REVIEW

Crop–weed complexes: the complex relationship between crop plants and their wild relatives

L. W. D. VAN RAAMSDONK* and L. J. G. VAN DER MAESEN†

*Centre for Plant Breeding and Reproduction Research CPRO-DLO, PO Box 16, 6700 AA Wageningen, The Netherlands; and †Department of Plant Taxonomy, Wageningen Agricultural University, PO Box 8010, 6700 ED Wageningen, The Netherlands

CONTENTS

Key-words: biosafety, classification, compilospecies, gene flow, introgression, phenetic analysis, phylogenetic analysis, phylogeny.

INTRODUCTION

It is obvious that each crop has had its wild parental relative. The relationship, however, can vary from a straightforward process of domestication of a crop out of the genetic variation of a single wild species to complex relationships between a crop and a range of weedy and wild relatives.

At first it is necessary to define domestication since the concepts of crops and weeds are linked to this process of adaptation to human needs. Domestication is the process leading to characteristics profitable for man which generally reduce the fitness of plants in natural habitats. A special case of a characteristic profitable for man is the reduction or even total incapacity to disseminate viable offspring (De Wet 1981; Harlan 1992; Van Raamsdonk 1993a). Thus, crops resulting from this process of domestication survive in dependence on man by means of special growing conditions and reproduction strategies. The decreasing capability of independent seed dispersal is due to characteristics such as non-dehiscence, non-shattering and requirement of seed vernalization. Also the lack of a seed dormancy period in some cases decreases the possibility of establishing the next generation. These characteristics are clearly found in seed-propagated crops or in crops domesticated for their propagules, such as cereals, pulses and fruits, as well as in vegetables (lettuce, cabbages) or in some tuber crops (beets; Simmonds 1979).

A large range of definitions of weeds has been given (Harlan 1992). These definitions focus either on the nuisance or unwantedness (human value criterion) or on adaptation or fitness (ecological criterion). A good example of an ecological definition is that of

Bunting (1960; quoted in Harlan 1992) which states that 'weeds are pioneers of secondary succession of which the weedy arable field is a special case'. In comparison to the given definition of domestication, we will define weeds as plants that are adapted to man-made habitats in the same way as crops, but which are still capable of disseminating their seeds on their own. This definition of weeds covers two different types of weeds, namely those which are evolutionary related to a crop and those which mimic an unrelated crop (Barrett 1983). In this review we will deal with only the first type.

Both definitions of crops and weeds are not clear-cut for several reasons. There are still crops which disseminate their seeds freely, such as culinary herbs, fodder grasses, clovers and some tuberous crops. Notwithstanding this feature they are considered a crop in the common sense. However, Simmonds (1979: 8) stated, referring to fodder grasses and clovers, '... it is arguable that many have yet to make the transition to domestication'. Regarding weeds, any intermediate state between entirely man-made habitats (greenhouses) and only weak disturbance (production forests, roadsides) exists. It is also important to realize that the naturalness of man-made habitats is influenced by the definition used. Williamson (1993) discusses the different indications of disturbance of waysides in a Dutch (De Vries *et al.* 1992) and an English (Raybould & Gray 1993) study with emphasis on the weediness of *Brassica napus* (oilseed rape). Similarly, the intermediate state of semi-shattering can be found, which means that the weed disseminates only a part of its seeds. The shattered seeds will infest the field in the next growing season, while the remaining seeds will be harvested and infest the sowing seed for the next crop generation (Harlan 1992). Moreover, 17 of the 18 most noxious weeds on a global scale are cultivated in other parts of the world (reviewed in Bartsch *et al.* 1993).

The shift from free shattering to non-shattering (cereals; Hancock 1992) or from dehiscent pods to non-dehiscence (pulses: Ladizinsky 1979) allows discrimination in archaeobotanical studies between seeds which were harvested in nature or from cultivated (weedy) plants and seeds of domesticated crops. Because of the importance and easy recognition of this feature in archaeobotany its present agricultural value may be somewhat overestimated (Harlan 1992). Similarly, allometric growth of fruits of domesticated plants also allows distinction between remnants of wild and domesticated plants.

In this paper attention will be paid to the patterns of variation which can be found in crop–weed complexes and to the different ways to analyse these patterns. The mechanisms which cause these patterns have been addressed partly by Van Raamsdonk (1995b). After the discussion of variation patterns some aspects of the classification of variation in crop plants will be addressed.

