The evolution of northern European crops

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Abstract

Agriculture was first initiated in SW Asia ca 10 000 BP. The first species to be domesticated were grasses in four major areas of the world. Evolution in crops can be divided into three distinct phases: 1. Domestication; 2. Migration and adaptation; and 3. Modern plant breeding. The presently cultivated crops in N Europe have a diverse evolutionary history and age and some examples are described in the paper. Northern Europe has had a restricted contribution to crop domestication but the area is rich in genetic resources of some groups, in particular forage grasses and legumes. For future food security a careful conservation and utilization strategy must be implemented.

SCI.DAN.H. 4 · 7 · FOOD, POPULATION AND HEALTH – GLOBAL PATTERNS AND CHALLENGES
THE ROYAL DANISH ACADEMY OF SCIENCES AND LETTERS · 2016

The dawn of agriculture and the first crops

The first deliberate cultivation of plants and thus the dawn of agriculture took place in the region of SW Asia called "The Fertile Crescent" (Zohary *et al.* 2012). That is the mountainous area in the Levant that comprises parts of present-day northern Israel, Syria, SE Turkey, northern Iraq and the Zagros mountains in W Iran. Some of the world's most important temperate crops entered the scene here, in particular wheat, barley, broad bean, flax and lentil. The archaeological remains are numerous and the evidences are strong that this took place around 10 000 BP when the crops where not only cultivated but also *domesticated*, which is when the plants were genetically changed from being well adapted to wild, natural habitats to being selected for the specialized biotopes of farm land (see below). The domestication process might have been a comparatively rapid event, perhaps only a couple of hundred years (Fuller *et al.* 2012). There was, however, a long "pre-domestication" period of several thousand years, since large amounts of older remains of wild species (particularly barley) have been found at human dwellings which do not show the characteristic traits of domestication. Humans had used many plant species for food and other purposes as hunters and gatherers and were certainly familiar with collecting, storage, and preparation for food, in particular of nuts and grass seeds before agriculture was implemented. The seeds of wild *Hordeum* (barley) and *Triticum* (wheat) were in some cases picked in great quantity for consumption (Harlan 1992, Savard *et al.* 2006).

During the early periods of domestication a large number of wild species were domesticated and many of our present crops dates back to this early period (10 – 4 000 years ago). Great civilizations such as the Sumerians and Egyptians in the west and The Chinese societies in the east based their progress on many of the main crops we know today, such as rice, wheat, flax, lentils, rice and several millets. Only a few agricultural crops have been domesticated during the last 500 – 1 000 years but more so among horticultural crops and ornamentals. Our forefathers prepared well for the further societal growth and migrations of people.

Grasses became cereals

Among the first crops to be domesticated were grasses and still after 10 000 years they are staple food for the majority of people in the world. In four major areas in the world and probably completely independent of each other and rather close in time, several species of the grass family (Poaceae) many not related were domesticated and became cereals. These four major areas of cereal domestications are:

- The Fertile Crescent has obviously been the oldest region for domestication and then for the cereals wheat and barley at ca 10 500 - 10 000 BP.
- About the same time or some centuries later, in an area at the mouth of the Yellow River in China rice and some species of millets became crops. Rice was domesticated in the lowlands and humid areas suited for cultivation of paddy rice. Two species of millets were domesticated namely *Panicum miliaceum* (common millet) and *Setaria viridis* (foxtail millet) in drier, more mountainous areas.
- From the wild relative teosinte (*Zea mays* subsp. *parviglumis*) maize (subsp. *mays*) developed in parts of C America ca 6-8 000 years ago. The first corns to be cultivated were small seeded and with small inflorescences, not the large, swollen, many seeded cobs we know today.
- In Africa sorghum (*Sorghum bicolor*) and pearl millet (*Pennisetum glaucum*) became crops. The problem here is the dating of the domestication process since there are only restricted numbers of archaeological remains for analysis. The domestication dates probably back to 5-6 000 BP.

There are several reasons why the small grass seeds were the targets for collecting in a large scale before the farming era started. The grass seed is a remarkable and complex organ with many advantages. It can be dried to low water content and in this stage the viability can be preserved and the seed can be stored for a long time. The seed is light and can easily be transported into other areas and thus promote the spreading of agriculture and the migration of people. The grass seed is comparatively nutritious containing a number of proteins and starches and for humans many essential minerals and vitamins even if it is by no mean a complete food supply.

