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Traditional maintenance breeding of landraces: 1. Data by crop

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Vidi lecta diu, et multo spectata labore
Degenerare tamen, ni vis humana quotannis
Maximus quaeque manu legeret

(The selected seed, improved through years and labour, was observed to reverse, unless the hand of man choose the biggest and richest ears each year).

Vergilius in Georgica I, 197, cited by H. de Vries, 1906. Soorten en varieteiten, Haarlem, 538 p.

Summary

Examples of the methods of traditional maintenance breeding of several crops, cited in literature, are presented. It is concluded that, although crops are grown all over the world, only few examples are sufficiently described. Only for maize some reliable data are available. Three explanations for this small number are 1. the farmers are not aware of their knowledge of growing crops (including traditional maintenance breeding), 2. the interviewers and other scientists are not acquainted with this farmer's knowledge, or 3. most farmers do not actually perform traditional maintenance breeding, as they and their ancestors probably have experienced that traditional maintenance breeding does not result in a better crop. They must have thought that seed replacement was a better method to maintain the yielding capacity of their crops.

Terminology: 'Maintenance breeding' (or 'maintenance selection') refers to all breeding measures taken to conserve the genetical composition of a variety, improved or not; where the term 'landrace' is used in the text it may also refer to a 'gardenrace'. In the following text 'maintenance breeding', in general, includes 'traditional maintenance breeding'.

Introduction

Farmers, gardeners and garden hobbyists put aside, for the next generation, a part of the harvested seed (in this text including seed ware). This activity has been applied since time immemorial and quite probably already soon after wild plants were domesticated. Depending on the crop and the man/woman, some selection may have been carried out to obtain a crop answering better to the wishes of the growers, communities.

Little information is available on seed replacement (Zeven, 1999) as well as on the traditional maintenance breeding, of landraces by the growers. An example is the information provided for flax (*Linum usitatissimum* L.) and hops (*Humulus lupulus* L.). The agricultural constellation of the Dutch province Gelderland in ca 1825 has been described (Roessingh & Schaars, 1996). Only for flax and hops did these authors find short references to the application of methods of multiplication and maintenance. Unfortunately, the 19th-century compilers did not feel the need to describe these methods, maybe, because they considered them to be common knowledge at that time or of no importance.

To obtain more information a questionnaire was sent to some 50 researchers. Some 30 answers were received of which some 20 communicated that no information was available. An extended search of the literature resulted in little published information on any handing-over of seeds of crops between people (Zeven, 1999). However, it is quite likely that in the first millennia of crop cultivation, neighbours, even when belonging to different ethnic groups, and conquerors adopted any better crop, any better form of it and any better method for growing and seed storage (for the next crop generation). Similarly, only a few descriptions of the quest for, and the obtaining of a better crop or form are mentioned. An example is the dispatch of plant collectors to the heart of Asia Minor in search of vines (*Vitis* spp.), figs (*Ficus carica* L.) and roses (*Rosa* spp.) by Sumerians around 2500 B.C.

Farmers are probably not well aware of their, often thorough, knowledge of agriculture in general and of their crops and the methods of their cultivation and storage in particular. However, they have built up and transferred this knowledge to the next generations during many millennia. They will adopt new knowledge, new crops and new cultivation and storage methods and new types of old crops or adapt indigenous ones. But, as they do not write about their unique knowledge, it looks as if they do not possess it. Moreover, a search of the literature showed that, apparently, quite a number of scientists discovered the existence of 'farmers' knowledge' and wished to report on this 'novelty'. As maintenance breeding is rare, most scientists are not aware of this absence. For that reason they did not refer to this type of breeding.

Farmer's knowledge

After a search through much early literature and consultation with many colleagues, it is concluded that farmer's knowledge and any activities of farmers to maintain landraces are rarely described. The results are compiled below. Farmer's knowledge is of all ages. In addition to the above mentioned early example, another is the expedition sent in 1495 B.C. by Queen Hatshepsut of Egypt to the land of Punt (= Somalia) to collect and transplant living frankincense trees (= cedar trees, *Cedrus* spp.) (Hepper, 1967). Queen Hatshepsut must have been a keen gardener. She must have obtained knowledge about this tree, most probably via advisors, who will have gained their knowledge from others who had visited Punt to trade in franckincense and other products of interest. This expedition was of such importance (to the Queen) that she had it depicted on the wall of the Temple of Thebes. Similarly, in the seventh century B.C. in the book Kuan Tzu is described that Duke Huan of Chhi (a part of the Shantung area) led an expedition to the territory of the Mountain Jung and brought back 'winter onions' and soybeans (Bray, 1984). Furthermore, support of the replacement of a (form of a) crop by another, is found in the writings by (Old-)Greek and (Old-)Roman authors (see top of article), who also describe selection activities. Some other examples are: in the former Roman Empire it was advised to use the best seeds, i.e. the heaviest seeds for the next crop; and Arabic writers as Ibn Al-Awwam, an agronomist from Sevilla, Spain, writing in 12th century, described how seed should be selected: the grains should be heavy, bright coloured, hard, and plump (Thurston, 1994). Fifteenth century data are provided by Lindemans (1952) who referred to a lease between a tenant gardener and the abbey Averbode in Belgium dated 1435, implying that, for the next crop, the tenant gardener should harvest seed of parsley (*Petroselium crispum* (Mill.) Nym. ex A.W. Hill), leek (*Allium porrum* L.), and cabbages (*Brassica oleracea* L.), and some 600 onions (*Allium cepa* L.). We may expect that such harvesting had to be carried out by all gardeners and farmers each year. Lindemans also described that the abbey Vorst, also in Belgium, purchased in 1475 'ayuynzade' (onion seed) and 'cambuys-coelzade' (cabbage seed). Elsewhere, and in modern times in Ethiopia, the presence of sound farmer's knowledge of storability of grains of sorghum landraces, with regard to storage pests, such as the rice weevil (*Sitophilus oryzae* L.) has been described by Awegechew Teshome et al. (1999a, 1999b).

Maybe, Fruwirth (1930) is the first to pay attention to maintenance breeding of landraces. He described that for cereals (in Austria) no maintenance breeding was applied. In 1943, Squire (1943), describing the landraces of rice (*Oryza sativa* L.) of the Mende in Sierra Leone, concluded that 'the subject (of traditional maintenance breeding) has received but little attention judging by the absence of records and collections' (cited by Richards, 1985). Unfortunately, Squire's conclusion is still true: the subject did not attract the attention of researchers. Squire's paper remained unobserved for some four decades, probably, because the time (World War II) and the type of journal (Sierra Leone Agricultural Notes) hampered a wide distribution to an interested readership. Identical conclusions were drawn by Johannessen et al. (1970) and Bradshaw (1975). Johannessen et al. said that 'gaps in the records of (Amer-)Indian ways of maintaining their improved varieties (of maize, *Zea mays* L.) probably reveal the observer's lack of awareness rather than that of the aboriginals', whereas Bradshaw wrote: 'the unfortunate point which is crucial to the whole of this problem is that the situation has not ever been looked at in sufficient detail to give a clear geographical picture of the genetic structure of any crop still in a primitive unimproved state.' Frankel & Soulé (1981) also 'touched' this point; they also reported that little is known of the deliberate selection of agricultural crops, and that for horticultural crops more knowledge is available. However, they did not elaborate on this interesting subject. Wilkes (1995) regretted that he and E. Anderson (1954), both collecting maize genetic resources, did not make a comparison between crops derived from a random ear sample (for research) and the sample selected by a farmer (next generation of the crop). Hence, Wilkes' conclusion that 'the ethnobotany of artificial selection has remained an ignored aspect of plant domestication' and 'artifical selection' by man. Although, in general, little (scientific) data on selection and maintenance of folk varieties by farmer-breeders is available (Cleveland et al., 1994), it is known that depending on the farmer and the gardener, as well as on the crop, maintenance breeding is applied. This type of breeding is carried out by selecting single plants or by (positive) mass selection. Continuous selection by some farmers for plants with desired characters is similar to the later proposed 'scientific' selection within landraces to select by 'seekers for the best plants' as suggested by Beyerinck in 1882 (Zeven, 1970). However, such phenotypic selection does not necessarily lead to high yielding lines.

Old knowledge is lost because farmers continuously adopt and adapt. This also is true for European farmers of the 16th century who had no knowledge about the ways neolithic farmers or farmers in Viking Times were growing their various types of einkorn and emmer wheat. And this also concerns so many other disciplines: the old knowledge is (almost, and often quickly) forgotten because young ones have not learnt it. However, the expression of the Adja in Benin should not be forgotten: 'It is with the old cord that one knits the new one' (Dangbegnon & Brouwers, 1990) . This saying indicates that the Adja farmers, and men and women in general, always experiment, and add new methods and information to the old ones forgetting with time the still older methods. But the selection activities to obtain a good (or better) yield next year, if applied, is of all ages. Transfer of farmer's knowledge goes mainly from parents to children. Although agricultural schools do very good work, the tricks of the trade will be learnt during the growing up on the farm. Muliokela (1997) stated that Zimbabwe has a relatively advanced seed industry. He provided an overview of the magnitude of types of selection, i.e. sources of seed is provided for this country (Table 1).