THE BIOLOGY OF CROP–WEED COMPLEXES

The recognition of crop–weed complexes dates back to Anderson (1952). He defined these complexes as 'a compound of crops, accompanying weeds and wild related species, mutually influencing each other by means of introgression' (Anderson 1952). Several authors have examined this phenomenon. More recently, Van der Maesen (1994) defined crop–weed complexes as a set of cultivated and related wild or weedy plants growing together and influencing each other through introgression. The main keyword in these and other definitions (Pickersgill 1981; Small 1984; Harlan 1992; Bartsch *et al.* 1993; Van Raamsdonk 1993a, 1995b) is introgression. This may occur at low levels (Van der Maesen 1994) but even a low level of gene flow between populations is proven to be

effective (Dobzhansky *et al.* 1977). Altogether eight different combinations of hybridization and introgression between two of the three components of crop–weed complexes were described. These combinations are wild × weed, weed × weed, wild × crop and crop × crop, each combination resulting in either supplementary weeds or supplementary domesticates, and wild × wild and crop × weed, which can result in both weeds and crops (Small 1984). Allogamy favours hybridization while autogamy generally prevents a substantial gene flow. It is to be expected that a majority of crops belonging to a crop–weed complex is at least partly outbreeding (Van Raamsdonk 1995b).

Three models of phylogenetic relationships between crops and weedy and wild relatives have been recognized. The first pathway implies that weeds evolve from a wild species and that the crop is a descendant of the weed. In the second pathway a crop gives rise to weeds, i.e. by means of escape and naturalization. According to the third pathway crop and weeds evolve simultaneously from a wild species (Pickersgill 1981; Bartsch *et al.* 1993). Since every step means a narrowing of the genetic basis due to genetic drift, crops of which the evolution is described by the first pathway may possess the least variability. A modification of this pathway is that the crop evolved directly from a wild species with weedy characteristics. In a number of cases where escapes of domesticated plants have been found (second pathway) hybridization between crop and wild relative took place initially. An example is *Beta vulgaris* (sugar beet; Boudry *et al.* 1993). On the other hand, in compilospecies a large variation compared to the individual wild relatives can be encountered (Harlan & De Wet 1963).

Accompanying weeds occur in a vast range of crop plants (Harlan 1992). However, not all these crop plants can be regarded as belonging to a crop–weed complex and proper delimitation of the range of the concept of crop–weed complexes should be made. In the next paragraphs a practical solution to this problem will be worked out in two ways: one way is to discuss crop examples along the entry of experimental approaches by which crop–weed complexes can be studied; the second way is to discuss the borderline between crop–weed complexes and isolated crops by means of specific crop examples with various levels of gene flow taken from two plant groups: woody plants and legumes.

EXPERIMENTAL APPROACHES

The design of experiments in the framework of biosystematic studies of crop–weed complexes is largely influenced by the evolutionary position of the objects. While the systematic position of crop, weed and wild relatives can be described in terms of a phylogenetic system, the classification of cultivars within a crop is generally not based on phylogeny or should not be based on such (Hetterscheid & Brandenburg 1995), hence phenetic methods are more suitable. An overview of both approaches in systematics is presented by Stuessy (1990). In the following examples both phenetic and phylogenetic approaches will be discussed. Most of these cases do not emphasize cultivar classification although variation within the crop will be treated. Cultivar classification is discussed in the paper of Hetterscheid *et al.* (1996).

Phenetic methods

Several premises have to be made for the use of numerical methods in cultivar classification. The starting point of a scientific study is generally a falsifiable hypothesis.

The existing classification can be used as a hypothesis to be tested and should therefore be excluded from the analysis itself. Phenetic methods such as cluster analysis and principal component analysis (PCA) are based on the analysis of variation without *a priori* assignment to categories such as taxa or culta and this offers the opportunity of comparing wild and domesticated material simultaneously. This simultaneous analysis is necessary because of the tight relationship between the different elements of crop–weed complexes (see e.g. Small 1984; Harlan 1992). The hypothesis can be tested by using it as an *a posteriori* overlay over the final results. Numerical methods allow recapitulation of the study because of their fixed algorithm. Cultivar classification is often based on only one or a few characters, while the mentioned numerical methods are explicitly multivariate. It is often necessary to extract one character from the range used to study the existing variation. Numerical methods indicate the contribution of every included character to the final distribution of the variation, which gives a basis for the choice of the most important character. Moreover, the support of the chosen character(s) by other characters can also be concluded from the results of numerical methods. The usefulness of phenetic methods for cultivar classification in the genera *Aster* and *Tulipa* is discussed by Hetterscheid & Van den Berg (1996) and Van Raamsdonk & De Vries (1996), respectively.