The evolutionary process in cultivated species

In nature evolutionary mechanisms including selection and subsequent adaptation to new environments or new conditions result in new life forms and new taxa in a never-ending process. It is based on genetic recombination and occasional mutations of genes, which creates new favourable types. Evolution in nature is usually a slow process in stable environments but is speeded up in periods of drastic and more sudden environmental changes. The evolutionary process in nature is also complemented by the action of random factors, such as random survival of new forms accumulating as neutral genotypes in a stable environment, which may be of an advantage when conditions are changed.

The same evolutionary factors operating in a wild organism are active also in an agricultural context. However, humans have partly replaced nature for creating new types of crops and domesticated animals not adapted to the wild stage but only for life in a manmade habitat - the agricultural ecosystem. During the domestication process and later (see below) the action of evolutionary forces are significantly increased (100-1 000 times) in comparison to what happens in nature. Man has selected which types are suitable for his purpose and are allowed to survive - and the strong selection for a special type leads to a simultaneous change. The lethality of unwanted types is no longer gradual as in nature but has gone up to 100 % in one generation.

The evolution of crop plants can be divided into three major phases in the ongoing story of alterations: 1. Domestication; 2. Migration, selection and adaptation; 3. Modern plant breeding.

Domestication

This phase is the transfer from the wild state to an agricultural ecosystem. During a comparatively short period (some centuries) the plants went through drastic genetic alterations with major phenotypic changes in rather few genes, a process called macroevolution. The changes for adaptation to the cultivation system affected biological system such as:

- *Loss of seed dispersal mechanism.* A wild plant must have an efficient dispersal mechanism of its seeds either by wind, water or by animals in order to survive. In cultivation all seeds can be harvested without loss and the plants have lost their shattering capacity and any special arrangements for dispersal (hairs, thorns, long awns etc, see Figure 3).
- *Even maturation and germination.* In cultivation all seeds can be harvested at the same time and all seed should germinate more or less simultaneously leading to an even development of the crop. This has lead to loss of successive maturation and seed dormancy, which predominates in nature.
- *From cross- to self-fertilization.* Many wild species have a higher degree of out-crossing, which promotes the development of genetic variation of importance for survival in a changing environment. For example, the wild progenitor of barley has up to at least 10 % of outcrossing whereas modern barley cultivars have less than 1 % out-crossing (Bothmer *et al.* 2003). However, a higher outcrossing rate often leads to a lower degree of fertilization and thus a lower seed set. In cultivation homogeneity in the offspring combined with high seed set is the preferred character.
- *Changes in life form.* In an agricultural context it is vital to get yield annually for food supply. Many domesticated crops emanate from biannual or even perennial ancestors and a shortened life cycle has been selected during domestication.

Migration, selection and adaptation

The second phase in the evolution of crops contains the further development and spreading of agriculture. It is a much more prolonged and slower process than the domestication. Cultivation together with the newly domesticated crops spread to new areas where the plants faced new climatic and edaphic conditions. New combinations of adapted traits were needed for the new environments, which include tolerance to other abiotic stresses such as frost and drought and changed day length. The crops faced the infection of new pests and diseases, which required particular resistance. The new habitats had also other edaphic conditions. New gene combinations and new mutations resulted in adaptation to the new surroundings. At the same time the new human category – the farmers – made their own selections for particular, preferred traits such as better taste, efficient growth and a higher yield or for other useful characteristics. In this way adaptation to very extreme conditions were possible (Figure 1).

The migration phase became a much more gradual process – influenced by several genes and alleles each one having a minor influence on the phenotype, called microevoltion. The major crops, such as the cereals were very successful and were eventually dispersed to suitable areas all over the world. The temperate cereals wheat and barley reached Scandinavia as early as 6 000 BP. Simultaneously they also spread eastwards and reached China ca 5 000 BP. In this gradual manner, new types, *landraces*, developed, which were well adapted to new conditions. The landraces were locally adapted often to very restricted areas. In this way a rich genetic variation, so called domesticated biodiversity, was created over time. The landraces were quite successful and when modern plant breeding started the initial material was the landraces.

