Biodiversity and Conservation (2006) 15:2673–2685
DOI 10.1007/s10531-005-5409-6

Towards a definition of a crop wild relative

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Received 15 October 2004; accepted in revised form 5 April 2005

Key words: Crop wild relative, Definition, Gene pools, Plant genetic resources, Taxon groups

Abstract. Crop wild relatives are an important socio-economic resource that is currently being eroded or even extinguished through careless human activities. If the Conference of the Parties (COP) to the CBD 2010 Biodiversity Target of achieving a significant reduction in the current rate of loss is to be achieved, we must first define what crop wild relatives are and how their conservation might be prioritised. A definition of a crop wild relative is proposed and illustrated in the light of previous Gene Pool concept theory. Where crossing and genetic diversity information is unavailable, the Taxon Group concept is introduced to assist recognition of the degree of crop wild relative relatedness by using the existing taxonomic hierarchy.

Abbreviations: CBD – Convention on Biological Diversity; COP – Conference of the Parties to the CBD; CWR – Crop wild relative; FAO – Food and Agriculture Organisation of the United Nations; GM – Genetic modification; GP – Gene pool; PGR – Plant genetic resources; TG – Taxon group

Introduction

The Convention on Biological Diversity (CBD 1992) and the subsequent International Treaty on Plant Genetic Resources for Food and Agriculture (FAO 2001) have proved a watershed in plant genetic resources (PGR) conservation in many ways, particularly by re-focusing conservation activities onto *in situ* conservation. *In situ* conservation, using the definition provided in the text of the CBD (Convention on Biological Diversity 1992), incorporates two distinct approaches: conservation of wild species in nature and on-farm conservation of domesticated varieties or breeds. Within the context of socio-economic plant diversity conservation, the change of emphasis away from further collecting of cultivated material for *ex situ* conservation in gene banks towards the *in situ* conservation of locally adapted land races and the wild relatives of crops within or outside existing protected areas, has necessitated the research and development of new conservation methods (Hawkes 1991; Maxted et al. 1997a).

The focus of crop wild relative (CWR) maintenance is conservation in genetic reserves, primarily due to the large numbers of species included and the difficulty of collecting and conserving *ex situ* their entire genetic diversity. CWRs are those species related to a crop, but what constitutes a CWR and how closely related to a crop does a taxon have to be to be considered a CWR? In the light of contemporary biotechnological advances in GM technology, most if not all species are potential gene donors to a crop. However, within the utilitarian sense of conservation for food and agriculture it remains important to be able to accurately define the relationship between a crop and its close wild relatives, so that conservationists competing for limited conservation resources may objectively prioritise taxa for study (Kell and Maxted 2003; Meilleur and Hodgkin 2004). This is a particularly pressing need given the current threats to genetic diversity from genetic erosion and extinction, as recognised by the Conference of the Parties (COP) to the CBD 2010 Biodiversity Target (www.biodiv.org/2010-target), as well as a number of other strategies and treaties, such as the Global Strategy for Plant Conservation, the International Treaty on Plant Genetic Resources for Food and Agriculture and the European Plant Conservation Strategy.

To meet many of the 2010 biodiversity targets[1] and the targets and requirements of other relevant strategies and legislation, we need to be able to assess biodiversity change; therefore, a clear baseline against which to assess change is essential. For Europe, for example, the European Community funded project, European Crop Wild Relative Diversity Assessment and Conservation Forum (PGR Forum – www.pgrforum.org) is making a significant contribution by providing the baseline information and the tools required to monitor this change. However, to continue working collectively and globally towards achieving the objectives of the 2010 Biodiversity Target, there is first a need to agree on what constitutes a crop wild relative, as there is currently no generally accepted definition.

