only after many years of adaptation).

In its range of cultivation within Central Europe, cultivated oilseed rape (*Brassica napus*) frequently invades segetal and ruderal habitats. (Rich, 1991) lists the habitats of feral oilseed rape for Great Britain and Ireland:

'A common yellow crucifer of roadsides, waste and cultivated ground, docks, cities and towns, tips, arable fields, riverbanks etc. Widely cultivated for seed oil or as a forage crop and consequently casual or naturalised wherever oilseed rape is grown on the British Isles.'

## **5. Crops showing weed characteristics**

Following (Schlink, 1994), almost all crops are able to appear as volunteers in the subsequent culture after remaining in the field by harvest loss. The trend towards short term crop rotation systems poor in species has stimulated the spread of volunteers. As well as weeds, volunteers of various crops compete with the cultivated crop for growing factors. Furthermore, they are a potential intermediate host of pests (and beneficial insects) in crop rotation systems.

### **5.1. Case study *Brassica napus*, oilseed rape**

This phenomenon is presented below showing data of oilseed rape (*Brassica napus*) by (Schlink, 1994) who extensively studied its *weed characteristics*. Concerning germinating ecology, *Brassica napus* has all requirements to establish itself as a „wild plant“ in an agrosystem with tillage or in a ruderal habitat. Furthermore, in its growth behaviour and in its high potential of reproduction, oilseed rape resembles segetal weeds and thus represents a typically competitive weed. In crop rotation systems including oilseed rape, the „unidentified“ volunteering rape is capable to pass through all developmental stages up to seed maturity. Seed loss before and during harvesting increases the seed stock in the soil even by seeds produced by volunteers. In this way, selection of enduring genotypes in the field is possible. Simultaneously, the seed stock in the soil is constantly enlarged by new genotypes due to rapid development of new varieties of oilseed rape.

Excerpts from a manual for experts in cultivation of oilseed rape in Top Agrar, Rapsanbau für Könnern (Schönberger & de Vries, 1991) p. 23:

Oilseed rape germinates like a weed. Under favourable conditions, it appears four or five days after sowing. Volunteering oilseed rape is problematic in the subsequent culture, whereby lost seeds may germinate over a long period of time and therefore may cause problems. Due to application of growth hormones, control of volunteering oilseed rape in cereals is no problem [per se]. But volunteering oilseed rape can become a leading weed, especially in dry zones. Because of its long germination period, its high competitiveness and difficulties in harvesting, herbicide application after germination will be necessary even if no weeds are present. Control of volunteering oilseed rape in culture of oilseed rape is very difficult. Therefore stands may vary greatly in their density which is negative for survival in wintertime and for quality, favours pest growth and depression of ripe plants.

#### *Soil seed bank:*

The ability of seeds to survive in the soil for a long period of time is caused by dormancy, germination biology and ecology, even under changing environmental conditions.

Following (Zohary, 1992), the spread of seed germination over two or more years is a common adaptation particularly of annual species. Partitioning of seed germination yield over two or more years is an effective device to buffer the otherwise crippling effects brought in by climatic fluctuations. But such allocation does not serve just to evade disasters. It also acts as a balance which buffers the selection in any particular year, and prevents extreme annual shifts in the genetic composition of the population.

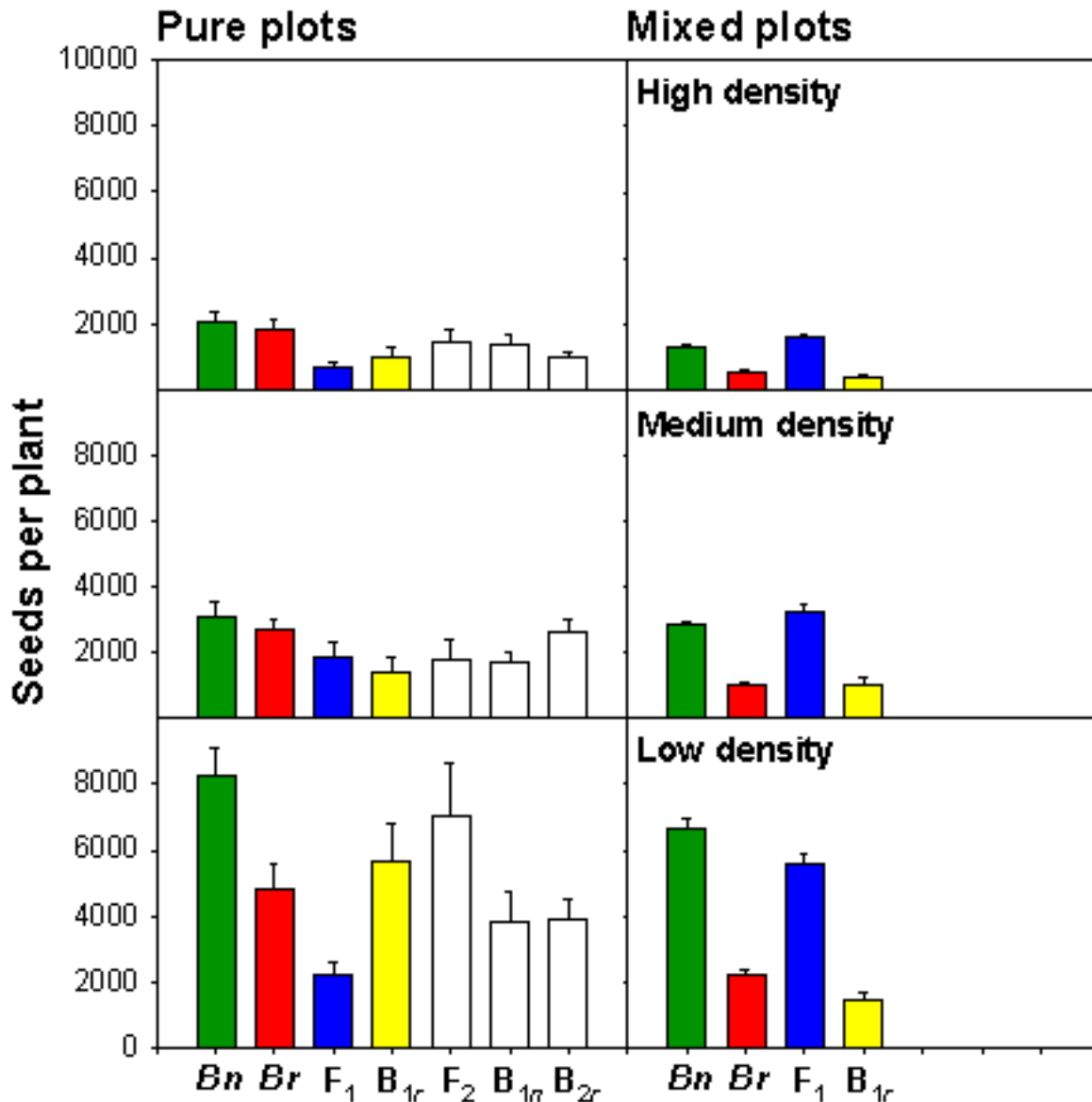
According to (Schlink, 1994), crop breeding generally selects well-germinating genotypes. Especially in the breeding of winter oilseed rape, which can be sown just after harvesting, high germination rates of fresh seeds might have been a secondary breeding goal. In contrast, seeds of oilseed rape are able to survive for a long time in the soil what has been

proven by model experiments using four different varieties. They have shown surviving rates of over 70% for a period of 1,5 years and of almost 60% after five years of exposition in the soil. These rates usually are met only by weeds. The surviving seeds of oilseed rape were sensitive to light which is characteristic for wild species that are adapted to segetal and ruderal habitats. Furthermore, the surviving seeds in the soil showed changes in their germination readiness due to a dormancy cycle induced by seasonal shifting of soil temperature. Such a survival strategy is well-adapted to ecological conditions in temperate zones. It is a typical characteristic of wild plants (Schlink, 1994), pp. 136-138).

According to (Schlink, 1994) , the strategy of eradicating volunteering crops in agrosystems, as it was followed some decades ago, is not reasonable, due to the fact that the supply of fresh seeds to the soil seed stock is guaranteed by the cultivation of the crop itself.

Even if seed loss during harvesting could be prevented, not all sown seeds would germinate under particular conditions as certain genotypes would develop a secondary dormancy and would therefore be added to the bank of dormant seeds.

As (Hauser et al., 2003) have shown it experimentally: Fitness of interspecific hybrids is sometimes highly related to their parents, despite the conventional belief that they are mostly unfit. F-1 hybrids between oilseed rape (*Brassica napus*) and weedy *B. rapa* can be significantly more fit than their weedy parents under some conditions; however, under other conditions they are less fit. To understand the reasons, the authors measured the seed production of *B. napus*, *B. rapa*, and different generations of hybrid plants at three different densities and in mixtures of different frequencies (including pure stands). *Brassica napus*, *B. rapa*, and backcross plants (F- 1 female x *B. rapa*) produced many more seeds per plant in pure plots than in mixtures and more seeds in plots when each was present at high frequency. The opposite was true for F-1 plants that produced many more seeds than *B. rapa* in mixtures, but fewer in pure stands. Both vegetative and reproductive interactions may be responsible for these effects. The results show that the fitness of both parents and hybrids is strongly frequency-dependent and that the likelihood of introgression of genes between the species thus may depend on the numbers and densities of parents and their various hybrid offspring in the population.