The phenetic method of PCA has been used to analyse the morphological variation within *Lactuca sativa* (lettuce) and between this crop and its wild relatives. The closest relative is *L. serriola*, while *L. virosa* and *L. saligna* are more distantly related (De Vries & Van Raamsdonk 1994; Fig. 1). Some additional variation on the molecular level was traced in *L. sativa*, which was not found until now in *L. serriola* (Kesseli *et al.* 1991; Michelmore *et al.* 1994). Two different evolutionary pathways can be proposed based on the morphological and molecular data. *L. sativa* originated either as a form selected out of the gene pool of *L. serriola* with simultaneous introgression from another species, or as independently selected species from a large ancestral gene pool, i.e. the first and third pathway, respectively, according to Pickersgill (1981). The differences in variation detected between *L. sativa* and *L. serriola* can be explained by assuming ancestral polymorphism in the second scenario (Soltis *et al.* 1992). Two diagonal axes have been recognized in the principal component plots based on morphological data (De Vries & Van Raamsdonk 1994). One can be referred to as the 'evolutionary' axis; the second, orthogonal one as the 'domestication' axis (Fig. 1). The latter is determined by a character combination including characters with as well as without domestication interest. The overlap in morphological variation between *L. virosa* and *L. serriola* appeared to be greater than between *L. sativa* and *L. serriola* after analyses of four different datasets. Only one *L. sativa* population resembled *L. serriola* significantly (Fig. 1). So, conspecificity of *L. sativa* and *L. serriola* (Frietema *et al.* 1994) is not supported by the study of De Vries & Van Raamsdonk (1994); the principal component plot in Frietema *et al.* (1994: 18) is similar to Fig. 1 with respect to the distinctness of the two species. After analysis of mitochondrial DNA variation in the tribe Lactuceae *L. sativa* and *L. virosa* show more common RFLPs than each of these two species share with *L. serriola* (Vermeulen *et al.* 1994). On the other hand, chromosome data do not indicate significant differences between *L. sativa* and *L. serriola* (Koopman & De Jong 1996). The floral structure of *Lactuca*, with a stigma growing through the anther tube with ripe pollen, ensures a high level of self-pollination. Introgression between *L. sativa* and *L. serriola* is not expected to be considerable in nature at levels that can be assumed in a crop–weed complex.
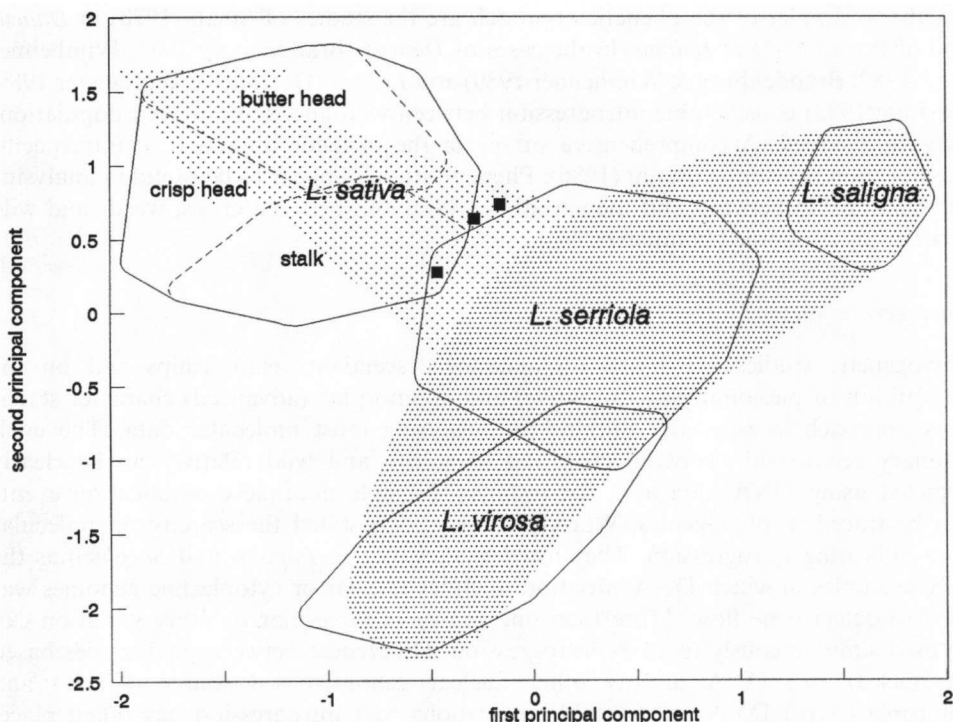
Fig. 1. Principal component plot of 252 *Lactuca* plants based on 63 morphological characters (adapted from De Vries & Van Raamsdonk 1994). Two diagonal axes are indicated. The area of the 'evolutionary' axis is shaded dark grey, the area of the 'domestication' axis is light grey. Solid squares: individuals of an intermediate accession.