Although lists of crop wild relatives exist, notably those proposed for Europe by Zeven and Zhukovsky (1975) and Heywood and Zohary (1995), and for individual countries by Schlosser et al. (1991) for the former German Democratic Republic and by Mitteau and Soupizet (2000) for France, no precise definition of what constitutes a crop wild relative is provided and the taxa have been selected subjectively on the basis of expert knowledge. Here we discuss previous CWR and Gene Pool concepts, and propose a working definition of a crop wild relative and how this definition can be applied.

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[1] Particularly targets 2.1, 'Restore, maintain or reduce the decline of populations of species of selected taxonomic groups'; 3.1, 'Genetic diversity of crops, livestock, and harvested species of trees, fish and wildlife and other valuable species conserved ....'; and 8.2, 'Maintain biological resources that support sustainable livelihoods, local food security and health care, especially of poor people'.

Crop gene pool concepts

From his observations of crops and their wild relative diversity Vavilov (Vavilov 1920, 1922) noted that similar patterns of variation were found between crops and their wild relatives in unrelated crop complexes. Comparative genomics have more recently revealed that both gene content and gene order are conserved widely across related species and genera, and this has been most thoroughly demonstrated in the grasses (Devos and Gale 1997). However, Vavilov's Law of Homologous Series, which preceded modern molecular genetics, was proposed to systematize such examples of parallelism (Vavilov 1920, 1922) and he illustrated his concept using patterns of variation among vetches, lentils and peas. These reproductively isolated genera each show similar patterns of variation, which are likely to have arisen as a response to similar natural and artificial selection pressures. The continuing importance of Vavilov's law is that it has predictive value, in that it can be used to try to identify desirable traits such as disease resistance or drought tolerance in related species. Thus Vavilov was one of the first to recognise the importance of conserving the breadth of a crop's genetic diversity, both within the crop itself, but also importantly within the wild species related to the crop, among which there could be natural or artificial introgression.

These views were formalised by Harlan and de Wet (1971) as the Gene Pool concept. Within each crop there was a potential pool of genetic diversity available for utilisation and a gradation of that diversity dependent on the relative crossing ability between the crop itself and the primarily non-domesticated species in the primary, secondary or tertiary Gene Pool of the crop. They distinguish three Gene Pools as follows:

- Primary Gene Pool (GP-1) within which GP-1A are the cultivated forms and GP-1B are the wild or weedy forms of the crop;
- Secondary Gene Pool (GP-2) which includes the coenospecies (less closely related species) from which gene transfer to the crop is possible but difficult using conventional breeding techniques;
- Tertiary Gene Pool (GP-3) which includes the species from which gene transfer to the crop is impossible, or if possible requires sophisticated techniques, such as embryo rescue, somatic fusion or genetic engineering.

Using the crop, cowpea (*Vigna unguiculata* (L.) Walp. subsp. *unguiculata)* as an example from a recent ecogeographic monograph of African *Vigna* (Maxted et al. 2004), then the Gene Pool concept may be applied as indicated in Table 1.

However, the division of the broader Gene Pool into its primary, secondary and tertiary units is only possible when extensive information is available on patterns of genetic diversity and relative crossing ability for the species in question.

Although applied widely to identify practical conservation and use targets, the Harlan and de Wet (1971) concept does have limitations (Maxted et al. 1997b): for instance, it necessarily requires an approximation of the relative ease

Table 1. Gene pool concept applied to cowpea (*Vigna unguiculata* (L.) Walp. subsp. *unguiculata*.).

Crop taxon	1° Gene Pool	2° Gene Pool	3° Gene Pool
V. unguiculata	A. *V. unguiculata* subsp. *unguiculata:* *Unguiculata* Group, *Biflora* Group, *Sesquipedalis* Group, *Melanophthalmus* Group B. All wild and weedy infra-specific *V. unguiculata* taxa	*V. nervosa*	Other *Vigna* species

Table 2. Numbers of plant species in the Euro-Mediterranean region and CWR and percentages of species in each CWR group (Kell et al. in prep.).