**Fig 5** The results clearly show a very pronounced influence of especially the frequency of parents and hybrids on their fitness. *B. napus*, *B. rapa* and backcross plants (F<sub>1</sub> ♀ x *B. rapa*) set many more seeds in pure stands than in mixtures and more seeds in stands with high frequencies of themselves. F<sub>1</sub> plants set many more seeds in mixtures and at low frequencies of itself. (Hauser et al., 2003)

## 5.2. Case study *Beta sativa*, sugar beet

In contrast to biennial sugar beet, in weedy annual forms specific alleles cause early development of stems and inflorescences already in the first year (Rauber, 1977). Feral, early shooting and blooming sugar beet cause certain problems in Switzerland. (Weedy hybrids between sugar beet and sea beet have not yet been found in Switzerland, they seem to be restricted to the Atlantic part of Europe). In case of development of ripe seed before the harvest period they can produce feral seed banks persisting for many years. Offspring of these seeds show again strong tendency to early shooting, therefore being a serious weed problem in sugar beet fields. According to (Bartsch, 1995) annual forms can be a result either of vernalisation during cold springs or evolve through introgression of dominant genes

causing annual forms from wild populations. This would contradict the opinion of Rauber previously cited. Compare also chapter 8. on genes for weediness.

## **6. Reversion of crops to wild types**

There is no reference to a case where crops would have totally been reverted to their wild type or where they would have lost all domestication characters (Sukopp & Sukopp, 1994). Centuries or even millennia of domestication obviously cannot be taken back easily.

According to the NRC Report on Field Testing (National-Research-Council, 1989), domesticated crops, such as wheat, maize and soybean, have been genetically modified in traditional breeding to such an extent that they can no longer compete effectively with wild species in natural ecosystems. These crops are unlikely to revert to a weedy condition upon further genetic modification. Some less domesticated crops such as forage grasses [and oilseed rape] are more likely to revert to a weedy condition.

However, the example below shows that a single gene change may be sufficient to revert a crop towards a wild type. This has been shown by a photograph of Schwanitz given by (Rauber, 1977) with the example of Maize, which turned into „corn-grass“ having a much smaller size in stem and leaf. Still, this is again not strictly a reversion into a wild grass.

In addition, (Sukopp & Sukopp, 1994) as well as (Bartsch et al., 1993) noted that in case of cultivars which have a low degree of domestication, one mutation can cause the weedy form which then successfully spreads. The loss of spikelet spindle toughness of cereals, for example, is sufficient for regaining the ability to spread diaspores (e.g. *Avena*).

Another example is *Avena sativa* with its fatuoid mutant: Loss of a combination of genes which suppress awn, pubescence and easy dehiscence of caryopses transform *Avena sativa* back into nearly wild plants, (Rösler, 1969). A thorough debate about morphological characters of domestication is given (in German) with lots of references in (Jacomet & Kreuz, 1999). In a lucid account the authors also refer to the confusing situation in nomenclature: Modern names as defined on grounds of a genetic analysis are coined by (MacKey, 1966; Szabó & Hammer, 1996) and others. Nomenclature of Hulled Wheats for instance has developed in modern names based on genetics and the names in use in archaeobotany.

## **7. Weeds evolving from hybridizations between crops and related wild species**

For general facts see chapter 3.

The NRC Report on Field Testing (National-Research-Council, 1989)) gives a list of case studies of crops becoming weeds after hybridization with wild relatives: Weedy beets in Western Europe; *Secale cereale* in California, where a weedy rye probably derived from a cross between *S. cereale* and *S. montanum* is leading to the abandonment of rye cultivation; Squash (*Cucurbita pepo*) - important in the Southern United States, already genetically modified; "Hybrid Grain Sorghum" and others.

### **7.1. Brassica napus, oilseed rape**

It is a biological fact that genes will escape from transgenic oilseed rape into the gene pool of *Brassica napus* which contains not only *B. napus* but also its relatives *B. rapa* subsp. *campestris* (L.) Clapham (= *B. campestris* auct.), *Raphanus raphanistrum* and other species.

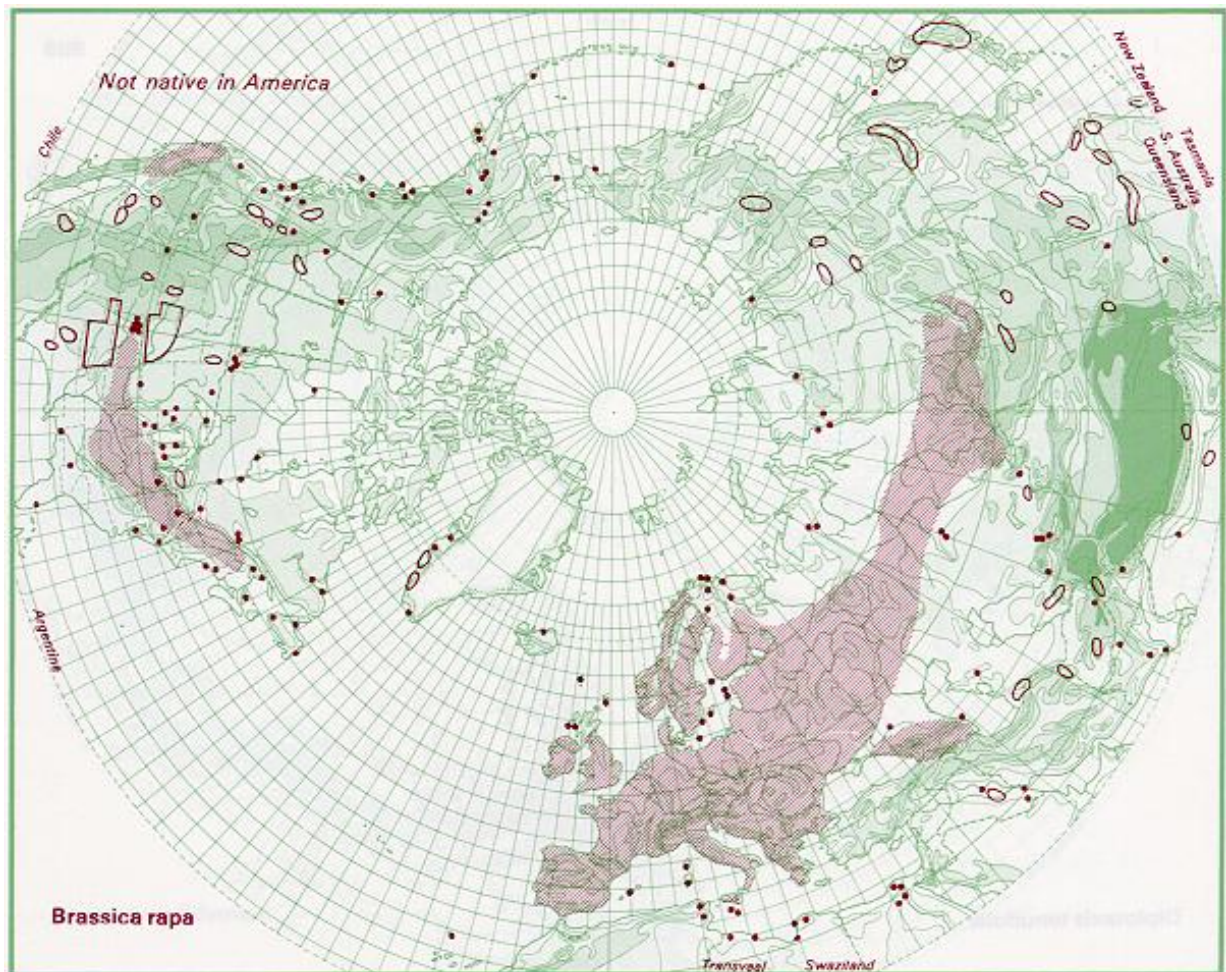
Introgression of genes of oilseed rape (*B. napus*) in natural populations of *Brassica rapa* subsp. *campestris*:

In an ongoing research program (Group of R. B. Jörgensen at Risö, (Mikkelsen, 1996), the behaviour of transgenic *B. napus* (herbicide tolerance, insect or fungal resistance) and *Brassica rapa* subsp. *campestris* is studied in natural habitats by screening populations over several years using non-destructive methods. Other populations are harvested yearly to

check biomass and seed production. Their experiments revealed transgene flow from oilseed rape to *Brassica rapa* subsp. *campestris* and introgression by backcrossing in the test field.

(Jorgensen & Andersen, 1994) underline the importance of weedy *Brassica rapa* subsp. *campestris*, a common weed in Northwestern Europe. (In Switzerland, re-discovered in 1995 by Pia Rufener Al Mazyad as a common weed in traditional mountaneous agriculture systems).

The biogeography is still somehow doubtful, and an important reason is the difficult recognition of the taxon. This also makes it clear that historical records are difficult to get and even if they would exist, they should be subject to thorough taxonomic scrutiny.