Table 1. Sources of seed for communal farmers in Zimbabwe in 1991, in % (Muliokela, 1997)

Source	Maize	Sorghum	Sunflower	Groundnut	Cotton
Farm-saved	2.1	56.1	50.4	71.5	3.0
Local farmer	–	8.8	19.5	11.1	1.5
Local trader	13.1	5.3	6.5	7.0	1.5
Local store	14.8	3.5	1.2	1.2	13.6
Others	70.0	26.3	22.4	9.2	72.4

From this table it is not clear whether the material of in the first two rows is on a landrace or cultivar level, and what is/are the original seed source/s of the 'Local farmer', 'Local trader' and 'Local store'. If one assumes that seed obtained from 'Local farmer' is very similar to 'Farm-saved', it may be concluded that for maize and cotton most seed is obtained from 'Others', whereas for groundnut most seed is '(similar to) Farm-saved'. Sorghum and sunflower represent an intermediate position in this respect.

I assume that a similar situation, be it for other crops, existed in countries like The Netherlands around 1900. Some crops were still grown from home-saved seed and others were already cultivated from seed (originally) provided by a breeding company or his agent. An example is the minor crop, the dry bean type of common bean (*Phaseolus vulgaris* L.), which is still grown from home-saved seed (Zeven, 1997, see below). In Ethiopia, no breeding is applied for faba beans (*Vicia faba* L.) and landraces still are the sole type grown by the farmers, even in the major faba bean regions. Similarly, breeding work for legumes and forage crops is often not carried out and hence all material is of ‘garden race’ level. But within a crop differences may occur. For instance, also for Ethiopia, for wheat (*Triticum aestivum* (L.) Thell.) in high-rainfall and low-rainfall zones the area under landraces is 15% and 73% respectively (Rishaw & Kugbei, 1997). These data support earlier conclusions drawn for any crop in any country, that the earlier breeding work started, the greater the area sown to cultivars of that crop will be. However, much depends on the ease of obtaining and maintaining seed for the next generation.

Examples of traditional maintenance breeding by crop

The degree of ‘contact’ of the farmer, his wife and relatives with individual plants or plant parts is of utmost importance for observing, ‘understanding’ and selecting plants before harvesting and/or plant parts after harvesting. ‘After harvesting’, in general, implies that desired plant parts are put aside and taken home. Hence, the link between the (favourable or unfavourable) growing site and the plant grown on that site will be broken, resulting in phenotypic selection for desirable characters. Selecting of material for the next crop will take place during cleaning or storing, or just before sowing or planting. Two examples of the latter are: farmers may add some red kernels to the yellow or white sowing seed of maize in the Americas to promote a ‘good’ crop (see below). Similarly, formerly, in Austria farmers growing a mixture of yellow- and purple-skinned potato landraces, would add tubers of one of the types if this type was considered to be under-represented (see below).

Maize, sorghum, millet, beans, minor crops (vegetables, spices and such) and many vegetatively propagated crops are examples of crops where the harvestable part is hand-picked, which makes selection before, during or after harvest possible. In many other crops, characterized by growing and harvesting in bulk, selection is rarely performed at all. Rice is a crop on which both types of harvesting may be used, each panicle being cut by hand as used to be the case in Indonesia, whereas in other countries it was bulk harvested. In Europe and probably elsewhere, in mediaeval times and earlier, wheat, barley (*Hordeum vulgare* L.) and rye (*Secale cereale* L.) were also harvested. by cutting first the ears and later the straw. This type of harvesting was applied to reduce the amount of seeds of pestweeds in the harvested seed. It also promoted a close contact between the farmer and the crop. Although little information is available, it may be assumed that farmers put aside attractive looking ears, and for other crops other plant parts, to be grown and watched separately, and when accepted, to be multiplied.

Crops

In the following part an overview of information extracted from the literature and from personal communications will be presented. The first examples deal with crops of which each plant can easily be observed and harvested by hand, resulting in a close contact between plant/plant part and harvester. As said before, rice is a ‘transitory’ crop. The last examples deal with crops which are bulk-harvested.

Maize (*Zea mays* L.). Most data are available for maize, because of the high number of investigators involved, the close contact between farmer and crop, and the easily observed single plants. The often-close association between the religion of the farmers and the many shapes, sizes and colours of the kernels, promoted the use of these characters by the farmers for landrace identification and, hence, maintenance. Thus, in Peru selection has been described as ‘an art’ (i.e. a skill, ACZ) and many races are maintained in a state of uniformity, at least with respect to colour, by rigorous selection’ (Anderson, 1947; Mangelsdorf, 1974).

As plants and especially ears are easily observed, positive mass selection can be carried out. Further, the existence of metaxenia and epistasis makes introgression of foreign, kernel colour genes detectable. The ties between the farmer and his maize crop are much stronger than between farmers and other cereals. Therefore, the maize specialist Anderson in 1947 stated that maize is a sensitive mirror of the people who grow it (Anderson, 1947; Mangelsdorf, 1974). Rigid selection for a type of seed by (Amer)Indians resulted in landraces, which are maintained as such. This is not only true for ‘varieties’ used for food, but also for those with another use. For example, in Guatemala, maize also is grown for other purposes by the Quechua farmers (Soleri & Cleveland, 1993). They maintain diverse varieties, such as ‘sweet varieties’ for native beer (‘chicha’) brewing, roasting, and others for preparing the native confection ‘pinole’. Black kernels of plants with deep purple rachis (‘cob’) are used for making tortilla and beer, and for medicinal-ceremonial purposes such as offerings to gods. In addition, plants with twin ears attracted attention too. It is naturally

Table 2. Association of kernel colour (landrace) and characteristics (Bohrer, 1994)

Landrace (kernel colour)	Growing period (months)	Yield	Taste and texture	Use
Yellow	$6\frac{1}{2}$	highest	poorest	animal feed
White	6	high	high	human food
Blue-purple	5	moderate	best	human food
Red	$4\frac{1}{2}$	low	low	reserve human food

(although often erroneously) assumed that plants with this character produce a higher yield type, i.e. assure a good crop. This character occurs quite commonly in landraces grown in Mexico and Guatemala, which may point to prolonged positive selection (Bohrer, 1994).

Farmers often grow more than one landrace at a time and apply methods to minimize hybridization. In one region of central Chiapas, Mexico, the maize farmers recognized 15 landraces by name. Some original components of such landraces may have derived from cultivars, of which some have become a landrace (*acriollada*, i.e. have become similar to a landrace (Bellon, 1991)).

In southwest U.S.A. the Hopi grew some deviating maize landraces among the two common ones. These deviating ones were obtained from North American and Spanish communities, whereas various Mexican 'varieties' must have been introduced during Apache raids (Anderson & Cutler, 1942).

So maize kernel types may 'migrate' ('travel', Johannessen et al., 1970) from one place to another, i.e. farmers had observed that maize plants of a certain field may produce ears with some kernels coloured like those in a neighbouring field. The causes may be metaxenia and epistasis, which phenomena may be conditioning the expression of dark grain colours in white kerneled landraces, as well as transport of kernels from one field to the other by animals.

To prevent this 'migration' farmers may grow landraces with different flowering times side by side, whereas those with simultaneous flowering are grown at some distance from each other. Special types for private use such as the blueish/blackish kerneled 'Negro'[1] are grown in isolated fields. However, according to Louette (1995) these farmers' fields would lose some genetic diversity because starting from 40 ears per field for the next crop is, according to her, insufficient. This conclusion is not generally accepted however (Zeven, in preparation). Furthermore, a constant introgression of genes from other sources will promote a continuous increase of the intra-landrace variation.

Gender also plays a role. With the Hopi, care of seeds from harvest until the next planting is the responsibility of women (Soleri & Cleveland, 1993). It appears that with increasing age of the farmer and his wife more landraces were maintained. For instance, three farmers younger than 30 years maintained an average of 5.0 landraces, 12 farmers being 30 to 60 years old kept 6.2 landraces, and 30 farmers older than 60 years maintained 6.8 varieties (Soleri & Cleveland, 1993). The difference may not be statistically significant, but the figures may indicate a trend. They may either indicate that, as a dying-out relic, i.e. the older farmers still maintain more landraces than younger ones. Or when a farmer becomes older he enjoys to maintain more landraces, whereas the younger farmer, probably, is not (yet) seeing the point of growing many landraces.