Floristic grouping	Number of species	Percentages of species
Euro-Mediterranean Species	30,729	100
All CWR species	23,818	77.5
Agricultural and Horticultural CWR	19,091	62.1
Forestry CWR	2798	9.1
Ornamental CWR	7388	24.0
Medicinal and Aromatic CWR	19,574	63.7

of hybridisation between the crop and the wild relative and it can only be used for designating conservation priority within a specific crop Gene Pool rather than both within and across different crop Gene Pools. Applications of this genetically based concept have been limited because more often than not, crossing ability and patterns of genetic diversity between crops and their wild related taxa are absent for all but the major crop complexes. If European and Mediterranean CWR are taken as an example; there are 23,818 crops and CWR species present in the region (out of a total flora of 30,729 species), see Table 2, and Kell et al. (in prep.). It is estimated that the Gene Pool concept could only be applied to approximately 226 out of the 1,025 genera, 22% of the total. The sheer number of crop species worldwide (7,000 species; FAO 1998) along with the potential total number of higher plant species (270,000 species, Groombridge and Jenkins 2002), each of which must to a degree be a crop wild relative, makes the possibility of obtaining the necessary genetic diversity information for all CWR taxa a distant reality, even with falling costs and ease of molecular genetic analysis. Also, when attempting to establish priorities for national PGR programmes, decision makers often need to set conservation priorities across the breadth of the entire flora covering numerous crop Gene Pools, not just in relation to a single crop, as proposed by Harlan and de Wet (1971).

What constitutes a crop wild relative?

A simple definition of a CWR would be a taxon found within the primary or more remotely the secondary Gene Pool of a crop, and between which gene exchange is relatively simple. Hybridisation occurs easily within this group, resulting in fertile hybrids with normal chromosome pairing and gene segregation. This simple application of the Harlan and de Wet (1971) concept remains functional for the crop complexes where hybridisation experiments have been performed and the pattern of genetic diversity within the Gene Pool is well understood. However, for the majority of crop complexes, particularly those in the tropics, the wild species related to crops have been described and classified using a combination of morphological characteristics, and the degree of genetic differentiation among species remains unknown. Where the data are available to objectively apply the Harlan and de Wet concept, it will remain the best assessment of what constitutes a crop wild relative. However, where the necessary crossing and genetic diversity data are unavailable there remains a need to find an alternative means of estimating the degree of relatedness of crops and their wild relatives.

Proposed application of taxon groups

PGR Forum has pragmatically circumvented the lack of crossing and genetic diversity data for the majority of European crops and related taxa by using the existing taxonomic hierarchy. This can be applied to define a crop wild relative's rank as follows:

Taxon Group 1a – crop
Taxon Group 1b – same species as crop
Taxon Group 2 – same series or section as crop
Taxon Group 3 – same subgenus as crop
Taxon Group 4 – same genus
Taxon Group 5 – same tribe but different genus to crop

For CWR taxa for which we have little or no genetic diversity data, the Taxon Group concept can be used to assist in setting conservation priorities. For example, if this concept were applied to the less well studied *Vigna* crop, zombi bean (*V. vexillata* (L.) A.Rich. var. *vexillata*), then the Taxon Group concept may be applied as indicated in Table 3.

When attempting to apply the Taxon Group concept it should be acknowledged that taxonomists do not always provide a detailed infra-generic ranking for genera when they publish a classification. Thus where certain levels of the taxonomic hierarchy are absent, the next higher Taxon Group should be applied. For example, if a crop is located in a genus where sections have not been defined but subgenera have, then the crop would be placed in TG1a, and other taxa within the same species (i.e. varieties or subspecies) as the crop would be placed in TG1b. It would not be possible to use TG2, but species found in the same subgenus would be members of TG3 and those in other subgenera in TG4. If no sections or subgenera had been defined, all species in

Table 3. Taxon group concept applied to zombi bean and its CWRs (*V. vexillata* (L.) A.Rich. var. *vexillata*).