**Fig 6 Brassica rapa: (Hulten, 1971) Circumpolar distribution: Scattered points: Isolated ruderal populations.**

*Brassica rapa* subsp. *campestris* possesses many agronomically important characters (e.g. yellow seed colour, pathogen resistance, cold tolerance) that are demanded in the breeding of *B. napus*. This together with the good cross-compatibility makes the species an attractive gene resource.

With efficient agricultural practice the wild form of *Brassica rapa* subsp. *campestris* is almost exclusively found as a weed in oilseed rape fields where herbicide elimination is not applicable. However, herbicide treatment in oilseed rape fields will be possible with the introduction of genetically modified oilseed rape with genes for herbicide tolerance. These genetically modified varieties are already in field testing and will be marketed within few years in Europe, in Canada herbicide tolerant canola is already on the market. When this

happens the wild form of *Brassica rapa* subsp. *campestris* could be endangered in a worst case scenario. But pragmatically it could also happen that the rare subsp. *campestris* becoming herbicide tolerant could save its existence.

In addition, weedy *Brassica rapa* subsp. *campestris* and its hybrids with oilseed rape could be disseminated with certified seeds. Herbicide tolerant oilseed rape might induce the evolution of a new weed (Jorgensen & Andersen, 1994) p. 1635:

As the gene for herbicide resistance is likely to be transferred to *Brassica rapa* subsp. *campestris* by hybridization and backcrossing, the use of this herbicide strategy will be inapplicable after a few years. Like many other weeds, *Brassica rapa* subsp. *campestris* is characterised by seed dormancy and longevity of the seeds. Therefore, *Brassica rapa* subsp. *campestris* with transgenes from oilseed rape may be preserved for many years in spite of extermination efforts. *Brassica rapa* subsp. *campestris* with other types of genes transferred from *B. napus* might affect natural ecosystems as well as the agro-ecosystem.

For an overview of additional hybridization experiments between oilseed rape and close relatives see chapter 2. hybridization and (Sukopp & Sukopp, 1994).

## **7.2. *Beta vulgaris*, Sugar beet**

Weed-beets, hybrids between sugar beet (*Beta vulgaris* ssp. *vulgaris*) and the wild type seaboot (*B. vulgaris* ssp. *maritima*) are more aggressive in culture than the wild type. This has been shown since the seventies. For an overview see (Madsen, 1994; Madsen & Sandoe, 2001) and (Pickersgill, 1981), as well as (Sukopp & Sukopp, 1994)

After Bartsch a main source of weediness after gene introgression is pollen transfer from *Beta vulgaris* ssp. *maritima* into seed production fields of *Beta vulgaris* ssp. *vulgaris* in the Netherlands and Northern Italy. Long term consequences cannot be evaluated from this study, but one result seems to be clear already now: Genetic diversity is not reduced by the constant and probably decades old gene flow from the cultivated beets to the wild coastal beets.

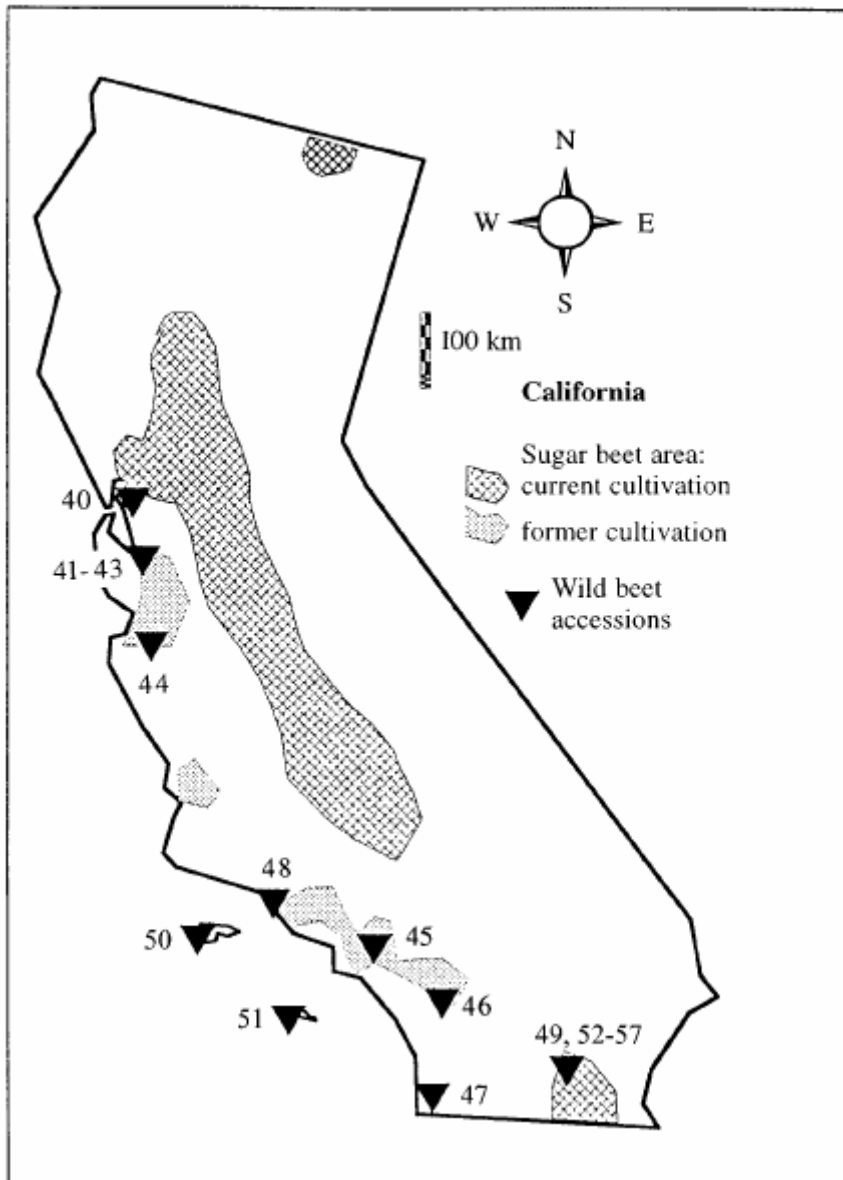
(Fredshavn et al., 1995) studied differences in the competitiveness of the *Beta*-complex when using transgenic *Beta*. There was no enhanced competitiveness observed.

Bartsch and his research group studied various aspects of beta populations and their relationship to wild species and feral populations.

Beside the insertion of various herbicide resistance genes into the beet genome, the transformation of beet to give resistance to the soil-born virus, beet yellow vein necrosis virus, which causes a serious disease called rhizomania, has been targeted extensively (Bartsch & Schuphan, 2002). In particular, rhizomania-resistant genotypes were examined for sugar beet as well as for sugar beet – Swiss chard hybrids. The beet's ecological performance was compared under various environmental conditions with regard to parameters such as competitiveness, winter hardiness and seed production. No difference was found in seedling performance even under virus infestation. The competitive performance of beet was tested against *Chenopodium album*, a common weed in sugar beet fields and young fallow. Field experiments carried out between 1993-2001 demonstrated that transgenic sugar beets often grew better than virus-susceptible beets, but only when the virus was present. The difference between susceptible and resistant beets declined as more competing weeds were placed nearby. No differences were observed in most cases if the virus was absent, but occasionally potential costs of resistance were reported for some transgenic events in sugar beet (Bartsch & Schuphan, 2002). Some of the experiments focused on over-wintering of transgenic and non-transgenic sugar beet at different locations in Europe representing mild to cold winters in the years 1994-1999. No survival differences were found even under virus infestation conditions. In conclusion, this experiments addressed primarily the ecological consequences of gene flow in a hybrid environment, since crop - variety hybrids were used as a model for crop – wild crosses in the experiments. By complementary use of transgenic and near-isogenic genotypes, direct comparisons were made in experiments, so that any difference measured was caused by the transgenic event.

For all cases examined, increased fitness effects were not found based on transgenic rhizomania-resistance genes (Bartsch et al., 2003).

UPGMA analysis showed overall that domesticated and wild beets form genetically coherent groups. Wild beets in California have two different origins, from European *Beta vulgaris* or from *Beta macrocarpa*. Population-level patterns of allozyme variation for wild California beets related to *B. vulgaris* suggest that those populations evolved from naturalized populations of the cultivated *B. vulgaris* ssp. *vulgaris* which had hybridized to varying degrees with the sea beets *B. vulgaris* ssp. *maritima*. (Bartsch & Ellstrand, 1999).



**Fig 7** Sugar beet cultivation areas and wild beet accessions in California (Bartsch & Ellstrand, 1999)

## 8. Genes of weediness

There is space for only a few examples for weediness genes here. Due to the fact that weeds have a large variety of characteristics, as is shown in paragraph 2., no definitive list can be given.

(Lupi, 1995) states in his BATS report that according to (Baker, 1974), weediness is a multicharacter attribute and the addition of one gene is unlikely to cause a crop to become a weed. In contrast, (Fitter et al., 1990) and (Williamson, 1988) suggest that the alteration of one gene may indeed be enough to change a crop into a weed. If a crop species has very few weedy characteristics, the addition of one or a few genes would be unlikely to cause the crop to become a weed problem. Special attention might be warranted where the crop has weedy characteristics or the added genes might be expected to improve the crops competitive ability in natural or agricultural ecosystems.