Common selection criteria concern: kernels obtained from the largest ears, ears with a minimum tapering, ears with the most rows of kernels, the depth of the kernel, and the absence of insect damage and diseases (Johannessen et al., 1970; Jensen, 1994). The kernel is an important plant part observed by the farmers: attention may be paid to kernels with a uniform shape, plumpness and tightness, their colour and size, and physical damage by insects and diseases, and their provenance. The growth period also is selection criterion. Such often rigourously applied selection criteria may result in a quite uniform landrace. A review of examples of each selection procedure is presented by Johannessen et al. (1970) and will not be repeated here. After removing the husks, flint kernels are preferred as the flint texture reduces insect damage. On the other hand, dent kernels are easier to grind, a job carried out by women. Another selection criterion is larger seed from the middle part of the ear. Selection for kernel colour is carried out as red is used for chichu, black for soft tortillas, and yellow for sale on the market. Kernels at the top or bottom of the ear are not used as the farmers believe that they grow into weak plants. This is a common practice in Meso-America (Johannessen, 1982).

The selection criterion of big(gest) or long(est) ear (i.e. many grains per ear) is, understandably, one of the major criteria for yield, as was described for the Central- and South-America, and reported for farmers in the USA (Zeven, 1979a), North-Portugal (V.P. Carnide, pers. com. 1995), Lithuania (J. Jaskonis, pers. comm. 1995) and Tanzania (E.E. Kanju, pers. comm. 1994). However, in Bénin the Adja maintain a landrace with small ears (Dangbegnon & Brouwers, 1990).

Hallauer & Miranda (1988) summarized data on correlation coefficients between characters affecting kernel yield, and found a low association between any yield component and grain yield per plant. This means that marking promising looking plants in the field or choosing the biggest ears after harvest may not result in a higher kernel yield per plant. Conversely, the correlation coefficient between plant length and ear length was high (r = +0.80) which shows that selection of long ears, which is a common practice, may result in due course in tall plants. Additionally, it should be remembered that the above data were obtained from plants grown in a regular system, whereas, in a farmer's field with its irregular soil fertility distribution, the plants grow in a scattered pattern. Selection for heavy kernels is also applied in Lithuania by scooping the seed (J. Jaskonis, pers. com. 1995).

In general, people in Central and South America associate varieties with light-coloured kernels with long growing season whereas dark-toned cultivars are destined for short growing seasons (Wilkes, 1995). A short growing period may be important in some environments. Thus, at the highland Puebla village of San Buenaventura Nealtican, Mexico one farmer was growing four varieties, each having its own purpose. The varieties were characterized by the kernel colour, length of growing period, relative yield, kernel taste and texture (Table 2). In this example the blue-purple-coloured landrace produced the highest yield. By sowing all varieties at the same time simultanous flowering was avoided and, also of importance, simultanous harvesting.

Certain types of maize function as 'fertilizers' of the next season's crop (Bohrer, 1994). For instance, in several regions special plant types are selected to be grown in the four corners of the field as 'guardians' to protect the crop. The Western Apache and Navajo select the tallest stalks with two or three ears. If such plants produce red kernels they are considered sacred as they 'fertilize' the other plants, and protect the crop against disease, storms and drought (Bohrer, 1994). Such 'fertilization' can be explained by the occurrence of metaxenia and epistasis in the main landrace. Some farmers do not plant red kernels in the field corners, but add, in case they are not already present, these seeds to the sowing seed. In some regions, red-striped maize kernels get special attention. In West Mexico they are called 'Sangre de Cristo', i.e. Christ's blood.[2] The Navajo add to the common type some striped seeds to 'ensure' yield (Bohrer, 1994).

Time of ripening is of importance to the farmers, because this character is often positively correlated with flowering time. Therefore, selection for various periods of ripening also induces selection for flowering period. This spread in flowering time may reduce introgression of foreign genetic material. (Un)consciously the farmers apply a method which promotes the maintenance of the landraces.

Other selection criteria applied are described for the Adja farmers of the Adja Plateau of Bénin who select certain types, for instance the landrace 'Djongo' which provides some yield on exhausted soil, and the landrace 'Bogan', because of its flood tolerance. Although the landrace 'Gbogboui' is flood sensitive, the character small ears is attractive and selected for. Some ten years ago the landraces 'Bogan' and 'Gbogboui' were replaced by a cultivar 'Carderbafo', which was selected for high yield and big ears, and good flood tolerance (Dangbegnon & Brouwers, 1990).

The following may appear a relativily new development, i.e. the selection within populations derived of, hybrid maize varieties. But because these hybrid varieties regress to landraces, I have included it. The ears produced by the hybrid varieties are, in some parts of India, too big to be used for roasting. Therefore, farmers select in the landrace-like populations maintained during several years from farm-saved seed for smaller ears and also for moderate tolerance to water stress (Maurya, 1989). However, the smaller ears could derive from inbred plants and from plants with the genotype for small ear. If this selection is severe it must have an effect on the frequencies of genes for small ear size, leading to an increase of the frequency of plants with small ears in the landrace-like progenies. Such a new landrace will be maintained by traditional standards.

Millet and sorghum. Millet (*Pennisetum americanum* (L.) Leeke) and sorghum (*Sorghum bicolor* (L.) are crops similar to maize. The ear and the panicle respectively are harvested by hand. As with maize, visual selection, often by the senior woman, is, in Kenyan EMI dryland and Tanzania, a common practice for millet and sorghum. Selection criteria are: large and full heads of grain (Cromwell, 1990; E.E. Kanju, pers. comm. 1994). In general, millet farmers in Africa select for long and compact ears with big kernels to obtain sowing seed (Ouendeba et al., 1995). Similarly, in India, the longest ear would be chosen (M.S. Ramanna, pers. comm., 1994).

For harvest seed the millet farmers will pick the best looking spikes. Laredo & Pernès (1985) add that 'The qualitative consequences of strong versus weak selection at the vegetative stage were not very important, especially when plants were partially self-pollinated' (= self-fertilized, ACZ).

The effect of cross-fertilization with wild plants greatly varies with field and year. Sometimes a field is close to a large group of wild plants, or wild plants grow in the field itself and farmers deliberately leave these and wild or weedy millet plants at the field side untouched as these plants are considered to increase variation of the crop. However, if the frequency of the weedy-looking plants is too high, the farmer will remove some of them during land preparation and also before flowering. The semi-wild F1 plants in the next crop also may cross with domesticated ones.

The farmer's acceptance of wild and weedy plants is found in Senegal, Niger, Namibia and probably elsewhere in Africa. If the distance between the field and wild plants is large the landrace is hardly contaminated or, better, enriched with 'wild' genes. Furthermore, the degree of cross-fertilization varies with years. Farmers must have experienced that any 'selection effort (for yield, ACZ) is not well rewarded' (Laredo & Pernès, 1985). These weedy millet plants were named in Niger (translated into French) '*père du mil*', i.e. the father of the millet, and in Sénégal '*mil de dieu*', i.e. god's millet (Grall & Levy, 1985). De Wet (1995) refers to these weedy plants occurring in West Africa and northern Namibia as shibras. According to Laredo & Pernès (1985) these actions promote the maintenance of the landraces of these cereals. However, this is difficult to understand, as the influx of wild genes will certainly increase genetic variation, and change the landrace.

In Southern Sudan and Northern Ethiopia all farmers, their wives and other members of the community discuss the development of the crop and point to the best panicles. But the women will take the final decision (Berg, 1993).

Potato. The potato (*Solanum* spp.) is another crop of which the harvester/planter has the propagules, i.e. the tubers, in his hands, simplifying selection by eye for some tuber characters (size, colour, colour pattern). Bitterness also is a selection criterion. However, little has been published about these and other selection criteria.

Because of this close contact and the age-old links with this crop, the farmers in South America love to experiment with new phenotypes. They obtain new material as gifts, payments or otherwise (Zeven, 1999) and select the types desired. Most phenotypes will be used for various manners of production and consumption, whereas others are used, e.g by the Quechua farmers, for cultural reasons (Soleri & Cleveland, 1993).

Three approaches are followed: 1. non-bitter potatoes grown separately from bitter potatoes, 2. within the non-bitter potatoes the farmer selects for certain types, grown in more or less pure fields, and 3. the farmers grow and maintain cultivars. For home use the farmers prefer to grow mixtures, selecting for tuber quality and tuber size, whereas other characters such as tuber colour and shape are of little importance. Brush et al. (1981) observed in ten fields in the Montaro Valley, Andes, the variation of the potato plants for ploidy level (Table 3).