Modern Plant Breeding

During the 19th century large, revolutionary changes of agriculture took place with, for example, land reforms, increased mechanisation, development of new

Figure 1. A genetically variable landrace of wheat in Tibet, at an altitude of 4 000 m.

farming technology and increased use of fertilizers. In this period there was also an increasing demand for better seed material for increased yield and yield stability, better quality properties and better disease resistance. Modern plant breeding was born and the first plant breeders were small, very local seed companies often with governmental support in many countries. The initial material was the older, well adapted but heterogeneous and genetically variable landraces often with uncertain yields. The methods practiced by the first breeders were simple selections. From genetically variable landraces plants with the best sets of characters were chosen and after some generations of continued selection a new cultivar was released. When Mendel's genetic inheritance laws were rediscovered in the year 1900 it became evident that further selections in already homogeneous and homozygous lines were not possible. The variability had been exhausted and new variation must be created. The next step was based on the ability to combine favourable traits from different parents by sexual crosses and the creation of new, genetically variable populations from which new circles of selections for producing the new cultivars could be performed.

Combination breeding and selection are more than 100 years old but they are still important in modern plant breeding. However, over the century these older technologies have been complemented with a number of other more sophisticated methods in the tool-box of the plant breeder (Kingsbury 2009). In each decade new and more efficient methods have been developed. Artificially induced mutations, chromosomal rearrangements and alterations in chromosome numbers (polyploidy), cell- and tissue-culture with fusion of protoplasts, which are single cells of different species for getting new hybrid combinations

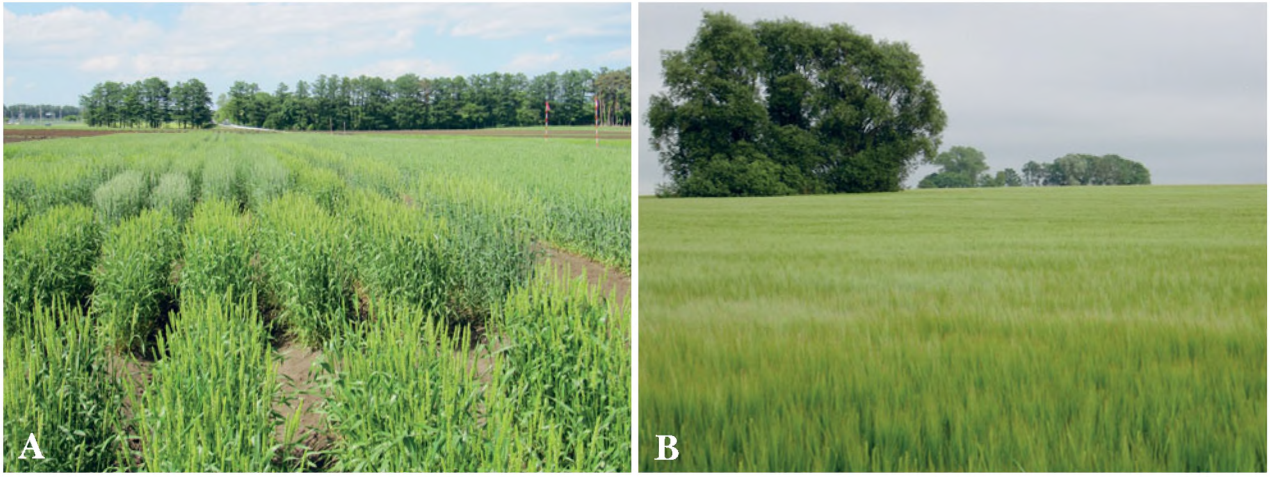

Figure. 2. Modern plant breeding. The genetic variation is present in the experimental fields of the breeder (A). A modern cultivar of barley is completely homogeneous and homozygous (B).

lead to the molecular era. Nowadays characterization of the whole genomes or mapping of genes has lead to effective marker-assisted breeding. In the mid of the 1980s the transformation technique was developed (Genetically Modified Organisms, GMO) for transfer of individual genes within and between species. The newest methods now in progress include how the function of single genes can be regulated. The evolutionary process has thus been speeded up considerably and man now controls in what direction the development goes.

The development of new methods in plant breeding is continuous and it is closely connected to the scientific development in genetics and related disciplines. In the old landraces the genetic diversity and heterogeneity were present in the farmer's field. The most obvious change from the times of the local landraces is that genetic variability is no longer present in the same way farmer's fields as was the case when landraces were grown. A modern cultivar of an inbreeding species is completely homogeneous and homozygous. The genetic diversity has been moved to the field trials of the plant breeders or in their stock of seed material (Figure 2). The major genetic variation in the crop species is now stored in the world's gene banks (see below).