Also in the above cited case of *Beta vulgaris ssp. vulgaris* Hoffmann et al. (1970) in (Rauber, 1977) state, that cultivar and weedy relative are identical except for one single allele B/B+.

## **9. Historical accounts on feral crops**

First it has to be stated that the data situation for crops, and even more so for feral crops is scanty.

A thorough debate about morphological characters of domestication is given (in German) with lots of references in (Jacomet & Kreuz, 1999). In a lucid account the authors also refer to the confusing situation in nomenclature: Modern names as defined on grounds of a genetic analysis are coined by (MacKey, 1966; Szabó & Hammer, 1996) and others. Nomenclature of Hulled Wheats for instance has bifurcated in modern names based on genetics and on the other side the traditional names in use in archaeobotany. Consequently, even on the simple base of names we always have to consider the view behind.

### **9.1. Methods of detection**

#### **9.1.1. Archaeobotanical methods**

Archaeobotanical methods are plentiful, they are extensively described with lots of examples in (Jacomet & Kreuz, 1999).

One of the most important methods is washing (elutriating) the samples in order to purify and concentrate all plant remains. It is worthwhile to examine critically the details of such purifying methods, since details in the procedure can heavily influence the results and resulting statistics.

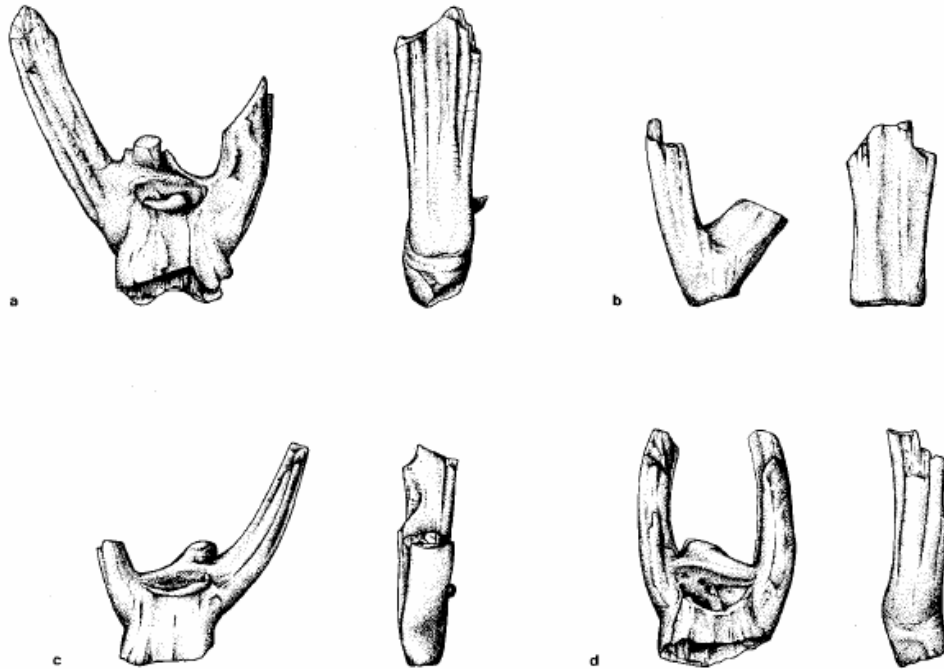


**Fig 8 Purification of midden plant matrix through hydroclensing. [www.nau.edu/~qsp/macrobotanical\\_lab.html](http://www.nau.edu/~qsp/macrobotanical_lab.html), Northern Arizona University:**



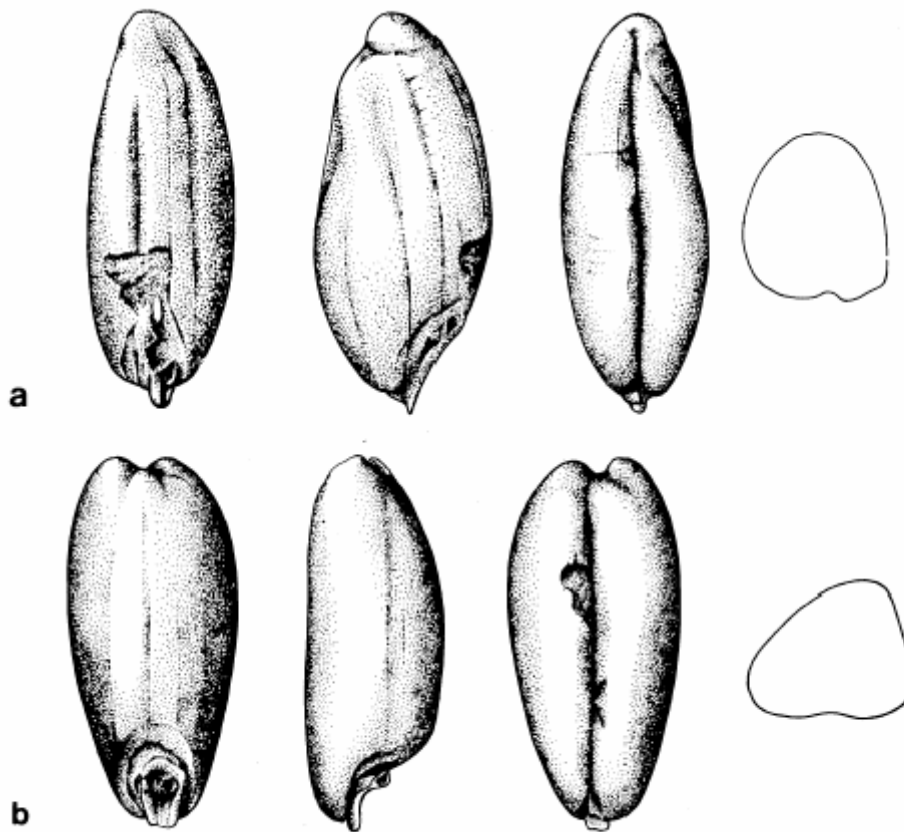
**Fig 9 Demonstration of proper midden analysis procedures [www.nau.edu/~qsp/macrobotanical\\_lab.html](http://www.nau.edu/~qsp/macrobotanical_lab.html), Northern Arizona University:**

After proper documentation, analysis can reveal lots of details, shown here with the example of Hulled Wheat (Padulosi et al., 1995)



**Fig 10** Charred hulled wheat chaff from Çayböyü, Turkey, dating to the Late Chalcolithic period (4th millennium BC). (a) Normal emmer spikelet fork, which originally came from the middle of the ear. (b) Terminal emmer spikelet fork – originally from the top of the ear. (c) Normal einkorn spikelet fork, with parallel glume bases. (Padulosi et al., 1995)

There is some agreement among archaeobotanists that well-preserved assemblages of spikelets or spikelet-forks and glume-bases can be reliably separated into einkorn, emmer and spelt. This does involve the assumption that the morphological groups we identify in ancient material match modern taxa. This is undoubtedly true in general terms: current-day einkorn, emmer and spelt can be distinguished from each other by the same character combinations which work on ancient material. However, archaeobotanists would not argue for complete similarity between modern Einkorns and ancient Einkorn.



**Fig 11 (Padulosi et al., 1995) Charred hulled wheat grains from Çayböyü, Turkey dating to the Late Chalcolithic period (4th millennium BC). The grains show the longitudinal grooves typical of hulled wheats, caused by the tightly investing chaff. a. Einkorn grain, with the typical spindle shape, pointed apex and pronounced ventral convex curve visible in the middle view. b. Emmer grain, with a blunter apex and straighter sides in all views. Note the typical asymmetric triangular cross-section.**

Identification of archaeological wheat remains was discussed at a meeting of 25 archaeobotanists in London in 1992 and the published account is a useful source of more details (Hillman et al., 2001; Hillman et al., 1993). In summary, the reader of archaeobotanical reports should bear in mind three points:

1. All identifications should be critically examined. Identification criteria should be presented in detail and backed up by illustrations. Poorly documented identifications should be treated with even greater caution, and the older literature must always be used with care. Identifications of charred material are not absolute and even desiccated material can be problematic.
2. Glume wheat chaff can, if abundant and well preserved, be identified with greater certainty than grain.
3. Identifications of hulled wheat remains can be identified with some certainty to ploidy level, but the use of terms such as einkorn, emmer or spelt does not imply full equivalency with current-day taxa.

The hulled wheats will be discussed as two groups. Einkorn and emmer were domesticated from wild ancestors growing in the Near East. These wild ancestors have been identified and much studied, and the area and time of domestication have been established with certainty. Spelt wheat, on the other hand, results from a hybridization that appears to have taken place

after the origins of agriculture, under cultivation. It has no single wild ancestor, and the area and date of its domestication are still unclear.

