Classifications of intraspecific variation in crop plants

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Introduction

Germplasm collectors must be thoroughly familiar with what is known of the variation present within their target taxon if they are to sample it efficiently. In crops this can be many times greater than in wild plants, especially for species which were domesticated early and have been widely spread around the world. Such variation is the result of both natural and artificial selection pressures. The latter may be conscious or unconscious, and result from the application of diverse agricultural practices and from the disparate and changing demands of growers for specific agronomic and other properties. Variation may be in morphological, anatomical, karyological, physiological, biochemical and molecular characters. Exploratory genetic diversity surveys using biochemical or molecular markers may be useful preliminaries to germplasm collecting (Chapter 6). Most relevant for the collector in the field, however, will be variation in morphological traits and in ecological adaptation. Making use of a scheme for the classification of the morphological variation within a crop can help collectors keep track of what they are finding and compare the diversity of different areas (Chapter 19).

The term 'intraspecific' is used here to refer to variation within a cultivated taxon, but it should be pointed out that the crop in a wild–weedy-crop complex is often given subspecific rank (e.g. Harlan and de Wet, 1971). Morphological intraspecific variation has been studied in many crops, though often for only a limited part of their geographic range or for a restricted set of characters. From 1978 to 1993 the literature on crop taxonomy (and evolution) has been reviewed in a series of publications by staff at the Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben. A full list of these reviews is given by Hanelt *et al.* (1993b). This series has now been discontinued, its task taken over by the new *Plant Genetic Resources Abstracts* (Chapter 13). Zeven and de Wet (1982) and Schultze-Motel (1987) summarize information on the taxonomy and evolution of different crops. Floras sometimes consider variation within crop plants, though never in much detail. However, there are also specialized Floras dealing only with cultivated plants (see below).

There is general agreement about the necessity and importance of such studies (Mansfeld, 1953; Baum, 1981) in both applied and theoretical applications, ranging from the investigation of the history of the domestication of plants and their subsequent evolution to the characterization of germplasm. However, the procedures used to develop the classifications and the resulting schemes themselves are extremely diverse and a generally agreed approach has not yet emerged (Hanelt, 1986). Two extreme types of schemes may be recognized:

- complex hierarchical taxonomic subdivisions of a cultivated plant taxon, with many infraspecific taxa at several taxonomic ranks between the species and cultivar level (e.g. Dorofeev and Korovina, 1979; Nechanský and Jirásek, 1967);
- relatively simple, non-structured, special-purpose schemes with a few main groups (e.g. de Wet, 1978).

Because selfing results in the splitting up of variation within a crop into distinct homozygous lines, autogamous species tend to be relatively easier to classify in detail into many groups than allogamous species. In the past, this has led to over splitting, a trend that has been somewhat reversed by genetic studies.

The different methods of approaching the infraspecific taxonomy of crops are discussed in this chapter in so far as they may be relevant to the needs of collectors. For further details, see Hanelt (1986) and Hanelt *et al.* (1993a). The focus is on the literature in languages other than English, which tends to be somewhat overlooked.

Classifications

A classification scheme for classifications of the intraspecific variation of crop plants has been proposed by Hanelt (1986):

1. Formal taxonomic classifications:
   (a) diagnostic–morphological;
   (b) phenetic–numerical;
   (c) ecogeographic.
2. Informal taxonomic classifications:
   (a) diagnostic–morphological;
   (b) phenetic–numerical;
   (c) genetic.
3. Mixed classifications.

Two principal types of approaches are distinguished, formal taxonomic and informal classifications. Whereas in the former formally recognized categories are used (more or less) according to the rules of the International Code of Botanical Nomenclature (ICBN) and the International Code of Nomenclature of Cultivated Plants (ICNCP), informal classifications use non-standard categories. In informal classifications, therefore, nomenclatural problems resulting from the use of the ICBN and the ICNCP (and the fact that the two codes are not always compatible (e.g. Brandenburg and Schneider, 1988)) are avoided. However, a broadly accepted designation of a group is not guaranteed and, therefore, communication of information on the material under study is more difficult.