Origin and developmental history of some northern European crops

The wealth of cultivated plants we presently grow have a very diverse background. They emanate from different times and different areas of the world and they represent different plant groups and different biological systems. Here a few examples of crops presently cultivated in northern Europe will be presented showing quite different developmental histories. The nomenclature here follows Aldén & Ryman (2009) and where references are not given specifically, these case studies draw on Harlan (1992) and Smartt & Simmonds (1995).

Barley

Barley *(Hordeum vulgare* subsp. *vulgare)* is one of the original, ancient crops emanating from the Fertile Crescent and it has a very simple developmental history (Bothmer & Komatsuda 2011). The ancestor (subsp. *spontaneum*) is still abundant and grows in suitable habitats in SW Asia. Domestication took place at the diploid level (2n=14) and the wild and cultivated forms are fully compatible with each other (Bothmer *et al.* 1991). Spontaneous hybridization may occasionally take place where they meet and the wild form is

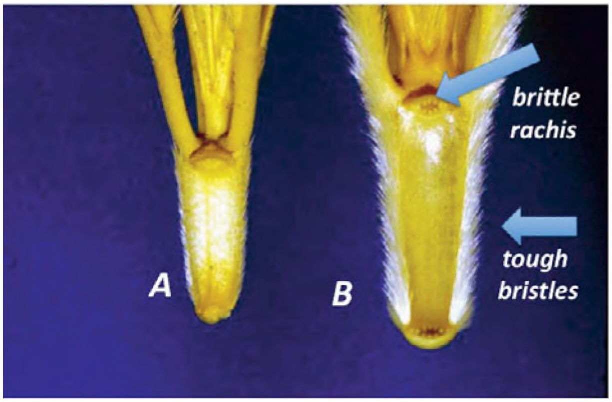

Figure 3. Dispersal units of two wild species of barley. A. *Hordeum murinum*; B. *Hordeum vulgare* subsp. *spontaneum*, the progenitor of cultivated barley. Both wild species have brittle spikes, which easily shatter at maturity and large bristles, which effectively adheres to the furs of animals for seed dispersal.

an important gene source for breeding with many interesting characteristics. The main traits differing the cultivated and the wild form involve the biological systems of reproduction and dispersal. Cultivated barley is mainly inbreeding, has a non-brittle rachis and has lost the seed dispersal mechanism whereas the wild form has a rather high rate of out-breeding. It is shattering with a very brittle rachis and very efficient structures for seed dispersal by animals (Figure 3).

Wheat

The history of wheat is much more complex than that of barley. Both cereals were domesticated at the same time (10 000 BP) but whereas in *Hordeum* a single crop developed several different species of wheat were domesticated including einkorn (*Triticum monococcum*), emmer and spelt wheat (*T. dicoccum*), and bread wheat (*T. aestivum*). The domestication has been gradual including many evolutionary steps such as polyploidization and interspecific hybridization. Einkorn and emmer were the oldest whereas bread wheat is much younger. Einkorn is diploid (2n=14) and emmer is tetraploid (2n=28) both occurring in a wild and in a domesticated form. Emmer probably developed through a hybrid between einkorn and a wild goat grass (*Aegilops* sp.) before it was domesticated. The last major step in wheat evolution took place around 4-5 000 years BP probably somewhere in present day Iran when emmer or durum wheat hybridized with another goat grass (*Aegilops squarrosa*) giving rise to the hexaploid bread wheat (2n=42). Still the details of this complex evolutionary history of the wheat are not completely understood.

Rye

In contrast to the primary cereal crops wheat and barley, rye is a secondary crop, which means that it became established as a weed in the fields of the other to cereals. When agriculture spread the weed migrated together with the crops. It was noted that the weed had large seeds, which often were contaminated with the seeds of the crops and the weed seeds could also be used as food. Gradually, selection for the best types took place. Dating for the domestication of rye is rather uncertain, but obviously it was a gradual process dating back at least to 4 000 BP. It is neither quite clarified where the original area for domestication is. According to different theories it happened either south or north of the Caspian and Black Seas on the migration route to Europe.

The evolution of rye took place at the diploid level (2n=14) and with various chromosomal rearrangements (mainly translocations) as the driving forces. It was a complicated process with several taxa involved. The cultivated crop (*Secale cereale*) is part of a species complex with weedy and wild forms. It comprises both in- and out-breeding forms originating from *S. montanum* with an eastern Mediterranean distribution. The original species is a perennial from which annual forms of the weedy type of *S. cereale* as well as the cereal crop were developed.