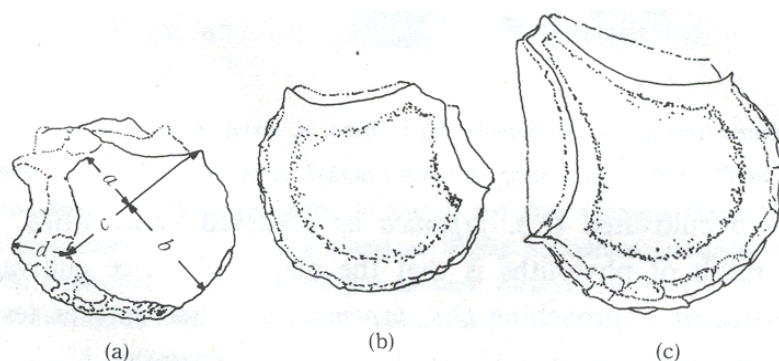
### 9. 1. 2. Pollen Analysis

Analyse pollen grains and other microscopical remains is well known and still widespread method used in many laboratories (Faegri et al., 1989). There is a plethora of literature, and no need to go into details. For our specific question about feral crops pollen morphology cannot offer any specific data, since it is not possible to discern single crop traits, it is even sometimes difficult to come down to species level. For specific archaeobotanical questions see [http://www.geo.arizona.edu/palynology/arch\\_pal.html](http://www.geo.arizona.edu/palynology/arch_pal.html). It is interesting to note that corn pollen provides, just as other recognizable crop palynomorphs, reliable indicators of early settlement in soil profiles. Corn pollen, as soon as produced by adjacent fields, can be detected at all levels in the Alps e.g., as has been shown by (Ammann, 1979)

### 9. 1. 3. Cyto- (Phyto)lith Analysis

Minute parts of silica in the cells of plants that are specific to certain parts of the plants. Phytoliths survive even after the plant decomposes or burns, which allows them to serve as efficient clues to archaeologists on harvesting periods and techniques, as well as different characteristics of food production. Phytoliths can also help differentiate between wild and domestic plant species. Hiroshi Fujiwara discovered phytoliths of rice in walls of Jomon pottery of Japan (c 500BC), which proved that rice cultivation existed at that time. He then analyzed the phytoliths in soil samples and determined an estimated depth and areal extent of the fields and the total yield of rice. (Sato et al., 1990; Wang et al., 1999; Wang et al., 1998a; Wang et al., 1998b; Zheng et al., 2003)

Much needed data were lacking because little has been preserved and analysis difficult. Many farm tools were excavated in many Chinese Neolithic sites without crops, a regrettable obstacle to the study of early cultivation. Phytoliths of crops and other plants were much more easily preserved in sediments and other sites than sporopollens, and easily identified. For this reason, phytolith analysis has become an important technique in agricultural and environmental archaeology, and will play a very important role in future studies of the origin and propagation of cultivated rice (Chen et al., 1995)



**Fig 12 Measurements and types of fan-shaped phytoliths from rice: a) parameters, b)  $\alpha$ -type, c)  $\beta$ -type (Chen et al., 1995)**

### 9. 1. 4. Analysis of Herbarium Specimens

The method has been developed in order to determine gene flow with morphometrics of hybrid specimens found in herbaria (Ammann et al., 1996; Frietema, 1996). These results, although derived from herbarium specimens, give a reliable picture on potential gene flow from crops towards their wild relatives, as long as hybrids can be analysed successfully with

morphometrical methods. The same methods can be used for the study of hybrid and feral crop populations. This remains to be done in a comprehensive style and it is obvious, that lots of data could be derived from this method. (Jacot et al., 2004). Molecular analysis have confirmed those results (Bianchi et al., 2002; Guadagnuolo et al., 2001a; Guadagnuolo et al., 2001b; Guadagnuolo et al., 2001c)

In closely studying the hybridization records in herbaria and their morphometrics, the dynamics of gene flow can be estimated. The dataset produced is valid for the decades the herbarium samples have been made, they can be reliable to give an impression of long term hybridization dynamics, as long as one remains critical about the sampling. Those results can also show long term dynamics in a more reliable way than short term measurements of the marking transgenes in the field, since those measurements are limited by cost and time consuming analysis. But on the other hand those herbarium results cannot reveal anything about the specific dynamics of the transgenes contained in the GMO crops.

Here some examples in the (non-transgenic) *Triticum aestivum* complex are given, all from (Jacot et al., 2004) (Figs 5-8). Wild Triticum species (or feral ones are generally not weedy in the agronomic sense, they grow profusely in ruderal habitats adjacent to wheat fields.

Hybrids between wheat and its wild relatives are generally rare, unlikely and often sterile.

There is little knowledge about the biology, the flowering behaviour and the reproduction system of the wild relatives of wheat. The artificially obtained hybrids show intermediate characters and remain usually sterile, except in cases of chromosome duplication within the *Aegilops ovata* – *Triticum durum* – Complex. Experiments also demonstrate low hybridization success and considerable differences between years and under different conditions. In the same study, (Jacot et al., 2004) established herbarium based morphometric studies.

Those morphometric studies take into account a high number of morphological characters, in the case of our study cited we used some 50 to 75 characters.

**Table 1 Morphological characters used to distinguish different species and hybrids of wheat in herbarium collections (Jacot et al., 2004)**

Distinguishing character	
stem	1- stem height [cm] 2- stem form
leaf	3- leaf length [0.5 cm] 7- leaf surface ventral
	4- leaf width [0.1 mm] 8- sheath form
	5- leaf form 9- auricle form
Spike	6- leaf surface dorsal
	10- spike length [mm] 15- spike: nr of fertile spikelets
	11- spike width (at middle) [mm] 16- spike: nr of rudimentary sp. bottom
	12- spike width (at top) [mm] 17- spike: nr of sterile sp. at top
	13- spike form 18- spike / plant color
14- spike density	
Internode	19- internode length 20- internode length at bottom
Rachis	21- rachis surface 23- rachis / spike fragility
	22- rachis edges
Spikelet	24- spikelet length [mm] 29- spikelet: nr of fertile florets
	25- spikelet width [mm] 30- spikelet's highest flower
	26- spikelet form 31- spikelets: total nr of awns
	27- spikelet surface 32- spikelets (upper): total nr awns
	28- spikelet: number of florets
Glume	33- glume body length [0.1 mm] 44- glume's 1. side t/a form
	34- glume body width [0.1 mm] 45- glume's 2. side t/a length
	35- glume body form 46- glume's 2. side t/a form
	36- glume keeling 47- glume's 4. t/a length
	37- glume form at apex 48- glume's 4. t/a form
	38- glumes concealing lemma ? 49- glume-awns length low
	39- glumes equilateral ? 50- glume-awns number upp

	40- glume: <i>number</i> of awns	51- glume-awns length upp
	41- glume's middle t/a length	52- glume awn position
	42- glume's middle t/a form	53- glume awn surface
	43- glume's 1. side t/a length	
Lemna	54- lemma body length [0.1 mm]	60- lemma's middle t/a length
	55- lemma body width [0.1 mm]	61- lemma's middle t/a form
	56- lemma body form	62- lemma's 1. side t/a length
	57- lemma nerves	63- lemma's 1. side t/a form
	58- lemma nerves convergency	64- lemma's 2. side t/a length
	59- lemma: <i>number</i> of awns	65- lemma's 2. side t/a form
	67- lemma-awns length upp	66- lemma-awns <i>nr</i> upp
Palea	68- palea length [0.1 mm]	70- palea form
	69- palea width [0.1 mm]	
Fruit	71- fruit length [0.1 mm]	73- fruit form
	72- fruit width [0.1 mm]	74- fruit unit
Fertility	75- fertility	

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t/a = ; upper spikelets = *nr*=number

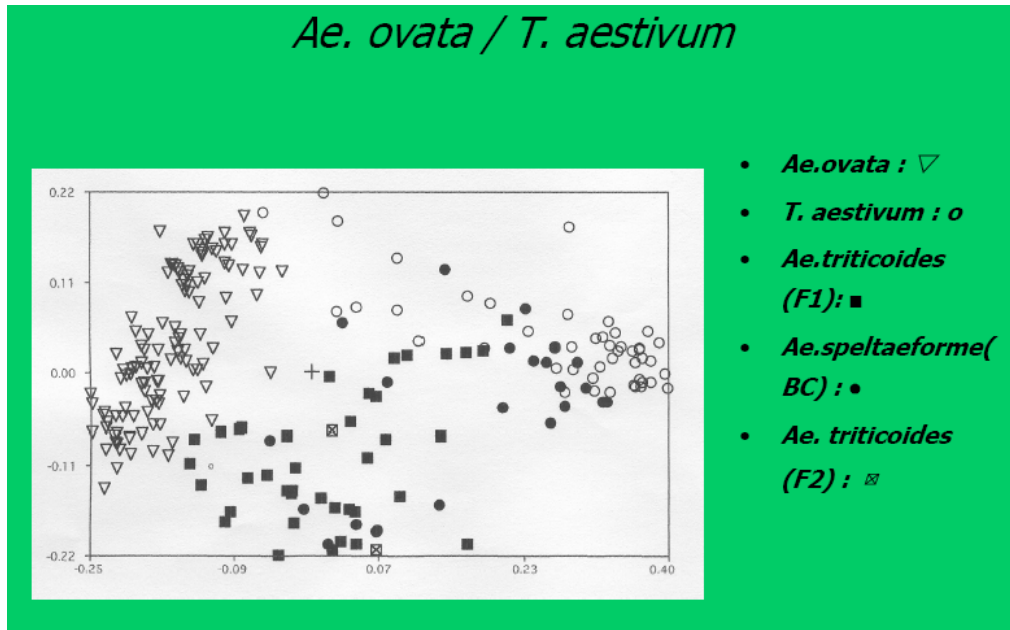
Studies on herbarium samples collected in the field reveal long term hybridization dynamics, but they cannot tell anything about the specific dynamics of transgenic crops and their wild relatives.