Formal taxonomic classifications

Diagnostic-morphological classifications

Usually these classifications are based on a few, easily recognizable morphological characters and allow a rapid overview of variation within a crop. Several major publication projects have been based on this type of infraspecific classification, e.g. the *Flora of Cultivated Plants of the Soviet Union* and *The Cultivated Plants of Hungary* (Máthé and Priszter, 1982). R. Mansfeld, the founder of the Gatersleben school of taxonomy, which has studied the infraspecific classification of several important cereal, legume and vegetable crops, provides a typical example with his morphological system of *Triticum aestivum* (Mansfeld, 1951). He considers 12 characters and organizes intraspecific variation into more than 400 varieties, each differing from related ones in only one character. Mansfeld's (1950) scheme for *Hordeum vulgare* is another example. Below the species level he applied the category of convariety (defined by Alefeld, 1866; cited by Helm, 1964) and accepted five, defined by major spike characters: convar. *vulgare* (convar. *hexastichon*), convar. *intermedium*, convar. *distichon*, convar. *deficiens* and convar. *labile*. Formerly, some of these convarieties had even been described as separate species (not least, by Linnaeus). There are some differences in geographic distribution and even some barriers among them which may indicate that this category has some biological significance. Varieties, of which 191 are described, are purely artificial entities, however. In fact, such classifications are as a rule rather artificial, especially at lower taxonomic levels.

The same principles have been applied to *Papaver somniferum*. Based on the classification of Danert (1958), Hammer (1981) developed a system containing three subspecies. Ssp. *setigerum* is the wild ancestor; ssp. *somniferum* and ssp. *songaricum* are both cultivated. The cultivated subspecies differ in having sulcate lobes of the stigmatic disc with dentate margins vs. flat lobes with entire margins. These characters have been considered as very important by *Papaver* taxonomists and also show clear geographic differentiation. The convariety level is defined by indehiscent vs. dehiscent capsules, another important character indicating different stages of domestication (Hanelt and Hammer, 1987). The variety level is based on seed colour, resulting from selection pressure under domestication, and other characters.

Such classifications can be very useful to the plant collector. Since the morphological entities they define can be recognized relatively easily, they can be used as the basis of field checklists. Rapid comparison of different areas with regard to the variation found there is possible and gaps in collections can be identified. Assessments of variation at different times based on such classifications have been used to estimate genetic erosion, for example in Sicily (Prestianni, 1926; Perrino and Hammer, 1983).

In some cases, the classifications are of restricted applicability because they deal with the cultivated flora of a rather restricted area (e.g. Máthé and Priszter, 1982). However, even country Floras of cultivated plants may employ a comprehensive concept of taxa, allowing them to be used for even a worldwide survey. The *Flora of Cultivated Plants of the Soviet Union* is perhaps the best example. Important recent contributions, in addition to the already mentioned *Triticum* volume are: Kazakova (1978), Makaseva (1979), Fursa and Filov (1982), Smaraev and Korovina (1982), Girenko and Korovina (1988), Kobyljanskij (1989), Kobyljanskij and Lukjanova (1990). The morphological classifications from the Gatersleben school are listed by Hammer (1981). In addition to the already mentioned *Hordeum vulgare*, *Papaver somniferum* and *Triticum aestivum* studies, there are works on *Beta vulgaris*, *Brassica oleracea*, *Glycine max*, *Linum usitatissimum*, *Lycopersicon esculentum*, *Nicotiana rustica*, *N. tabacum* and *Pisum sativum*.

A potential problem with such schemes is that the availability of the publications describing them may be limited. Many are not available in English and may be difficult to obtain. As a result, some older classifications, such as that of Percival (1921) on *Triticum*, are sometimes used even today in the English-language literature.