Taxon group 1a (= crop)	Taxon group 1b (= same species)	Taxon group 2 (= same section)	Taxon group 3 (= same subgenus)	Taxon group 4 (= same genus)	Taxon group 5 (= more remote genera)
V. vexillata var. *vexillata*	*V. vexillata* *var. angustifolia* var. *davyi* var. *dolichonema* var. *lobatifolia* var. *macrosperma* var. *ovata*	Section *Plectotropis* *V. kirkii*	Subgenus *Plectotropis* Section *Pseudoliebrechtsia* *V. nuda* *V. longissima*	Subgenus *Vigna* Subgenus *Haydonia* Subgenus *Ceratotropis* Subgenus *Lasiospron* Subgenus *Sigmoidotropis* Subgenus *Macrorhyncha*	*Phaseolus* *Dysolobium* *Lablab* *Macroptilium* *Oxyrhynchus* *Physostigma*

the same genus as the crop would be placed in TG4 and those in other related genera in TG5.

Knowledge of differences in crop and wild species ploidy levels also has an impact on the application of the Taxon Group concept. Even if a taxonomist considered two species closely related, placing them in the same section on the basis of morphological similarity, differences in ploidy level may cause difficulties in the survival of hybrids and therefore in utilisation. However, as indicated above, wherever the Gene Pool relationships are well understood, for instance, in cases where cytogenetics and ploidy levels have been studied, the Gene Pool concept would have priority and the Taxon Group concept would not be applied.

Application of the Taxon Group concept assumes that taxonomic distance is positively related to genetic distance. Flint (1991), Heywood (1994) and Johnson (1995) all point out that this relationship may not hold because of inconsistencies amongst taxonomists when describing species; species are not all separated by the same, standard genetic distance. Nevertheless, it is believed that the taxonomic hierarchy is likely to be an approximation of actual genetic distance and therefore, for practical purposes, classical taxonomy remains an extremely useful means of estimating genetic relationships.

Specifically in relation to the PGR Forum project, it was initially intended to apply the Taxon Group concept to the Euro + Med Plantbase database for the European and Mediterranean flora by automatically tagging each taxon record as to which crop the taxon was related and to which Taxon Group the individual taxon belonged. However, the Taxon Group tagging of all Euro + Med Plantbase taxa was ultimately not possible because the series, section and subgeneric hierarchy of the genera included were not linked to individual species in the database structure. However, a sample of the genera were linked manually to demonstrate how the Taxon Group concept could be applied, see Kell et al. (in prep.) for further discussion. Application of the Taxon Group concept in this form to taxonomic databases is seen as essential to enable the comparatively large number of CWR taxa to be prioritised for conservation action, however, the application of the concept to individual CWR genera can be easily achieved using the accepted classification. It should also be noted that the Taxon Group concept can be utilised to prioritise 100% of crop and CWR taxa for conservation action, as long as the existing classification of the genus contains infra-generic structure, as opposed to the approximate 22% of crop and CWR taxa that can be prioritised using the Gene Pool concept.

Proposed definition of a crop wild relative

If it is accepted that the Gene Pool concept together with the Taxon Group concept proposed above provide the best pragmatic means available to determine whether a species is a CWR, a working definition of a crop wild relative is possible:

A crop wild relative is a wild plant taxon that has an indirect use derived from its relatively close genetic relationship to a crop; this relationship is defined in terms of the CWR belonging to Gene Pools 1 or 2, or taxon groups 1 to 4 of the crop.