From those morphometric analysis, here two examples:

1. The complex of hybrids between *Triticum aestivum* and *Aegilops ovata*. **Fig. 5 and 6**
2. The complex of hybrids between *Triticum aestivum* and *Aegilops squarrosa*. **Fig. 7 and 8**

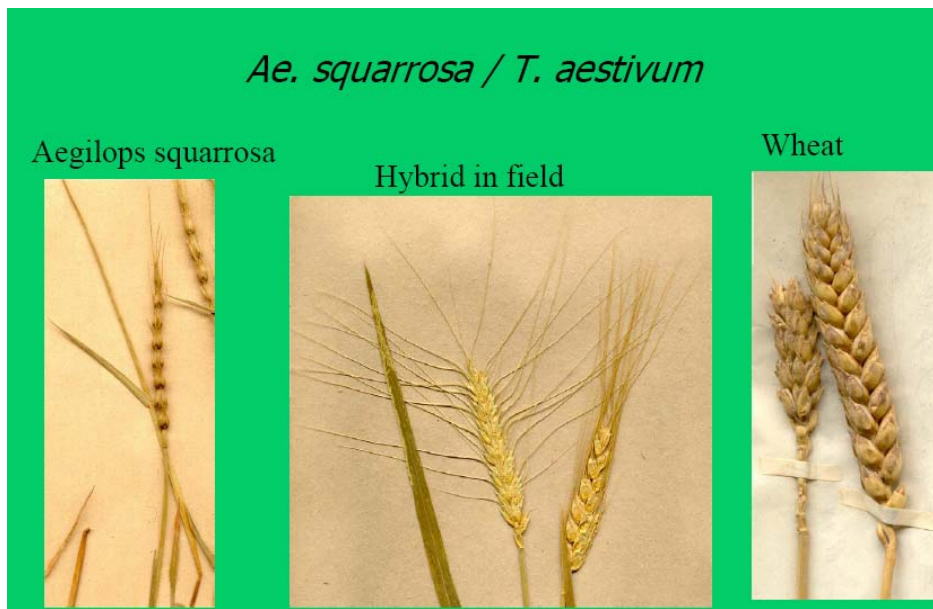


**Fig 13** Exo-feral hybrids in herbaria: *Triticum aestivum* x *Aegilops ovata* (Jacot et al., 2004). The hybrids show intermediate characters. With permission of the publisher

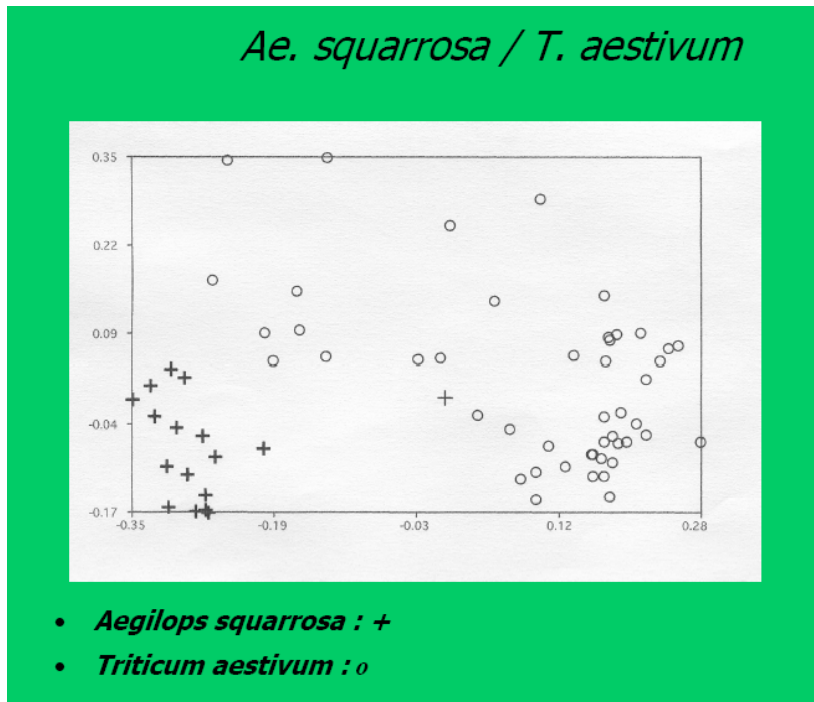


**Fig 14** Scattergram of morphometrics in the *Aegilops ovata* x *Triticum aestivum* complex (Jacot et al., 2004). The scattergrams of this figure and the following ones show a principal component analysis of some 60 characters involved in the measurements. Therefore the dynamics of the hybridization is based on a full set of visible and measured (counted) characters of the herbarium specimens chosen over many decades and localities. It involves several hybridogene taxa as shown in the figure. With permission of the publisher

*Aegilops ovata*: ▽, *Triticum aestivum*: ○, *Aegilops triticoides* (F1): ■, *Aegilops speltaeforme* (BC)●, *Aegilops triticoides* (F2): ☒



**Fig 15** Exo-feral hybrids between *Triticum aestivum* and *Aegilops squarrosa*, specimens from herbarium (Jacot et al., 2004) with permission of the publisher

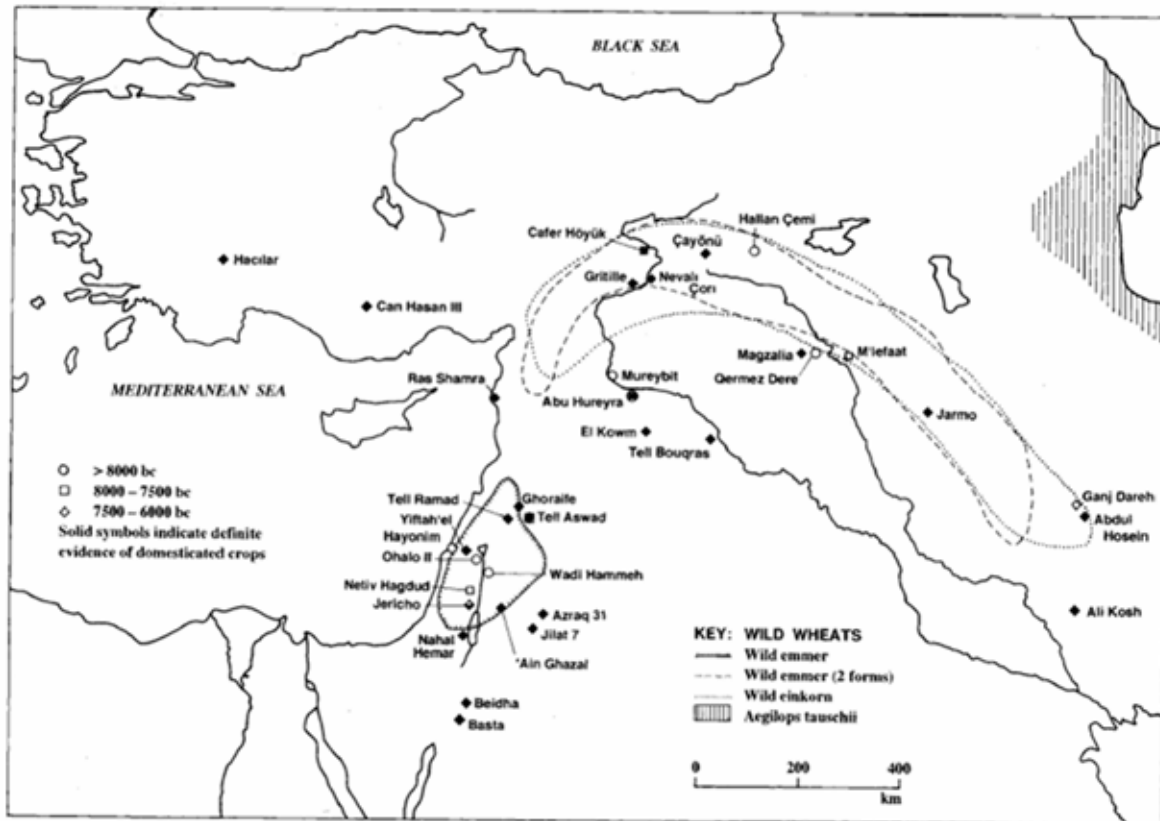


**Fig 16** Scattergram of morphometrics of hybrid specimens *Triticum aestivum* x *Aegilops ovata* (Jacot et al., 2004) with permission of the publisher

*Triticum aestivum*: O, *Aegilops squarrosa*: +

## 9. 2. Some results of archaeobotanical studies, restricted to the example of Hulled Wheat.

Once the wild ancestors of einkorn and emmer had been identified, it became clear that the domesticates would most likely have been taken into domestication in the same area where the wild ancestors grew. There are two main sources of information for the distribution of wild cereals during the period of domestication around 10 000 years ago: the current distribution of wild cereals, and archaeobotanical finds of wild cereals from pre-agrarian sites.