In a Nordic context rye together with turnip (*Brassica rapa*, see below) has been an important element. These two species were the main crops in the slash-and-burn farming system in remote, meagre areas mainly in C and N Scandinavia with poor farming under several hundred years, until the end the 19^{th} century (Emanuelsson 2009).

Figure 4. Wild and cultivated Brassicas in southern Italy. A. *Brassica rupestris*; B. An old landrace of leafy kale (*Brassica oleracea*).

Brassica crops

The genus *Brassica* comprises a number of cultivated species and types all interrelated and showing much genetic diversity. Most wild *Brassicas* are perennial or biannual and with a European, W Asiatic and N African distribution whereas the cultivated ones are annual. The genus, and particularly the domesticated species, shows a reticulate evolutionary pattern including several examples of interspecific hybridization followed by chromosome doubling. Most species are thus interrelated. One example of this pattern is rapeseed (*Brassica napus*), which is a natural hybrid, probably recent, between wild kale (*B. oleracea*) with 2n=18 and wild turnip (*B. rapa*) with 2n=20. The hybridization was followed by spontaneous chromosome doubling giving rise to rapeseed (2n=38). Other cultivated crops in *Brassica* are for example Black mustard (*B. nigra*), Ethiopian mustard (*B. carinata*) and Indian mustard (*B. juncea*).

B. oleracea was domesticated in historic times in the Greek-Roman area around 3 000 BP. In Greece and southern Italy a number of closely related wild species occur. During domestication in S Greece and in Calabria and Sicily in southern Italy diversification to different forms such as leafy kales, cabbages, broccoli and cauliflower can be followed in ancient literature in the period (Maggioni *et al.* 2010). All these cultivated forms are fully interfertile (Bothmer *et al.* 1995). The original, wild type was probably a leafy kale similar to the wild types growing in the area today, which are woody, perennial shrubs (Figure 4). Plants of *B. oleracea* occur in wild habitats at the Atlantic coast (France, N Spain and Britain) leading to a theory that kales and coles were domesticated here in Celtic times. However, newer research shows that it is more likely to assume that the central Mediterranean Greek-Roman area was the locus for domestication (Maggioni *et al.* 2014). The different coles became important foodstuff for the Romans and when the empire extended westwards the legionaries brought the coles with them for cultivation in the newly conquered areas. The *Brassicas* have a very efficient reproduction and are effective to compete with other species in certain habitats, particularly in and around cliffs. The so called wild *Brassica oleracea* still growing in or around cliffs in the Atlantic region thus represents older escapes from cultivation which have naturalized in these maritime cliffs.

Sugar beet

Whereas the domestication history of the new industrial crop, sugar beet (*Beta vulgaris* var. *altissima*) is of recent origin, the domestication of its relatives in the same species has a much longer history. The ancestor of all forms of the cultivated beets (*Beta vulgaris s. lat.*) is the low grown, prostrate somewhat fleshy sea beet, *B. maritima* native to stony beaches at the Atlantic and N Mediterranean coasts. The first domestication was for consumption of the leaves and took place in pre-Roman time (ca 4 000 BP) in the Mediterranean. It developed to leaf beets, chard or Swiss chard (mangold) (var. *cicla*), of which the leaf petioles are enlarged and swollen and nowadays eaten as a delicacy (formerly it was poor man's food!). The next step in its evolution was the development of forms with swollen upper parts of the roots with fodder beet (var. *crassa*), which was important for animal feed up to the 1950s and red and other edible beet roots (var. *esculenta*). This happened probably in historic times but the dating is rather uncertain.

Sugar beet has an increased sugar content in comparison to the beet roots from which it was selected. This took place in France around 1780. The first beets from which sugar was extracted had a sugar content of 5-6 %. A century later breeding had resulted in a sugar content of ca 18 %. During the last century, up to present, no increase in sugar content has occurred – it is still 18-20%. Obviously one has reached a biological limit for the sugar content. However, breeding for other traits such as beet size and shape, seed structure, growing efficiency and disease resistance has much increased the sugar yield per hectare.