Phenetic–numerical classifications

These classifications consider a large number of characters. Various multivariate mathematical methods are used to calculate similarities among types and identify groupings. There are several examples (reviewed by Schultze-Motel, 1987) but none is particularly convincing in the context of formal taxonomy.

Ecogeographic classifications

Such classifications have been developed by the Vavilov school based on the hypothesis that, in an area where selection pressures by environmental factors, cultivation practices, progagation methods, etc. are relatively homogeneous, a crop will tend to have a certain genetic integrity (Vavilov, 1940). An example of ecogeographic classification is that proposed by Flaksberger (1935) for *Triticum aestivum*, which includes two subspecies, 15 proles and six subproles.

New taxonomic categories have often been introduced. Groups are largely defined by their geographic origin and by characters which reflect the agricultural and ecological conditions to which they are adapted (e.g. reproductive phenology, pest and disease resistance, growth characters, etc.). In general, field experiments are necessary to verify the results and to incorporate new accessions into such a classification. Therefore, they may not be directly applicable during the collector's fieldwork. However, they may be very useful for the characterization of collections, facilitating use of the material by breeders. There is still no bridge between formal ecogeographic classifications and the use of an ecogeographic approach in fieldwork (Chapter 14).

Informal taxonomic classifications

Diagnostic–morphological classifications

There is no example of this kind of approach describing the full extent of variation within a crop. There are, however, some regional studies. The classification of French bush bean cultivars is one. They have been arranged into three categories, i.e. groups, sections and classes (Anon., 1983). Pod characters (11 character states) are used for the differentiation of groups and sections, and leaf colour, pod length, colour of unripe pods and length of bracts (12 character states) for the differentiation of classes. The resulting system comprises five groups, 14 sections and many classes. Another example, also from *Phaseolus vulgaris*, shows that the input of biochemical methods (in this case, phaseoline types) can lead to phylogenetically more relevant groupings within an informal classification of the diagnostic–morphological type (Hammer, 1992).

Phenetic–numerical classifications

One of the best examples of this type of classification is the study of the South American cultivars of cassava (*Manihot esculenta*) by Rogers and Fleming (1973). They used 55 character states and defined 19 groups of cultivars. Within these groups there is a high degree of phenotypic similarity, and evidently also considerable genetic similarity. New material can be easily incorporated into the proposed classification scheme. However, the evaluation of the basic data for this type of study is very time-consuming.

Genetic classifications

This type of classification is only possible in crops whose genetics have been well studied, such as *Pisum sativum* (Blixt, 1979), where the genes responsible for the expression of many different characters are known. In peas there has also been an attempt to combine a formal diagnostic and a genetic classification (Lehmann and Blixt, 1984). It is difficult to incorporate new material into such classifications. Test crosses are necessary and multifactorial characters cannot be included at all. Somewhat different are classifications based on genomic composition. An example is that of Simmonds for the edible fruit-bearing bananas (Simmonds, 1966; Simmonds and Weatherup, 1990). These are classified by reference to ploidy (2×, 3×, 4×) and the genomic contribution made by two diploid wild species (AA *Musa acuminata* and BB *Musa balbisiana*). Some 15 characters are used to distinguish among cultivar groups.

Mixed classifications

There is no single classification approach suitable for all possible demands. Different aims can be achieved with different types of classifications. A combination of classifications has been proposed by Hanelt (1972) for *Vicia faba*. A formal diagnostic classification into two subspecies, three varieties and six subvarieties, based mainly on seed size, form and structure of pods, was combined with an informal classification into 14 races, based mainly on ecogeographic data. A similar approach has been used for *Citrullus lanatus* (Fursa, 1981).

Conclusions

It is well known that most of the more important and widespread crop species are characterized by an enormous amount of intraspecific variation. Familiarity with this is essential for the effective collecting of plant genetic resources. There are many publications on the infraspecific taxonomy of crop plants, but many have been written in languages other than English, in particular the papers of the Vavilov school. A variety of methods have been proposed for the classification of crop plants. Most appropriate for collectors seem to be ones based on easily recognizable characters of the gross morphology. Variation in such characters can be used to establish taxonomically formal or informal diagnostic classifications. These will be no less useful for the later management of collections than for the collector in the field.