While the CWR definition may most commonly be applied to species used in food and agriculture, the concept is equally applicable to ornamentals, medicinal plants, and forestry species. A broad definition of a CWR would be any taxon belonging to the same genus as a crop. Applying the proposed Taxon Group concept, it would be a member of TG1 to TG4. Harlan and de Wet (1971) apply a similar breadth to their Gene Pool concept for ease of usefulness of related species, commenting that the secondary Gene Pool is equivalent to generic limits of the crop. However, the use of this broad application of the Taxon Group concept would result in the inclusion of a very large percentage of known taxa. If the European and Mediterranean floras are taken as an example, 77.5% of species in the Euro + Med region (Euro + Med Plantbase, www.euromed.org.uk) would be regarded as CWR. Therefore it is important to underline that being a crop wild relative is itself a relative concept and that there is a need to estimate the degree of CWR relatedness, if for no other reason than to assist in establishing conservation priorities. Therefore, taxa which belong to GP1B or TG1b and TG2 may be considered close CWRs of higher priority, and those in GP2 or TG3 and TG4 more remote CWRs afforded lower priority. Those in GP3 and TG5 would be excluded from being considered CWRs of that particular crop. Therefore it can be argued that application of the Gene Pool and Taxon Group concepts to determine whether a species is or is not a CWR is pragmatic, and that the two concepts used together can be applied to establish the degree of crop wild relative relatedness and thus assist in establishing conservation priorities. This strategy has been applied within the European CWR project, PGR Forum (www.prgforum.org).

The concepts combined could also be of value in assessing ‘risk’ of genetic pollution of CWRs by genetically modified and conventional modern crop varieties. Risk can be assessed using combined estimations of hazard and exposure (Wilkinson et al. 2003). Exposure is a quantifiable estimate of the probability of the hazard occurring. Combining the Gene Pool and Taxon Group concepts can provide a basis for estimating the likelihood of gene flow occurring, even in poorly studied taxa where genetic information is minimal or absent.

The Gene Pool and Taxon Group concepts applied to a crop and its wild relatives would ideally be expected to be congruent, but as discussed above and acknowledged by Harlan (1992), inconsistencies among taxonomists when describing species mean that where both taxonomic and genetic information is available the two concepts may not match perfectly. This can be illustrated by applying the Gene Pool and Taxon Group concepts for two European crops and their wild relatives as is shown in Table 4. It is interesting to note the close correlation between the application of the Gene Pool and Taxon Group

Table 4. Application of gene pool and taxon group concepts for the crops *Vicia narbonensis* and *Beta vulgaris* and their wild relatives.

Crop	Gene pool concept					
	GP1A[a]	GP1B	GP2	GP3		
Narbon bean	*Vicia narbonensis* L.	*V. narbonensis* L.	*V. kalakhensis* Khattab, Maxted & Bisby	All other *Vicia* species		
	var. *narbonensis*	var. *salmonea* (Mout.) H. Schäfer var. *jordanica* H. Schäfer var. *affinis* Kornhuber ex Asch. & Schweinf. var. *aegyptiaca* Kornhuber ex Asch. & Schweinf.	*V. johannis* Tamamschjan in Karyagin *V. galilaea* Plitm. & Zoh. in Plitm. *V. serratifolia* Jacq. *V. hyaeniscyamus* Mout.			
	Taxon group concept					
	TG1A[b]	TG1B	TG2	TG3	TG4	TG5
Narbon bean	*V. narbonensis* L.	*V. narbonensis* L.	Sect. *Narbonensis* (Radzhi) Maxted	All non-section *Narbonensis* (Radzhi) Maxted	All *Vicia* subgenus *Vicilla* Schur species	*Lens* Miller, *Lathyrus* L., *Pisum* L. and *Vavilovia* A. Fed. Species
	var. *narbonensis*	var. *salmonea* (Mout.) H. Schäfer var. *jordanica* H. Schäfer var. *affinis* Kornhuber ex Asch. & Schweinf.	*V. kalakhensis* Khattab, Maxted & Bisby *V. johannis* Tamamschjan in Karyagin *V. galilaea* Plitm. & Zoh. in Plitm.	*Vicia* L. subgenus *Vicia* species		

Table 4. Continued.