The total number of phenotypes for all ten fields is not given. Each 'field variety' is a mixture of plants with different tuber shapes, colours, textures, and flavours. Except for field 7 the tetraploid plants are the commonest ones. As the farmers are not aware of ploidy, tetraploid plants apparently do have more attractive characters, such as larger tubers, to select for than plants with other ploidy levels. No pentaploid plants were observed. Seed tubers are selected for quality characters (such as storability, cookability, taste, resistance and tolerance) and size rather than for shape and colour. In another field 46 phenotypes were scored. As trading goes over distance of some 50 km, some favourable phenotypes are common in all regions. Each carry specific names used over very large areas (Brush et al., 1981). Although several reports

Table 3. The number of phenotypes, plants and their distribution over three ploidy levels of 10 fields in the Montary Valley, Andes (Brush et al., 1981) . The * is added by me to indicate the highest frequency

Field no.	No. of phenotypes	Number of plants per ploidy level			Total no. of plants
		2×	3×	4×	
1	23	27	40	511*	578
2	19	30	15	115*	160
3	11	30	7	115*	152
4	7	–	235*	12	247
5	6	–	35	45*	80
6	13	24	11	136*	171
7	11	5	–	391*	396
8	5	–	–	217*	217
9	30	82	18	486*	586
10	18	14	16	273*	303
Total		212	377	2301	2890
%		7.3	13.0	79.6	100

mention that tuber colour is not an important selection criterion, it is certainly used as a character to recognize varieties (i.e. clones).

Formerly, in the Netherlands farmers grew many forms of potato (more than 14 named landraces are mentioned). Many appeared quite similar, others differed to some extent. These many forms will have been propagated by selecting (probably for tuber characters, i.e. after harvest, ACZ) (Roessingh & Schaars, 1996) . This was also carried out by a farmer near Potosi, Bolivia, who preferred to grow a mixture of some 24 types to increase yield stability (A.M. van Harten, pers. com. 1974) . Maybe the mixing of two skin colour types, yellow and purple, by women in Austria in earlier times, in such way that both types were present in a desired ratio in the seed ware of the next planting (R. Schachl, pers. comm. 1985), was a relic of mixing more types. In the Netherlands, in the province of Zeeland, the farmers were advised in 1860 to use small tubers for seed potatoes (Van Hertum, 1860). At that time the decrease in potato yield was explained by planting too small seed potatoes. Van Hertum suggested that an experiment should be done to compare 1. big tubers, 2. two halves, 3. big tubers with three eyes, the other eyes being removed, 4. normal tubers, 5. small tubers with two in one plant hole. The treatment ‘two halves’ will have been an economic one, viz. to increase the amount of planting material. However, I have not seen any report of anybody having carried out such an experiment. If done, it could have been discovered that the use of half tubers might result in an increase of yield as was observed by farmers in subtropical China. By cutting the tuber its dormancy and apical dominance disappears, which results in plants with several stems. But, in China, this method also resulted in the spread of *Pseudomonas solanacearum*. The farmers selected for phenotypes with small effect of this disease-causing agent (He, 1998). Seed tuber cutting is also reported from North America (Allen et al., 1992), some regions in Pakistan (Geddes, 1989) and India (Shashirekha & Narasimham, 1989).

In other countries, such as Ecuador, the farmers chose the smaller tubers for planting (Crissman & Uquillas, 1989).

In Pakistan, depending on the region, seed potatoes of *desi* (landraces) and cultivars, either from previous storage in a pit, bought on a market or imported from elsewhere, are used (Geddes, 1989). In Sind and Southern Punjab, the number of farmers multiplying own material is quite small, presumably because of the lack of healthy seed potatoes. If healthy seed potatoes are obtained they will quickly degenerate due to viruses, spread by aphids (Geddes, 1989). Maybe, the farmers found that by storing the seed tubers in the loft of the house, where the temperature rises above 40 °C, the virus infection of the plants grown from these tubers was reduced. Most authors who had noticed the absence of any seed ware selection will not have reported it. An exception is the publication by Crissman & Uquillas (1989); they described for Ecuador a case where all phenotypes were planted without any effort of positive or negative mass selection. The reasons are not presented. I assume that experience had shown that the extra effort did not result in a higher yield.

Cassava. Little is known about maintenance breeding in cassava (*Manihot esculenta* Crantz). Although a certain amount of selection within-the-field is daily routine, the preparation of planting of a new cassava garden gives the farmer’s wife the most important opportunity to review, cull and expand the assortment of clones. The size and range of the assortment differ per woman. Older women, in particular, take pride in their knowledge and ownership of a range of clones, and they may serve as distributors of the rarer clones to younger women (Bostert, 1984). In Tanzania, selection characters are plant habit, leaf shape, (young) leaf colour, tuber shape and colour (E.E. Kanju, pers. comm. 1994).

The Aguaruna maintain over 100 landraces (i.e. clones) without clear pragmatic reasons. However, diversity in the field is limited as only four clones make out about 70% of the number of plants. All other clones were maintained at a low frequency. Some clones are cultivated for roasting, some for beer-making and some for putting a good foam on the beer (Boster, 1984). One selection criterion is the root colour as it is used to characterize clones for beer-making and for eating (boiled or roasted). So beer clones, should have a yellow root, as they grow more rapidly, produce larger roots, have more fiber, have a greater tendency to get hard and rot rapidly after harvest. The character quick rotting is desirable for beer-making. It is probably associated with the ease of fermentation (Bostert, 1984). Cassava with bitter tubers yield more and better starch. The increased bitterness made the tubers less attractive for insect pests, allowing the plants to be left longer in the ground as reserve supplies (Lathrap, 1977). This is true for many parts in the world.

Sweet potato. Sweet potato (*Ipomoea batatas* (L.) Poir. in Lam.) can be multiplied vegetatively and in several regions also sexually. The latter results in a great number of genotypes in which the peoples of the Pacific selected and maintained good ones vegetatively. Hence, the great variation within a large world collection for many characters, but not for chromosome number: all clones had 90 chromosomes (Yen, 1963). Desired characters are good tuber taste, short growing period, large tuber (high yield), rapid vining to suppress weeds and reduce soil erosion, resistance to diseases and pests, long duration of harvesting, and ability for long storage (Lightfoot, 1987).

Taro. Taro (*Colocasia esculentum* (L.) Schott) is a vegetatively propagated crop. According to Handy (1940) 'all Polynesians (i.e. farmers, ACZ) have powers of observation and discrimination which led to separating variants or mutants and to conscious selection, as they do now for all vegetables' and their varieties. Due to these selection activities many varieties (in 1913 ca 170, 1940 ca 80) were created and maintained. Although most varieties are commonly used, some are grown for food of the chiefs, some for medicine, and some for ceremonies. Selection criteria are not described.

Brassica crops. Maintenance breeding of fodder cabbage ('chou fourrager') (*Brassica oleracea* L. var. *acephale* (DC.) Alef.) in France is applied by farmers by positive mass selection. The farmers select on individual plant basis. As each farmer has slightly different selection criteria, the field 'populations' differ somewhat from each other. However, these field 'populations' belong to the same landrace. On a larger scale, landraces of the Department de Nord differ from those of the Department de Pas-de-Calais (du Crehu, 1957).

The same must be true for the self-fertilizing summer cauliflower (*B. oleracea* var. *botrytis* (L.) Alef.). Due to its early flowering no hybridization with the other, later-flowering cabbages (*B. oleracea* var. *capitata* (L.) Alef.) and kales occurs. Similar mass selection activities must take place to maintain the various morphotypes within garden cabbages ('Précoce de Louviers', 'Drum head' and 'Pointed head') and within marrow stem kale ('quite pure', 'half-marrow stem kale' and 'leafy') (Margelé et al., 1995).

In Lithuania too, each grower developed his own selection of cabbage (J. Jaskonis, pers. comm. 1995).

Perpetual kale (*B. oleracea* L. var. *ramosa* DC.) exists of diploid and tetraploid clones. Many clones lost the ability to flower and have to be propagated by (often rooted) branches. Other clones flower occasionally, but seeds may be produced only after hybridisation with other *B. oleracea* forms. The many clones differ for several characters such as chromosome number, chemical composition and flowering habit, but resemble each other morphologically (Zeven et al., 1989). Any difference of plant size, induced by various numbers of genomes, as observed in so many other crops, were not maintained by selection and disappeared with time as was observed for other crops (Butterfass, 1987). Most growers grow one clone only. If a grower looses a clone, new planting material (branches) will be obtained from neighbours or relatives.

Japanese radish. Japanese radish (*Raphanus sativus* L. var. *hortensis* Becker) is grown in southern Kyushu, Japan. In spite of a continuous selection landraces are very polymorphic. Farmers select especially for root colour and further for healthy plant, plant size and root shape. Root colour is important because farmers have different purposes for different colours. Negative selection is applied for pithy, early flowering and very big root. Further, some landraces such as 'Mera' have pinnatifid leaves, and for this landrace this character is also selected for.