References

Anon. (1983) *Description et essai de classificaton de variétiés de Haricot Nain.* INRA, Versailles.

Baum, B.R. (1981) Taxonomy of the infraspecific variability of cultivated plants. *Kulturpflanze* 29:109–239.

Blixt, S. (1979) Some genes of importance for the evolution of the pea in cultivation (and a short presentation of the Weibullsholm-P.G.A. collection). In: Zeven, A.C. and A.M. van Harten (eds) *Broadening the Genetic Basis of Crops*. pp. 195–202. PUDOC, Wageningen.

Brandenburg, W.A. and F. Schneider (1988) Cultivar grouping in relation to the International Code of Nomenclature for Cultivated Plants. *Taxon* 37:141–147.

Danert, S. (1958) Zur Systematik von *Papaver somniferum* L. *Kulturpflanze* 6:61–88.

de Wet, J.M.J. (1978) Systematics and evolution of *Sorghum* sect. *Sorghum* (Gramineae). *American Journal of Botany* 65:477–488.

Dorofeev, V.F. and O.N. Korovina (eds) (1979) Psenica [Wheat]. In: Breznev, D.D. (ed.) *Kul'turnaja Flora SSSR*. Vol. 1. Kolos, Leningrad.

Flaksberger, C.A. (1935) Wheat. In: Wulff, E.V. (ed.) *Flora of Cultivated Plants*. Vol. 1. State Agricultural Publishing Co., Moscow and Leningrad.

Fursa, T.B. (1981) Intraspecific classification of water-melon under cultivation. *Kulturpflanze* 29:297–300.

Fursa, T.B. and A.I. Filov (1982) Tykvennye [Cucurbitaceae - *Citrullus*, *Cucurbita*]. In: Breznev, D.D. (ed.) *Kul'turnaja Flora SSSR*. Vol. 21. Kolos, Moscow.

Girenko, M.M. and O.N. Korovina (eds) (1988) Listovye ovoscnye rastenija [Leafy vegetables - asparagus, rhubarb, sorrel, spinach, purslane, garden cress, dill, chicory, lettuce]. In: Dorofeev, V.F. (ed.) *Kul'turnaja Flora SSSR*. Vol. 12. Agropromizdat, Leningrad.

Hammer, K. (1981) Problems of *Papaver somniferum* classification and some remarks on recently collected European poppy land-races. *Kulturpflanze* 29:287–296.

Hammer, K. (1992) Neu- und altweltliche Bohnen. *Vorträge für Planzenzüchtung* 22:162–166.

Hanelt, P. (1972) Die infraspezifische Variabilität von *Vicia faba* L. und ihre Gliederung. *Kulturpflanze* 20:75–128.

Hanelt, P. (1986) Formal and informal classifications of the infraspecific variability of cultivated plants - advantages and limitations. In: Styles, B.T. (ed.) *Infraspecific Classification of Wild and Cultivated Plants*. pp. 139–156. Clarendon Press, Oxford.

Hanelt, P. and K. Hammer (1987) Einige infragenerische Umkombinationen und Neubeschreibungen bei *Brassica* L. und *Papaver* L. *Feddes Repertorium* 98:553–555.

Hanelt, P., G. Linne von Berg and M. Klaas (1993a) Taxonomische Untersuchungen zur infraspezifishchen Variabilität bei Kulturpflanzen. *Vorträge für Pflanzenzüchtung* 25:212–227.

Hanelt, P., R. Fritsch, K. Hammer, J. Kruse, K. Pistrick and J. Schultze-Motel (1993b) Taxonomy and evolution of cultivated plants: literature reviews. *FAO/IBPGR Plant Genetic Resources Newsletter* 91/92:24.