**Fig 17** Distribution of archaeological sites in relation to the distribution of wild wheats. Only those Epipalaeolithic and Neolithic sites dating to before 6000 BC with available archaeobotanical reports are shown. Solid symbols indicate definite evidence of domestication; empty symbols indicate sites that are non-agrarian or of uncertain status. Full details are given in Table 2. Distribution of wild wheats in primary, truly wild, habitats is shown, but small populations of wild einkorn on Mount Hermon in southern Lebanon and of wild einkorn and emmer in Transcaucasia are not shown. Note that wild emmer in the Levant consists of pure *T. dicoccoides*; in the northern Fertile Crescent both *T. dicoccoides* and *T. araraticum* are present (indicated by the dashed line). The western extension of primary habitats of *Aegilops tauschii* is shown, around the Caspian sea. (Padulosi et al., 1995)

### Einkorn

A relatively extensive discussion about one specific complex of ancient, modern and feral taxa is given here, in order to demonstrate that we are far from a final analysis of the situation: it is not enough to arrange a few scattered findings into a logical system of evolution, we need the population genetics approach and a multivariate data analysis in the whole range of those fascinating crop taxa. This situation is summarized in (Padulosi et al., 1995): Today wild einkorn and wild emmer seem obvious candidates as wild ancestors of, respectively, einkorn and emmer wheat, because of their morphological similarity and ability to intercross. However, this has only been apparent for a hundred years or so, after a series of botanical discoveries whose history is discussed by Aaronsohn (1910), (Schiemann, 1951, 1956) and (Feldman, 1977). Wild einkorn (*Triticum boeoticum*) was discovered in Greece and Turkey in the mid-19th century, and by 1900 was widely accepted as the ancestor of domesticated einkorn wheat. *Triticum urartu*, the second diploid wild wheat, was named in 1938 by the Armenian botanist, Tumanian. It grows throughout the Fertile Crescent as a minor admixture of *T. boeoticum* on outcrops of basaltic soil (Waines et al., 1993). Unlike *T. boeoticum*, it has not spread outside the Fertile Crescent as a weed of disturbed ground. It is morphologically similar to *T. boeoticum*, but *T. urartu* can be consistently distinguished on the basis of anther length, the presence of a third lemma awn and caryopsis colour

(Johnson, 1975; Morrison, 1993; Waines & Barnhart, 1990). Crosses between the two taxa result in sterile hybrids. Overall the evidence points to *T. urartu* as a separate species. *T. urartu* is not a candidate species as a wild ancestor for domesticated einkorn (Jaaska, 1993; Waines & Barnhart, 1990), but may be a parent of *T. dicoccoides* (Dvorak et al., 1988).

### **Emmer**

The wild ancestor of emmer was not identified until 1873, when Körnicke found part of a spike of *T. dicoccoides* in a collection of wild barley, *Hordeum spontaneum*, made on Mount Hermon in southern Syria. However, it was Aaron Aaronsohn's discovery from 1906 (Aaronson, posthumous) onwards of abundant wild emmer in Israel that led to general acceptance of its role as the wild ancestor of emmer. Two morphologically distinct forms of *T. dicoccoides* have been recognized (Poyarkova, 1988; Poyarkova et al., 1991), a narrow-eared, gracile form native to the whole range of wild emmer, and a wide-eared, robust form of more restricted distribution. Although both forms are found in weedy habitats such as roadsides, both mostly grow in primary, undisturbed habitats. Unlike wild einkorn and barley, wild emmer has conspicuously failed to spread outside the Fertile Crescent. Its current distribution is therefore believed to be more representative of its early Holocene distribution than that of the other wild cereals. As with wild einkorn, wild emmer consists of two morphologically similar but reproductively isolated tetraploid species, *T. dicoccoides* and *T. araraticum*, the latter first recognized in the 1930s and named by (Jakubziner, 1958). *T. araraticum* has been identified as the wild ancestor of *T. timopheevi*, a rare domesticated glume wheat found in Georgia.

Whether the widely accepted theory that salinization of soils in Mesopotamia can be linked to the decline of Emmer is in the light of new scrutiny of the original data put into question.

The only study known to have compared yields found that one variety of Indian emmer wheat yielded much more than barley under a number of salinity levels (Hunshal et al., 1990). In view of modern-day emmer's adaptability to poor soil conditions, it is possible that some forms of ancient emmer were resistant to saline conditions.

This combination of ambiguous texts, lack of archaeobotanical data, and lack of agronomic characterization of hulled wheats equally affects virtually all studies of ancient historical agriculture. (Padulosi et al., 1995)

Some maps showing the present day knowledge of the distribution of some selected historical wheat taxa: They indirectly will reveal important localities on feral populations.

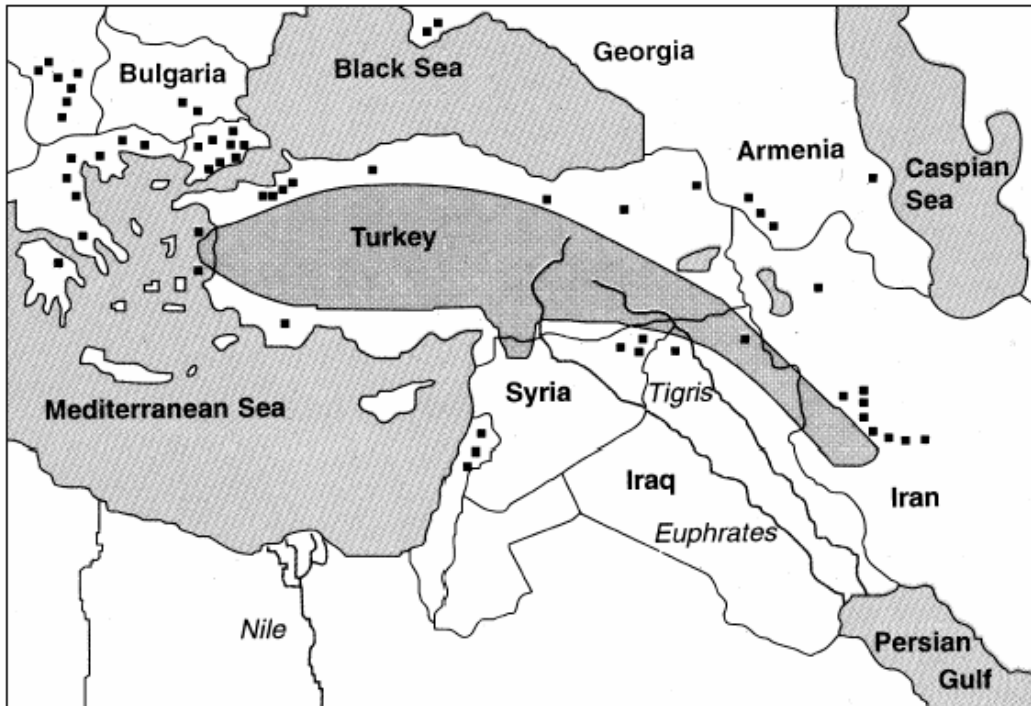


Fig 18 Shaded area represents the main centre of origin of *Triticum boeoticum*, wild progenitor of *T. monococcum*; dots indicate areas of secondary importance where *T. boeoticum* also has been found (Harlan & Zohary, 1966).