Before flowering farmers transplant some 10–20 selected plants to one site. With coloured strings they mark the root colour of the plant. Per household 5000–26000 seeds may be produced. Interestingly, these practices were already described in 1697 (Yamaguchi & Okamoto, 1997). Any tendency to inbreeding is counteracted by cross-fertilization with pollen grains of plants of neighbouring gardens and run wild plants.

Red pepper. In Middle-America various types of red pepper (*Capsicum annuum* L.) were selected and maintained, probably by conserving the fruits of these desired types. Landraces exist within each fruit type. In France, the non-pungent sweet or bell type is maintained. In Hungary the colour of the pointed fruits does not indicate the intensity of pungency, which led to considerable confusion. The creation of an association between fruit colour and pungency (pale immature for sweet and green for pungent) was therefore suggested (Pickersgill, 1986).

Other vegetables. In Lithuania, seeds of cucumber (*Cucumis sativus* L.) were kept during the winter in small bags which the women hung on their necks. They believe that the steady temperature promoted female flowering (A. Lekavicius, pers. comm. 1995). Whether this belief is true and based on experience or not, this 'conservation method' prevents frost damage of the seeds!

Farmers in Cuba produce seed of pumpkin (*Cucurbita moschata* Duch. ex Lam.) by growing their own material side by side with material obtained from neighbours (Rios-Labrada et al., 1998). Reasons are not mentioned. The gardeners must have experienced that a continuous exchange of plants and, consequently, of genes (i.e. preventing inbreeding), results in a better crop. In the same country, onion (*Allium cepa* L.) bulbs were hung near the stove to become smoked. This would promote a better quality, and later a healthier and higher yielding crop (A. Lekavicius, pers. comm., 1995). Of course, the covering by soot and tar-like products prevents damage by pests and diseases.

Garlic (*Allium sativum* L.) growers in the Drôme, France select for big cloves, as they have discovered that the plants derived from such cloves suffer less of onion yellow dwarf virus. However, in SW France all plants become infected and a truely tolerant clone is needed (C.M. Messiaen, pers. comm. 1996).

Turmeric. For the landrace 'Wynadan' of turmeric (*Curcuma domestica* Val.) a bright orange inner colour is selected for because of its assumed association with a high amount of curcumin. This desirable colour is already described in the old folk literature of the Malabar region of Kerala, India (B. Sasikumar, pers. comm. 1995). Whether this association truly exists, is not reported. However, age long selection may have resulted in the origin of genotypes with linked loci for colour and curcumin production.

Common bean. The first introductions of the common bean (*Phaseolus vulgaris* L.) into Europe took place at the end of the 15th century or during the first decade of the 16th century. But, as seeds are attractive and easily transportable, many more introductions from nearby or faraway sources may have taken place (Zeven, 1997). In The Netherlands, the dry seed type of the common bean is grown in fields and gardens. Each grower maintains his own material by taking a few healthy, bush-type plants which are stored in the shed. Selection criteria at time of harvest are healthy plants with disease free, good looking pods. At the time of threshing the appearance of the seed (colour (pattern), size, shape, diseases, pests) plays a role (Zeven et al., 1999). Zeven et al. (1999) observed that most unimproved (and improved) accessions were (semi)shiny, which may indicate that growers (and breeders) select for this seed skin character.

If sowing seed is lost neighbours will provide new seed. Yield level is difficult to assess and of limited importance, as a grower will cultivate more plants if he wishes to obtain more yield. Within regions growers have, apparently, the same selection criteria, resulting in apparently regional and uniform land- and gardenraces (Zeven, 1979b, see map). These are mainly characterized by seed colour (pattern), seed size and seed shape. After natural (and legitimate) hybridization between various seed types, followed by human selection, new, but similar types were obtained. They all belong to one large group (Zeven et al., 1999): the 'Dutch bush bean land/gardenrace group'.

In some African countries farmers prefer mixtures of seed types. If they conclude that in their mixture a certain component (seed size, colour type) is overrepresented they will remove seeds of that component. Table 4 shows the percentage of seeds stored, kept for sowing and removed, and divided over seed size and soil fertility type (Sexton et al., 1994).

These figures show, as expected, that the seeds obtained from infertile soils are in general smaller than

Table 4. The percentages of small and large seeds in stored seed, sowing seed and removed seed, divided over provenance (fertile or infertile soil) (Sexton et al., 1994)

	Stored seeds		Seed used for sowing		Removed seed	
Seed size	small	large	small	large	small	large
soil type						
fertile	40	60	30	70	77	23
infertile	81	19	75.5	24.5	92	8

those from fertile soils. The high percentage of small seeds will have a genetic and an environmental background. These figures also show that the sowing seed composition is manipulated to increase the component of the desired, large seed. This is done by removing in both seed samples the small seeds. Landraces in Malawi, judged for plant habit and seed type, may consist of either two to three components or be more complex mixtures. As farmers do not rigorously select, except when rejecting shriveled, weathered, diseased or pest infected seed at planting time, heterogeneity for other traits will increase with time (Adams & Martin, 1988). For Central Africa, Voss (1992) mentioned an association between landrace and soil and intercropping type. For instance, for less fertile soils they choose mixtures consisting of small seeds, and for very fertile soil mixtures consisting of large seeds. We may conclude that seed size is a character selected to maintain the landraces.

Negative correlation coefficients are observed between seed size (seed weight) and overall growth (White et al., 1992), and with yield per area (White & Gonzáles, 1990). The regression coefficient indicated that an increase of 0.1 g in weight per seed sown 'provoked' a decrease of 140 kg in seed yield per hectare, which is 0.56 g per plant. This decrease is not large enough to be observed by gardeners and therefore they may choose bigger seeds, believing that a positive association exists between seed size and plant yield.

The colour of the seed may have an effect on the composition of the emerging plants. For instance, Powell et al. (1986) observed that in dwarf French beans the white-seeded accessions had a lower mean field emergence (67%) than black- and brown-seeded accessions (91%). Therefore, a grower should account for the greater loss of white seeds during emergence, when composing the mixture of sowing seed. In the field, however, plants derived from white seeds are in a genetic advantage because of linkage between genes conditioning white seed skin and resistance to bean common mosaic virus (Temple & Morales, 1986).

Although the common bean is a self-fertilizer, some cross-fertilization with plants of the same and of other types takes place (Zeven, 1997), the latter resulting in an increase of variation counter-acted by selection.

Yam bean. The yam bean, also known as ahipa and parodi (*Pachyrhizus apiha* (L.) Harms), is a self-fertilizing crop. The main characters selected for are oval tuber shape, and a tuber weight of 1000-1500 g. Two selection strategies are applied in Bolivia for seed propagation:

1. the common procedure is positive mass selection: the farmer selects the most vigorous plants within the field for seed production and removes the flowers of the remaining plants in order to stimulate tuber growth;
2. a less applied, more laborious procedure for seed production is leaving the first pod on each plant, followed by the removal of all subsequently produced flowers (Orting et al., 1996). For this latter method no mention is made of any purposeful selection.

Orting et al. (1996) explain that the first procedure leads to a decrease of variation, whereas the second leads to a genetically rich landrace. By selecting for vigorous plants according to procedure 1 and the presence of self-fertilization one may indeed select for the plants with the same or similar genotypes. After several generations this would certainly lead to uniformity of the crop. The ideal plant type would be a vigorous one with a few flowers, and high tuber yield, as pruning is laborious, but, except for plant habit, Orting et al. (1996) do not indicate whether any selection for the above mentioned characters is carried out. Number of flowers can only be observed on the field, whereas tuber size is judged after harvest and before planting.

In both procedures, after marking a sufficient number of plants and pods, the farmer may, unconsciously, select against late plant flowering. This would lead to uniformity of flowering time. Plants selected according to procedure 2 may produce big seeds, as intra-plant competition between the aboveground parts is reduced. The bigger seeds may produce bigger plants producing good or bigger tubers. The population is, however, genetically not improved for bigger tubers. with the Single Seed Descent method in mind, this procedure, if one fruit of all plants is taken, could be named Single Fruit Descent method.

Rice. Rice (*Oryza sativa* L.) is a 'transitory' crop as in several countries hand-picking of panicles on sawahs is still commonly done by women by cutting off each panicle with a small knife, whereas in other countries rice is bulk-harvested. The single panicle harvesting results in a close contact between harvesters and their plants. They may select goodlooking panicles for the next crop.

In 1943, in Sierra Leone, F.A. Squire (1943) pointed out that rice farmers and their families recognized some 20 rice varieties (probably landraces, ACZ) 'unerringly'. Squire continued that the farmers take every precaution to keep the 'varieties' pure. Seed rice is reaped from the centre of fields while the borderline between the fields of different 'varieties' is eschewed. This means that the farmers observed that the next year generation of landraces derived from mid-field plants due to low frequency of off-type plants, responded better to the 'variety description', than if derived from plants of the field border.