Harlan, J.R. and de Wet, J.M.J. (1971) Towards a rational taxonomy of cultivated plants. *Taxon* 20:509–517.

Helm, J. (1964) 100 Jahre Kulturpflanzentaxonomie. Dr Friedrich Alefeld zum Gedächtnis. *Kulturpflanze* 12:75–92.

Kazakova, A.A. (1978) Luk [Allium]. In: Breznev, D.D. (ed.) *Kul'turnaja Flora SSSR*. Vol. 10. Kolos, Leningrad.

Kobyljanskij, V.D. (ed) (1989) Roz [Rye]. In: Dorofeev, V.F. (ed.) *Kul'turnaja Flora SSSR*. Vol. 2, Part 2. Agropromizdat, Leningrad.

Kobyljanskij, V.D. and M.V. Lukjanova (eds) (1990) Jacmen' [Barley]. In: Kriveenko, V.I.

(ed.) *Kul'turnaja Flora SSSR*. Vol. 2, Part 1. Agropromizdat, Leningrad.
Lehmann, Ch.O. and S. Blixt (1984) Artificial infraspecific classification in relation to phenotypic manifestation of certain genes in *Pisum*. *Agri Hortique Genetica* 42:49–74.
Makaseva, R.Ch. (ed.) (1979) Zernovye bobosye kul'tury [Grain legumes]. In: Breznev, D.D. (ed.) *Kul'turnaja Flora SSSR*. Vol. 4, Part 1. Kolos, Leningrad.
Mansfeld, R. (1950) Das morphologische System der Saatgerste, *Hordeum vulgare* L. s.l. *Züchter* 20:8–24.
Mansfeld, R. (1951) Das morphologische System des Saatweizens, *Triticum aestivum* L. s.l. *Züchter* 21:41–60.
Mansfeld, R. (1953) Zur allgemeinen Systematik de Kulturpflanzen I. *Kulturpflanze* 1:138–155.
Máthé, I. and S. Priszter (1982) *The Cultivated Plants of Hungary*. Akadémiai Kiadó, Budapest.
Nechanský, F. and V. Jirásek (1967) Systematische Studie über kultivierte Sommerastern (Gartenastern) - *Callistephus chinensis* (L.) Nees (Asteraceae). *Preslia* 39: 122–150.
Percival, J. (1921) *The Wheat Plant. A Monograph*. Duckworth & Co., London.
Perrino, P. and K. Hammer (1983) Sicilian wheat varieties. *Kulturpflanze* 31:229–279.
Prestianni, P. (1926) *I Frumenti Coltivati in Sicilia*. Commissione Provinciale per la Propaganda Granaria di Caltanissetta, Caltanissetta.
Rogers, D.J. and H.S. Fleming (1973) A monograph of *Manihot esculenta* with an explanation of the taximetric methods used. *Economic Botany* 27:1–113.
Schultze-Motel, J. (1987) Numerisch-taxonomische Studien an *Triticum* L. und *Aegilops* L. zur Theorie der Klassifizierung von Kulturpflanzen. *Kulturpflanze* 35:53–97.
Simmonds, N.W. (1966) *Bananas*. 2nd edition Longman, London.
Simmonds, N.W. and S.T.C. Weatherup (1990) Numerical taxonomy of cultivated bananas. *Tropical Agriculture* 67:90–92.
Smaraev, G.E. and O.N. Korovina (eds) (1982) Kukuruza [Corn]. In: Breznev, D.D. (ed.) *Kul'turnaja Flora SSSR*. Vol. 6. Kolos, Moscow.
Vavilov, N.I. (1940) The new systematics of cultivated plants. In: Huxley, J. (ed.) *The New Systematics*. pp. 549–566. Oxford University Press, Oxford.
Zeven, A.C. and J.M.J. de Wet (1982) *Dictionary of Cultivated Plants and Their Regions of Diversity*. PUDOC, Wageningen.