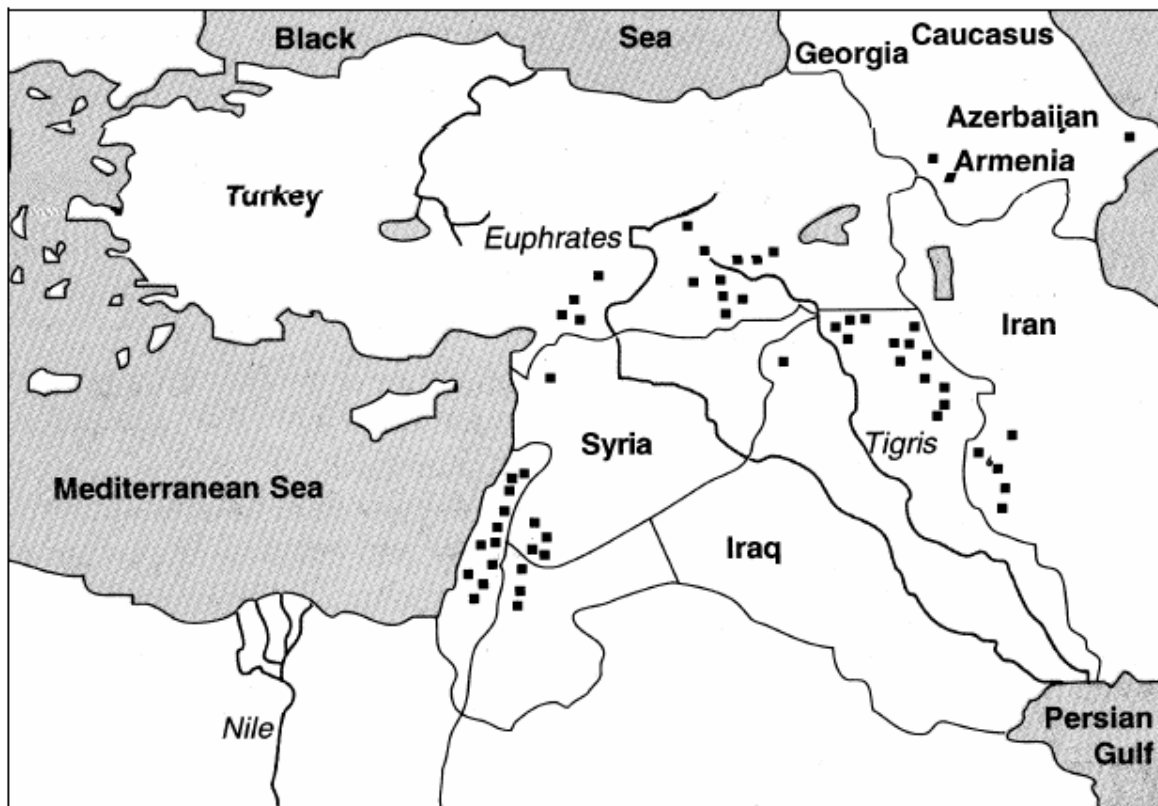
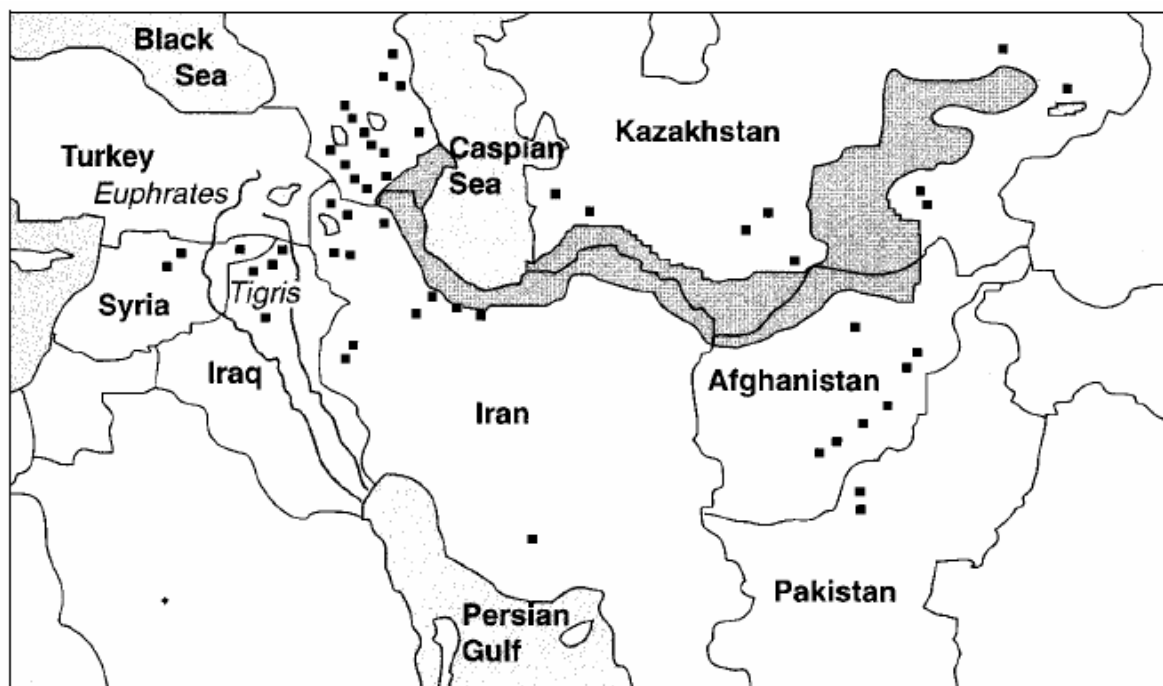


Fig 19 *Triticum dicoccoides*: Dots indicate the presence of *Triticum dicoccoides*, progenitor of *T. dicoccon* (Harlan & Zohary, 1966)



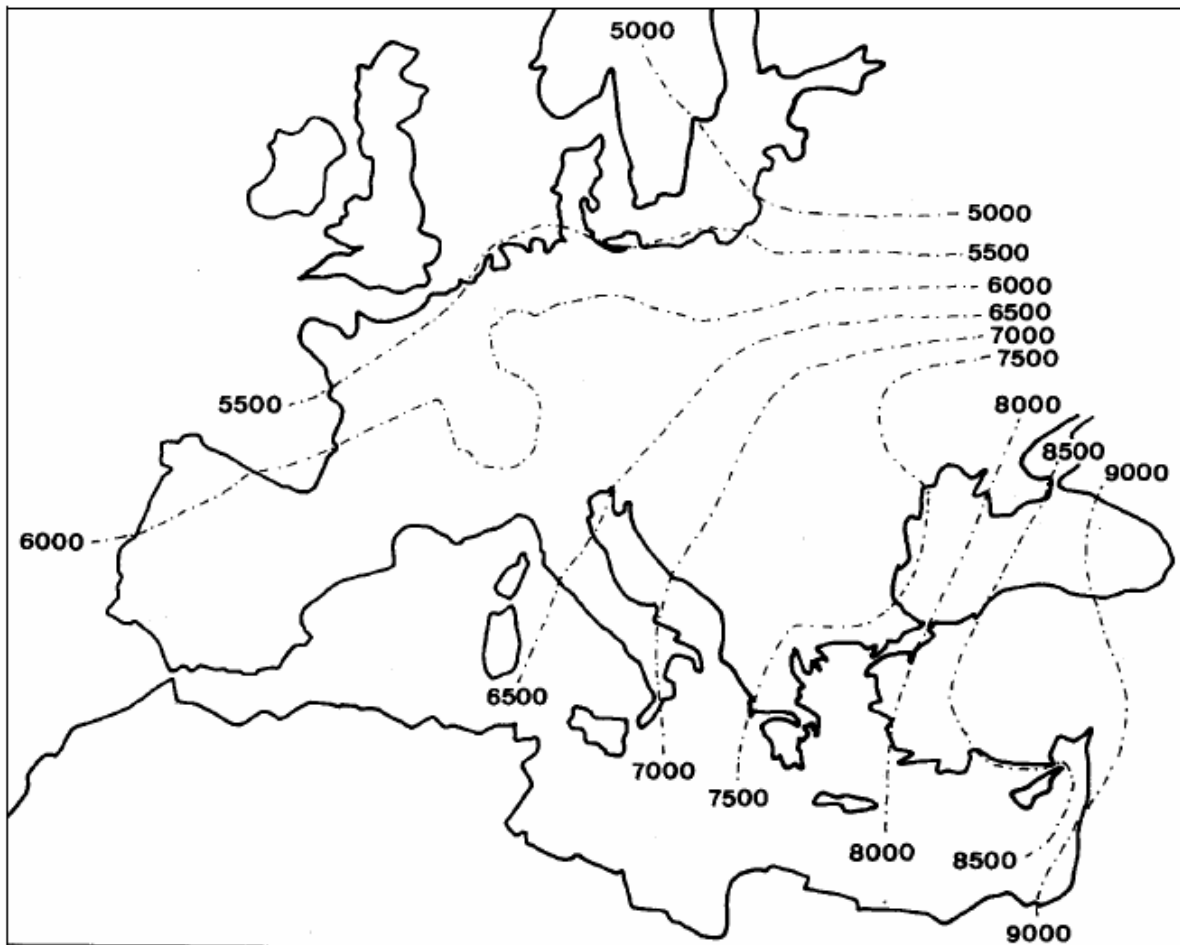
**Fig 20** Shaded area represents the centre of origin of *Aegilops squarrosa*, donor of D genome and progenitor of *Triticum spelta*. (Padulosi et al., 1995)

(Padulosi et al., 1995) conclude:

From this short review on the ecogeographical distribution of hulled wheats some considerations arise:

- spelt, emmer and einkorn are spread, in decreasing order of importance, in several countries, mainly of Europe, Near East, central Africa and north America
- good information on the cultivation of these old crops is available for only a few countries, whereas for most of the others is scarce or almost completely lacking
- only a few and rarely specific expeditions have been carried out to collect these species in their centres of diversity
- in many cultivation areas native populations are often extinct or mixed with other germplasm and/or replaced by modern cultivars, showing that the risk of genetic erosion is very high
- characterization and evaluation data are available only for a part of the world collection

This means in our case of feral crops: There is still a lot of work to be done to trace and understand feral wheat populations all over the world. Due to the fact that each crop and its wild and feral relatives have multiple origins it will be necessary to conduct lots of regional and local studies, and after having done this it might be possible to find common ground for the definition of feral populations and individuals and proceed to some generalizations, keeping in mind that the complexity of history and migration, partly due to human activity, will only allow for a highly selective and thus basically insufficient data set.



**Fig 21** The spread of agriculture into Europe. The isochrones mark the first appearance of agricultural, Neolithic villages; note that they spread out from the Near Eastern heartland. The isochrones are in radiocarbon years before present. (Padulosi et al., 1995), adapted from Ammerman and (Cavalli-Sforza et al., 1993).

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