During the drying period on the field the crop is carefully rogued before the seed is harvested and put away for the next planting. Again, rogueing is, in general, the work of women and children. Although it is suggested that the selection criteria applied are the propensity for quick growth and high yield these characteristics are less easily selected for than characters such as certain bush types. In fact, the farmers carry out mass selection by selecting for useful characteristics. Furthermore, they like to experiment with new or unfamiliar planting material. With respect to this last point many improved varieties released by the Department of Agriculture have been absorbed into the local planting stock and sometimes modified by selection by farmers to suit local conditions (Richards, 1985).

Harvesting by panicle in north Sierra Leone always is necessary, because of contamination with off-types. The farmers explain the fact that contamination occurs as 'God had made it so'. They and their family members select panicles for further observation and, if favourable, for multiplication. Selection is commonly occurring as each farmer tries out new 'varieties' from time to time (Richards, 1986).

As in Sierra Leone, gender played (and plays?) a role in Sarawak, where women of the Iban hill tribe may take a major part in the selection work. The senior woman chooses panicles which are put in a separate container and are separately threshed, winnowed and stored. Such special containers protect the stored sowing seed from rodents. She and the other women know what is stored and so what will be sown. Often twice the amount needed for sowing is stored in case of mis-sowing or mis-harvest (Freeman, 1955).

For rice, as for cassava, age of the persons involved may also play a role in the choice of the selection method and the material selected. In Thailand, seed selection was carried out by the older farmers for each variety separately by selection for big, healthy panicles (Dennis, 1987). They are, probably, better informed on the landrace characterics than younger persons.

Soybean. Soybean (*Glycine max* (L.) Merr.) also is a 'transitory' crop, as it is grown on a small as well as on a large scale. On a small scale, farmers observe the plants and their seeds during harvesting and threshing. Because of this close 'contact' between farmer and crop I have listed the soybean here. But such a close contact is limited in countries such as U.S.A. and Canada.

In Indonesia, a rich variation of home grown material derives from a cultivar 'no 29', introduced in 1924 from Taiwan. After its introduction it spread widely among the farmers, who made their own selections. These farmers, populations now differ in earliness and yield capacity, and in general the local selections yield more than the original 'no 29'. This may be a result of adaptation to regional conditions. Farmers select before harvest for plants that are early and disease and pest free, and after harvest for seed shape, seed colour and taste (Siemonsma & Linnemann, 1988). Also in Indonesia, a reduction in germination occurs after some 60 days. To bridge the long time gap between the harvest and the sowing of the crop during the main season, a system, called JABAL (Jalinan Arus Benih Antar Lapang = seed flow between fields, Siemonsma & Linnemann, 1988; Linnemann & Siemonsma, 1989), has been developed by some farmers to produce sowing seed during the off season which is used for the main crop.

In the U.S.A. and Canada so-called 'Public Soybean Varieties' are free for cultivation. They may or may not become contaminated with foreign pollen grains and seeds, and maintenance breeding may or may not be applied by farmers (Bernard et al., 1988).

Bread wheat and durum wheat. Little information on bread wheat (*Triticum aestivum* (L.) Thell.) and durum wheat (*T. durum* Desf.) is available. For instance, as no information is available on the breeding history of bread wheat landraces in the valleys of Nepal, it is difficult to tell whether the phenotypic differences among landraces between and within valleys (Damania, 1985) resulted from human selection, natural selection, or from a recent introduction of other landraces. The archives of the leper house of Middelburg, province of Zeeland, the Netherlands, dating from 1559, reported that sowing seed reached a higher price than bulk seed. This points to a better quality of the first, which may have been obtained by multiplication of selected material, or more likely by cleaning and sifting (Boerendonk, 1935; Zeven, 1990). In the 19th century, farmers in the same province, growing the bread wheat landrace 'Zeeuwse', preferred sowing seed of the same landrace, multiplied on the Island of Walcheren. There it was known as 'Walcherse'. Unfortunately, the motive(s) of the farmers is (are) not given. It could be that on Walcheren, for unknown reasons, the grains were less infected by smut (*Ustilago tritici*).

R. Plot reported for Oxfordshire in 1677 how farmers were developing varieties of bread wheat by culling and propagating the most productive grains and selling the seed in other regions. The first variety he mentioned was 'first propagated from some few ears of it pickt out of many Acres, by one Pepart near Dunstable about fifty years ago' (i.e. ca 1627, ACZ). It was 'sowed by it self till it amounted to a quantity, and then proving Mercatable is now become one of the commonest grains of this Country, especialy about Oxford' (Allen et al., 1992, citing R. Plot). One wonders what degree of contaminations took place during these 50 years of multiplication.

Plot continued to report that the new 'Corn' yielded sometimes 20 for one. So if one assumes a sowing quantity of some 80–100 kg/ha the yield might occasionally be 1600–2000 kg/ha. This is high in comparison with the normal yield at that time of some 750 to 1000 kg/ha. The report also suggests a yield of some 45 bushels/acre (Allen et al., 1992), which is ca 115 bushels/ha. If one accepts 1 bushel equals 36.4 liter and 1 liter weighs 0.72 kg, the yield would have been ca 3000 kg/ha. This also is an extremely high yield for that time and may rarely have been obtained. I presume some exaggeration to promote seed sale was involved.

Similar yields were obtained for the highest yielding lines selected for yielding capacity around 1910 from the Dutch winter wheat landrace 'Gelderse Ris'. Grown under the present day growing conditions these lines yielded some 1600–2400 kg/ha (Zeven, 1990). These figures indicate the genetically conditioned maximum yielding capacity of these lines. The yield of the landrace 'Gelderse Ris' grown under poor conditions would have been much lower.

Mass selection of winter wheat is carried out in Austria by choosing easily recognizable phenotypic features. To maintain the improved landrace 'Sipbachzeller', long, awnless ears with red kernels were selected. And because of the poor baking quality white-kernel is not desired. Because of the positive relation between red kernel and less sprouting-in-the-ear, maybe, by selecting for red kernels the farmer unconsciously selected for resistance to sprouting-in-the-ear. Furthermore, nature strongly selects against sprouting-in-the-ear, and consequently against white kernel colour. In general, differences exist because some farmers select better than others. Any surplus will be sold (Schachl, 1981). However, after heavy hail storms in the early part of the 20th century which destroyed many landraces, many farmers turned to cultivars (Werneck, 1935, cited by Schachl, 1981).

Wheat farmers in the Kulu valley, North India also selected for big ears to obtain seed for next sowing (M.S. Ramanna, pers. comm., 1994).

In Ethiopia, durum wheat is bulk-harvested and broadcast sowing is used (Pecetti & Damania, 1996). Nature 'selects' for uniformity, for stem rust resistance, long coleoptile, short stature, and adaptation to low soil fertility. Man unintentionally selects for time of maturity.

On Cyprus, hand-picking before harvesting was carried out for some 50 years and especially by durum wheat farmers. These farmers used to select single plants, multiplied their seed and shared with neighbours. They were extremely efficient in doing so. This resulted in the presence of the same durum phenotypes all over the island (Zeven & Waninge, 1989). Durum landraces were contaminated with 'recently' bred material, which included Australian bread wheat cultivars (introduced before 1920). As some tetraploid plants resemble bread wheat, selection for durum plants, will also exclude these tetraploid 'bread wheat' plants (Zeven & Waninge, 1989).

On the whole, in the Mediterranean areas bread wheat plants easily replace durum plants in durum landraces and should be removed on the field to avoid an almost complete change to bread wheat (Bennett, 1973).

Little information is available on the selection criteria and the methods of multiplication durum wheat on Cyprus. Although the durum wheat variety 'Kyperounda' was not completely suitable to the growing conditions of Cyprus, farmers preferred this late maturing variety as they could finish the barley harvest before attending to the durum crop. At present, mechanized harvesting shortens the harvest period resulting in selection for earlier maturing durum varieties. In addition, 'Kyperounda' had excellent quality for pasta and also for bread making. In West Cyprus the durum landrace 'Tripolitico' was grown as the plants of this landrace suppress weed growth. Due to the use of herbicides it could be replaced by modern cultivars (A. Hadjichristodoulou, pers. comm. 1996).

Hand-picking of seed after harvest is done by Bedouins in Israel. They grow a mixture of durum and bread wheat (and occasionally barley) plants. Bold and amber-yellow kernels are preferred. By visual selection for long grains with amber-yellow kernels, which reach a higher price on the market, these kernels are put aside. However, as no maintenance breeding is carried out most landraces produce small kernels with poor colour only (Blum et al., 1987). Maintenance of diversity on the wheat fields of the Bedouins often is a result of their farmer's knowledge, built up in many centuries. They have learned that mixtures ensure yield stability in their environments (Beharav et al., 1997).