Crop	Gene pool concept					
		var. *aegyptiaca* Kornhuber ex Asch. & Schweinf.	*V*. *serratifolia* Jacq.			
			V. *hyaeniscyamus* Mout. *V*. *eristalioides* Maxted			
Crop	Gene pool concept					
	GP1A	GP1B	GP2	GP3		
Beet	*Beta vulgaris* L. subsp. *vulgaris*	*B*. *vulgaris* L.	Section *Procumbentes:*	Section *Corollinae*:		
	Cultivar groups: leaf beet, garden beet, fodder beet, sugar beet	subsp. *maritima* z(L.) Arcang.	*B*. *procumbens* Sm.	*B*. *lomatogona* Fisch. et May.		
		subsp. *Adanensis* (Pamuk.) Ford-Lloyd & Williams	*B*. *webbiana* Moq.	*B*. *macrorhiza* Stev.		
		B. *macrocarpa* Guss. *B*. *patula* Ait.	*B*. *patellaris* Moq.	*B*. *corolliflora* Zos. ex Buttler *B*. *intermedia* Bunge *B*. *trigyna* Waldst. et Kit. Section *Nanae*: *B*. *nana* Boiss. et Heldr.		
	Taxon group concept					
	TG1A[c]	TG1B	TG2	TG3	TG4	TG5
Beet	*Beta vulgaris* L. subsp. *vulgaris*	*B*. *vulgaris* L.	Section *Beta*		Section *Procumbentes*	

Cultivar groups: leaf beet, garden beet, fodder beet, sugar beet	subsp. *maritima* (L.) Arcang.	*B. macrocarpa* Guss.	*B. procumbens* Sm.
	subsp. *adanensis* (Pamuk.) Ford-Lloyd & Williams	*B. patula* Ait.	*B. webbiana* Moq.
			B. patellaris Moq.
			Section *Corollinae*
			B. lomatogona Fisch. et May.
			B. macrorhiza Stev.
			B. corolliflora Zos. ex Buttler
			B. intermedia Bunge
			B. trigyna Waldst. et Kit.
			Section *Nanae*
			B. nana Boiss. et Heldr.

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[a] Gene pool concept for *Vicia narbonensis* is taken from Enneking and Maxted (1995).

[b] Taxon group concept for *Vicia narbonensis* is derived from the classification provided in Maxted (1993).

[c] Taxon group concept for *Beta* is derived from the classification provided in Ford-Lloyd (2005).

concepts for the crops and their wild relatives, particularly for *Vicia narbonensis*, but also for *Beta vulgaris* and its wild relatives. Although the accepted classification of *Vicia* utilises the full taxonomic hierarchy (i.e. series, sections and subgenera are designated), for *Beta*, the taxonomic rank subgenus has not been used, therefore, no taxa can be included in Taxon Group 3 (= same subgenus) and all remaining *Beta* taxa not present in section *Beta*, which contains the crop, are grouped in Taxon Group 4 (= same genus but excluding the section containing the crop). The correlation between the application of the Gene Pool and Taxon Group concepts and the flexibility of applying the Taxon Group concept even where the full taxonomic hierarchy has not been applied underlines its usefulness. However, it should be stressed that where both genetic and taxonomic information are available, genetic information should be given weight when defining crop wild relative relatedness. Application of the Taxon Group concept is pragmatic and will prove very helpful in defining the degree of relatedness of a wild species to a crop for the bulk of plant species where genetic diversity data is absent but the Taxon Group concept is a more subjective assessment than direct comparison of genetic diversity.

Acknowledgements

The concepts discussed in this paper were stimulated by PGR Forum (the European crop wild relative diversity assessment and conservation forum – EVK2-2001-00192 – www.pgrforum.org), funded by the EC Fifth Framework Programme for Energy, Environment and Sustainable Development, and as such we would like to acknowledge the support of other members of the forum, specifically L. Guarino, J. Iriondo, H. Knüpffer and T. Hodgkin.

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