Garlic

Already in Egyptian time fully domesticated garlic (*Allium sativum*) was present and remains of bulbs and stalks have been found in Pharaonic tombs and are well preserved by the very dry conditions. The morphology and structure of the ancient plants are remarkably similar to the garlic cultivated today. The domestication history of garlic is incompletely known but it seems that it was domesticated already ca 7 000 BP. One particularly interesting condition is that garlic is sterile. It sets no seeds and is multiplied vegetatively by the bulbs, which was the case already in ancient times. No wild forms of the species *A. sativum* are known. The closest wild relative might be the central Asiatic species *A. longicuspis*. It is a tetraploid species (2n=32) with a restricted distribution in Central Asia whereas garlic is diploid (2n=16). The evolutionary history is thus obscure since there is a considerable distance from C Asia to Egypt in the Mediterranean from where the ancient garlic is known and there are no other intermediate forms.

Strawberry

Fragaria is a widespread genus with around 20 species distributed in Eurasia and America. The more or less tasty fruits of most species have certainly been picked and eaten everywhere the different species grow. The European representative of wild strawberry, *F. vesca* (2n=16) was highly praised by Linnaeus not only for its taste but also for its medicinal use. However, this species was not involved in the development of the cultivated strawberry, *F. ananassa*, as often believed. Instead two American species are the ancestors and the hybridisation took place recently. *F. chiloensis* (2n=56) was introduced to The Netherlands in the early 1700s and half a century later the N American *F. virginiana* (2n=56) came to Europe. Around 1750 the hybrid between the two species was made, also in The Netherlands, and in the offspring a favourable combination was selected resulting in the cultivated strawberry. In later years also other species, including *F. vesca*, have been used in breeding particularly for introducing the delicate taste of the other wild taxa.

North European contribution to evolution and crop diversity

Northern Europe has had a restricted contribution to crop domestication in general. For some plant groups, however, the area has been and still is important. It is a centre of diversity for crop wild relatives and for old landraces of many crops with origins elsewhere the area is important as a genetic resource.

Even if seeds of many forage species mainly of legumes, domesticated in C or S Europe were imported to the Scandinavian countries already at the time of Linnaeus (early 1700s) the area has in later years contributed much to the breeding of new cultivars. This is the case particularly for many forage grasses such as *Dactylis glomerata* (cock's foot), *Phleum pratense* (timothy), *Poa pratensis* (Kentucky bluegrass or common meadow-grass) and some species of *Festuca* (fescue), which are native in the wild Scandinavian flora. For centuries they have regularly been harvested for hay and during the last 100 years they have been the target for intense breeding efforts here. The species have successively been domesticated, bred and cultivated in most of the agricultural land in the Nordic area. Also legumes, particularly the species *Trifolium medium* (red clover), *T. repens* (white clover) and *T. hybridum* (alsike clover), have extensive distributions in the Nordic region and these species, even if not directly domesticated here, are common elements in the wild flora and thus of great importance to preserve and utilize in breeding programs.

Other genera where Scandinavia houses important genetic resources are the temperate cereals wheat, rye, oats and barley (local landraces and older cultivars), black currant (*Ribes nigrum*), rhubarb (*Rheum rhabarbarum*), as well as many other fruits, berries and kitchen vegetables. The evolutionary process and natural selection for the area have over the years created a rich genetic diversity in our crops during the long history of agri- and horticulture.

The future of food supply and food security

Even if genetic diversity connected to our crops is large we are nevertheless rather vulnerable for the future food supply from the plant kingdom in a global context. Totally there are around 300 000 species of higher plants in the world. It has been calculated that around 7 000 of those can be used by man for food and other purposes and ca 120 species are of national importance.

Only 30 species stand for 90 % of human calorie uptake and, even more of concern, only three species – rice, wheat and maize – are used for 60 % of the global calorie uptake. If a serious pest or other external causes such as drought or flooding strike one of the major three staple crops, which actually has happened, it may result in a serious challenge for the food security in certain areas or globally. Richness in availability of genetic diversity within crops is the best insurance. The future will be complex with many new situations such as climate change, overpopulation, hunger and escalating environmental problems. We will need a new green revolution aiming at a sustainable intensification in agriculture with among other things increased urban or peri-urban cultivation. The continuous production of new cultivars of established major crops and better utilization of minor crops for all kinds of agricultural systems is necessary.

The large genetic diversity in our crops and wild relatives has been created over the whole history of man as a farmer. The 10 000 years of an ongoing evolutionary process in our crops will continue and hopefully contribute to further genetic variation. The present and future supply of new genetic material for breeding may however be vulnerable why collecting and preservation of genetic resources still is important.

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