In Europe, emmer wheat (*T. dicoccum* Schrank.) was formerly an important winter crop. When its importance decreased, farmers used this wheat as spring-sown crop only. Unconsciously they selected for spring habit resulting in many landraces around 1900 (Hillman, 1981). The difference in development of the plants grown in a population, derived from a mixture of emmer wheat accessions, obtained from Germany, and grown on clay soil at Wageningen and on loess soil near Cologne, was astonishing. At Wageningen, the plants remained small, whereas in Germany the plants were robust. This indicates that this mixture was adapted to its 'native' loess soils. Such adaption may have taken place during its cultivation on this soil type during some 4–5 millennia. Maybe this explains why emmer wheat never became an important crop in the Netherlands where loess soils are limited to the very southern part (A.C. Zeven, unpublished).

A good seed weight/size of the landrace was also maintained by the Romans (White, 1970) and probably everywhere where wheat and other cereals were and are cultivated. They – the Romans – obtained sowing seed by throwing the seeds in the air and collecting the heavy grains. These grains would have been produced by plants with the genotype for heavy grain, or by vigorous healthy plants. The latter plants could happen to grow on a good spot, carry genes for resistance and tolerance, or be escapes. Maybe, by experience the Roman and other farmers knew that sowing heavy grains results in a good crop.

Rye. According to Bieleman & Roessingh (1994) the only rye (*Secale cereale* L.) landrace of the Drente province in The Netherlands originated by natural selection only, as no human selection was carried out to maintain the landrace. Due to bulk harvesting any 'contact' between farmer and plant disappeared. Rarely, some 'good-looking' ears were given to farmers in neighbouring villages. Some of the recipient farmers would sow the grains to satisfy their curiosity hoping to improve their own seed lots. One should realize that such good-looking ears could derive from plants growing on a favourable spot, and from positive heterosis for 'good-looking'. Furthermore, due to cross-fertilization, the plants derived from these ears were half-sibs. Such 'presents' had no effect on genetic improvement of the crop.

Some dealers traded in rye seed. Those farmers who could not pay for the sowing seed had to hand over a part of the harvest seed. So in 1805, a Dutch trader, living in St. Petersburg, Russia, asked his wife in the Netherlands whether the 'lent-out' rye (sowing seed) already was returned (as harvest seed) (Meeuwse, 1996). Maybe, each lot of harvest seed was genetically slightly different. The trader, probably, would not care to keep the various returned seed lots separated and would issue a mixture to new buyers and 'borrowers'. Further, any local differentiation would be undone by cross-fertilization between rye plants of neighbouring fields. The result was one landrace grown over a large area. As this landrace was the only one grown, it had no landrace name.

On the Veluwe, the Netherlands the rye winter landrace 'Kruiprogge' ('creeping rye') was cultivated. This type was not developed by man, but by nature, as the erect young plants were, during the winter, eaten by deer. Those with a creeping habit had a smaller selective disadvantage than the erect plants.

An example of human induced natural selection is the origin of the landrace 'Amelander'. On the North Sea island Ameland, northern Netherlands, a transitory rye was unconsciously developed before 1900. Formerly, the inhabitants were mainly fishers. When they returned too late in autumn to prepare the land and sow rye they would do so in the spring. This resulted in a landrace with sufficient winter hardiness and absence of vernalization requirement. Elsewhere in Europe, farmers probably grew winter rye only, as archeological remains of rye seeds do not indicate that two clearly separate lots of rye seed, viz. seed of winter rye and seed of spring rye, were preserved.

Barley. Jönsson et al. (1994), in Sweden, studied during three years which barley (*Hordeum vulgare* L.) characters had a high correlation with yield per plant and hence, could be used as selection criteria. Most characters require methods either too laborious, or unsuitable for use in the field or on the farm. This holds, probably, for hectolitre weight, but grain size (often positively associated with 1000-grain weight), is unknowingly selected for by farmers during sieving and winnowing. What has been said for the preference of sowing heavy seeds of wheat by the Romans and others (see above) holds for barley too. On the other hand, grain weight of barley was such a stable character that it was used as a weight measure, called grain (1 grain = 0.0648g).

In Ethiopia, barley is an important crop. Much variation can be found within fields and between fields, as can be observed by the frequencies of various morphotypes. Occasionally uniform looking fields are found. Differences between fields are caused by those farmers and their families who prefer to maintain for various reasons, their own stock. Only when their own stock is destroyed do farmers turn to another stock. During cultivation over a longer period it seems that rare morphotypes, such as naked type, disappear (Zemede Asfawa, 1988, 1990). This could happen only if either man or nature strongly selects against this character. Zemede Asfawa (1988, 1990) adds that the frequency of plants with low hardiness, low yield and little adaptation also decline with time. However, whether this conclusion is based on observations is not mentioned. Farmers prefer landraces with big grains for food, and with small grains for beverages. Further, Zemede Asfawa (1988, 1990) described how farmers wanting white grained barley may carry out negative mass selection before harvest, and positive mass selection during (and after?, ACZ) harvest. No information is presented on the method(s) applied by the farmers. Nature, for instance, 'carries out' negative selection for genotypes with early maturing, brittle rachis types; the ear propagules drop before harvest, after which they are either plowed under (causing the seeds to germinate at the wrong time, ACZ), or eaten by cattle.

Oats. In Finland around 1900, Axelson (1908) reported a farmer of oats (*Avena* spp.), who had sold the best part of his seed lot and would use that remaining for his next year planting. Another, who had obtained seed of 'foreign oats' would mix it with home-grown seed 'to improve the blood' of the latter. According to Axelson (1908) no attempts were made at that time to maintain the improved oats. Axelson continued: 'This case is by no means an exception. – it also shows the complete lack of understanding, that exists in many places concerning the seed question' (translation by H. Ahokas, 1999, pers. com.). It could be argued that these and other farmers could quite well explain their action, for instance, to get instant money. They probably realized quite well that a possible poor crop could develop next season, but they had no other option.

Bulk-harvested cereals. In addition to the information provided on wheats, rye and barley, more information is available for cereals in general. For instance, in the Netherlands, Cordes (1855) advised that plants of cereals which are selected for the production of sowing seed should remain on the field until the seeds are completely ripe. No information is available whether farmers followed this advice. A late harvest could probably result in seed damage, loss by (hail) storms and sprouting-in-the-ear. Probably, based on farmer's knowledge and irrespective of any 'official' advice, the farmer and his neighbours harvested when they thought it to be the right time. It would have depended on 'weather forecast' based on their own insight, and on availability of labour. However, negative selection would have occurred for early seed drop. Identical to the activities of the Romans (see sections on wheat and barley) Van Hertum, working in the province Zeeland, the Netherlands, advised in 1860 to use big seeds for sowing cereals. In Austria mostly no maintenance breeding was carried out. Even no winnowing or the use of a sorting machine was applied; a part of the harvest seed was used as sowing seed (Biebl, 1927).

Hillman (1981) was surprised by the fact that in spite of some 10,000 years, i.e. 10,000 generations of selection, there is still substantial variation for height and ripening in landraces of cereals. But it should be remembered that farmers initially harvested the cereals by hand and little attention was paid to height. Further, it should also be remembered that within a field individual plants tend to mimic each other to some extent. Those being a little early or a little late, become a little later or earlier respectively (Anon., 1857). The same is true for plant length. Those being a little shorter increase their length. Of course, very short/very long and very early/very late is a too large gap to bridge by the plants. This phenomenon has received little attention (A.C. Zeven, unpublished).

Man also influences the time of ripening by much earlier/later sowing or harvesting. The landrace becomes adapted to the wishes of the farmer.

Rose rootstocks. In the Netherlands, up to some 30 years ago, millions of rose rootstock plants (*Rosa* spp.) were annually propagated for rootstock production especially of plants used for cut rose production (Leemans, 1964). Each nursery population of rootstocks still is a (sub)landrace (de Vries & Dubois, 1987, 1988), i.e. populations belonging to the same selection (i.e. landrace) are sublandraces. In 1964, Leemans (1964) described 18 landraces (selections). Although this number is dramatically reduced now some of them are still in use.

The rootstocks were grown from seeds sown in rows in open fields. The resulting density is some 80,000 plants/ha. Seeds are obtained from plants grown in 'seed gardens' where several hundreds of mother plants of a certain landrace (selection) are growing. Heterogamy results in quite uniform fields and in the next population resembling their parental 'selections'. However, because 'selections' of the same or other *Rosa* species are planted in the same 'seed garden', and flower simultaneously, hybridisation between 'selections' occur. At the end of the season rose fruits ('hips') of true-to-type plants are harvested and seeds extracted for the next generation.

Some negative mass selection is applied on the field each season, removing those plants which obviously differ too much from the landrace type. But quite a lot of variation remains unobserved. Thus, each multiplication may add some new variation, resulting in less uniformity of the populations as multiplications increase (de Vries, 1993), with additional differences between nursery populations within the same selection. After harvest the individual plants are graded 'by eye' according to their root collar diameter in several classes. As this is phenotypical selection, the plants within one diameter class may still differ genetically for diameter (and for other characters as well). These genetic differences within a diameter class may show up in different degrees of development of the buds and grafts of rose cultivars, e.g. in the flower yield (de Vries & Dubois, 1988).

When the rootstock grower wishes to start a new seed garden he commonly takes rootstocks of the 8–12 mm diameter class (de Vries, 1993). As said, variation may occur between nursery population and a further increase of variation is promoted by exchange of material by rootstock growers visiting each other. As the growers like to add good material of others to their own nursery selection during such visits a few ripe 'hips' may be handed-over (D.P. de Vries, pers. com., 1999). Depending on the number of 'foreign hips' in comparison with the own harvest and on the level of difference between the nursery populations such action may cause a blurring of any grower's preference for a certain type, and an increase of the level of variation.

In conclusion, for this type of rootstock production two events of selection occur: 1. negative mass selection in the field, and 2. phenotypic selection for plants of the 8–12 mm diameter class to be planted in a new seed garden. A remarkable point is that any preference of a nurseryman is counteracted by him adding material from fellow-nurserymen.

White clover. In the Netherlands, in the thirties of the 20th century, a farmer maintaining the white clover (*Trifolium repens* L.) landrace 'Fries-Groninger' (syn. 'Dutch White'), did not carry out any selection (Lettinga, 1977). However, during the growth severe competition between the clover plants occurs resulting in the elimination of up to 90% of the plants (Annicchiarico & Piano, 1997). In the seventies of the same century the only farmer-maintainer of this landrace removed, on advice of the Agriculture Extension Service, plants with reddish/pinkish flowers (Zeven, 1991).

Red clover. In Switzerland the farmers take seed of red clover (*Trifolium pratense* L.) only from fields older than two years as they found that the plants which survived are more hardy (Nüesch, 1976). So, although they do not carry out selection work themselves, they use natural selection to their advantage.

I have not found any information on the maintenance breeding of the now extinct Dutch landraces 'Maasklaver' and 'Roosendaalsche'.

In the U.S.A., after the introduction of landraces from Europe, natural selection took place resulting in landraces adapted to the new conditions. For example, mainly smooth-leaved landraces from Europe developed under the presence of leafhoppers into landraces with mainly hairy plants (Pieters & Hollowel, 1937). These authors did not present data on the maintenance of these new landraces. Such information is given by Taylor & Quesenberry (1996, citing Westgate & Hillman, 1911). Seed for sowing was produced by choosing only fields where a 'goodly' number of heads had at least 25 seeds each. Lower numbers indicated a low seed production and the field was used then for hay making. The farmers followed the safe way of seed production, because a low seed number per flower may have a genetic or/and environmental background.

Lucerne/alfalfa. In Perugia, Central Italy, landraces of lucerne (*Medicago sativa* L.) are still commonly used as they, in their native area, outyield (exotic) cultivars. The farmers take the seeds of the best fields observed two or three years after establishment. In addition to these home-grown and multiplied landraces, sowing seed of officially registered landraces and maintained by the Ministry of Agriculture is traded (Falcinelli et al., 1994).

In France, farmers try to obtain 'sufficient' home-grown seed. However, in 'bad years' they obtain new seeds either from friends or from the seed trade. In the last situation this seed could come from other regions in France, other European countries, or North and South America. In the first years the foreign varieties are not sufficiently adapted to the French growing conditions, but in due course they will (Julier, 1996). During their adaptation they change from allochthonous into autochthonous landraces (Zeven, 1998). These foreign varieties also act as sources of 'foreign' genes enriching the autochthonous landraces.

Grasses. Formerly, sowing seed of grasses was obtained by sweeping the barn floor or hay-loft. In the Netherlands, at the turn of the century grass seed 'production' was carried out by inhabitants of the village of Didam, province of Gelderland, who cut (often without permission of the owner) ripe grass inflorescences on estates and similar areas. The grass bushes were dried and sold to traders who threshed the plants. This seed was sold in the Netherlands and exported as well (Verhey, 1945). By doing so, they unconsciously selected for (early) flowering, for seed-production, and, hence, for less leafy plants. The latter is a disadvantage as the farmers bought the seed with the intention to create meadows and hay-fields.

Gender

We have already described how the farmer and his wife may have different responsibilities for the maintenance of the landraces. Examples have already been presented for maize, sorghum and rice. In many communities women control crop processing and the family store. They often select the plant material to be used for the next planting. This means that they store this material separately from the material to be consumed or sold. Another example is for Ghana, where women are able to identify and select elite types in many crops (Bennett-Lartey & Akromah, 1996). According to Anon. (1989) man decides what to sell, but this can hardly be so in the markets which are, in general, controlled by women. Although different gender roles exist for selection in other crops, we found for potato only one reported case in Austria (see above).

Caste

In Nepal a case is described where the Mehata (Koiri) caste is involved in the maintenance of potato varieties (Rhoades, 1985). Apparently, the other castes are excluded from this activity.

Natural selection

Although it is not the subject of this paper, several cases of the effect of natural selection on the genetic composition of landraces have been described above.

Discussion

The above reports and citations of traditional maintenance breeding by crop were collected by consulting a very large number of publications from all parts of the world. Although it is realized that most scientists are not (sufficiently) aware of the presence and scale of farmer's knowledge and their application of maintenance breeding, I conclude that on a global scale little traditional maintenance breeding was applied. The same conclusion for Europe was drawn earlier by Fruwirth (1930). Maize is perhaps the only crop where traditional maintenance breeding is carried out all over the world, be it especially described for Central and South-America. This is presumably due to the growth habit of this crop, with a number of traits which are easily observable, the possibility of harvesting single plants and ears and of picking large kernels. Further its 'beauty and traditions' (Galinat, 1996) must have intensified traditional maintenance breeding.

The level of knowledge and of experience of farmers about the maintenance of landraces differs from one to another, and it changes for many of them with time. Some farmers, have a better understanding than others of their crops and the methods of cultivation. And for various reasons, some farmers are unable to carry out (each season) any maintenance breeding.

Nature selects for survival of the population (i.e. the (sub)landrace). This, to a certain extent, satisfies mankind, as survival implies a high yield stability. Even when grown on the same field for a long period, growing conditions differ each year as no year is the same as a previous one. Consequently, the optimum composition of a sublandrace is continuously under selective pressure.

The transition zone between traditional maintenance breeding of a landrace and applying formal breeding is quite wide. If the farmer selects certain types within the landrace he applies formal breeding and the result will be a so-called improved landrace, i.e. a cultivar. Consequently, all activities to genetically improve a landrace, as is described for wheat for The Netherlands (Zeven, 1970), and Ethiopia (Melaku Worede & Hailu Mekbib, 1993) and for rice for the Philippines (Salazar, 1992), have resulted or will do so in formal breeding of cultivars.

Conversely, if the farmer applies no traditional maintenance breeding or slight by carrying out some positive or negative mass selection, the landrace will be maintained as such. Furthermore, in the absence of traditional and formal maintenance breeding, any improved landrace, any cultivar, including a hybrid variety, will regress with time into a landrace. The cause is natural selection pressure for survival, i.e. yield stability.

In addition to the intensity of traditional maintenance breeding by man the number of genes conditioning the expression of a certain character play a role in any change of the frequency of occurrence of that character. The higher this number the smaller the effect of man's breeding activities. Consequently, polygenically controlled characters will retard man's selection activities. He will be more successful with oligogenically inherited characters.

Selection by different farmers or ethnic groups (Spagnoletti et al., 1984) may, in the long run, result in (slightly) different looking (sub)landraces. Such sublandraces still belong to the same landrace. Similarly, such different selection pressures may result in different landraces, which together belong to one landrace group (Zeven, 1986). If a strong selection pressure is applied for one character, such as seed colour of common bean, the resulting population, is, still a landrace, being uniform for one or a few characters. The same holds when nature selects for (or against) a certain character as red (or white) kernel of wheat, the colour being associated with resistance (or susceptibility) to sprouting-in-the-ear. Farmers and their families are continuously discussing their crop, as was described for sorghum (see above) By doing so farmer's children in the whole world receive their first training in 'agriculture' at home (Berg, 1993). But because '(traditional) maintenance breeding' is, in general, rarely applied by the parents, children are not trained in this matter.

Conclusion

The almost world-wide absence of application of traditional maintenance breeding could find its origin in the blurring effect of cross-fertilization (of cross-fertilizers: growing half-sibs and inter-landrace hybrids) and in the effect of natural selection being much larger than that of human selection. Maybe, the commonly applied seed replacement (Zeven, 1999) substituted the need of traditional maintenance breeding or replaces it.

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Notes

1. Which name was given to this type before Africans became known to the Indians?
2. It would be interesting to know its name in the pre-Christian era too.

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