The morphological variation in the *Capsicum baccatum* and the *C. annuum–chinense–frutescens* complexes has been studied extensively by Pickersgill *et al.* (1979). Minimum spanning trees and principal coordinate plots show considerable variation and a near continuum from wild to semi-domesticated and domesticated. We have also frequently found intermediate forms between *C. annum*, *C. frutescens* and *C. chinense* among germplasm accessions (Van Raamsdonk & De Vries, unpublished results). These identifications were based on a composite key abstracted mainly from Smith & Heiser (1975), D'Arcy & Eshbaugh (1974), McLeod *et al.* (1982) and IBPGR (1983). In both complexes parallel evolutionary trends from wild to domesticated forms were traced. The crops of the complexes can be distinguished, but the wild components show overlapping morphological variation. Isozyme variation indicates at least three parallel domestication events, which resulted in forms assigned to as *C. baccatum* var. *pendulum*, *C. annuum* p.p. and *C. pubescens*, respectively (Doebley 1989). Cross-fertilization is promoted by protogynous flowers (Pickersgill 1991). Introgression between the different parts of the crop–weed complexes in *Capsicum* is abundant (Pickersgill 1991; Zijlstra *et al.* 1991).

Cluster analysis of isozyme variation and tuber skin and flesh colour revealed extensive gene flow in the entire Andean gene pool of *Solanum tuberosum* (potato) due to hybridization and selection and to migration (trade) (Quiros *et al.* 1992). Further studies of *Solanum* will be reported by Van den Berg *et al.* (1996).

Other examples of the phenetic approach are the studies of Small (1978) in *Daucus* and of Loos (1993) in *Lolium*. In the cases of *Daucus* (Brandenburg 1981; Wijnheimer *et al.* 1989; Brandenburg & Wijnheimer 1989) and *Lolium* (Den Nijs & Wardenaar 1989; De Jong 1992) considerable introgression between wild and domesticated populations may be assumed. A comprehensive survey of the phenetic approach to infraspecific classification is given by Baum (1986). Phenetic studies appear to be useful in analysing the relationship between and the variation within and between crops, weeds and wild relatives in crop–weed complexes.

Phylogenetic methods

Phylogenetic studies are based on ancestor–descendant relationships and on the recognition of plesiomorphic (primitive) and apomorphic (advanced) character states. This approach is especially suitable for analysing most molecular data. The evolutionary relationship between crop and its weedy and wild relative can be clearly depicted using DNA data and, for instance, possible multiple domestication events can be traced in phylogenies. Whitkus *et al.* (1994) stated the scarcity of molecular data indicating introgression. They listed studies of *Iris*, *Populus* and *Sorghum* as the only examples in which DNA variation in either nuclear or cytoplasmic genomes was used to detect gene flow. More than one source of molecular or other variation can be used simultaneously to study introgression. Differences between phylogenies based on nuclear (n-) DNA or any other nuclear genome-based source of data and chloroplast (cp-) DNA are probable indications that introgression has taken place. This is due to the absence of recombination in cpDNA and to the almost exclusive uniparental (maternal in most cases) inheritance of cpDNA (Rieseberg & Brunsfeld 1992). This phenomenon is of particular interest for the study of crop–weed complexes.

Comparison of nDNA (ribosomal DNA differences) and cpDNA trees of the genus *Helianthus* unravels several types of hybridization and introgression (Rieseberg 1991; Rieseberg *et al.* 1991; Fig. 2). The annual oilseed crop *H. annuus* (sunflower) is capable of hybridization with a range of related species (Heiser 1965, 1969). The species *H. anomalus*, *H. deserticola* and *H. paradoxus* are considered to be hybrid derivatives of *H. annuus* and *H. petiolaris* since they show the nDNA variation of both these species (Fig. 2a; Rieseberg *et al.* 1993). The type of cpDNA of these hybrid species indicates the maternal parent. Populations of *H. anomalus* possess the cpDNA type of both parental species (Fig. 2b) which points to the inclusion of both reciprocal crosses in the parentage of *H. anomalus*. Introgression of cpDNA from a related species took place in four different species (Fig. 2b). The genetic background of the nDNA did not change as far as could be inferred from the ribosomal gene sequences (Fig. 2a). In all four introgression events *H. annuus* appeared to be involved. Sunflower, together with its relatives and their weedy hybrid forms, can be considered as a crop–weed complex. On the other hand, hybridization and introgression do not explain all the incongruencies between the two trees. The position of *H. bolanderi*, *H. debilis* ssp. *silvestris* and *H. argophyllus* is different in both trees, presumably due to other factors. The example of the annual *Helianthus* species indicates the usefulness of comparing nDNA and cpDNA phylogenetic trees (phylograms) for the study of crop–weed complexes, but incongruencies can be caused by other mechanisms than hybridization or introgression.
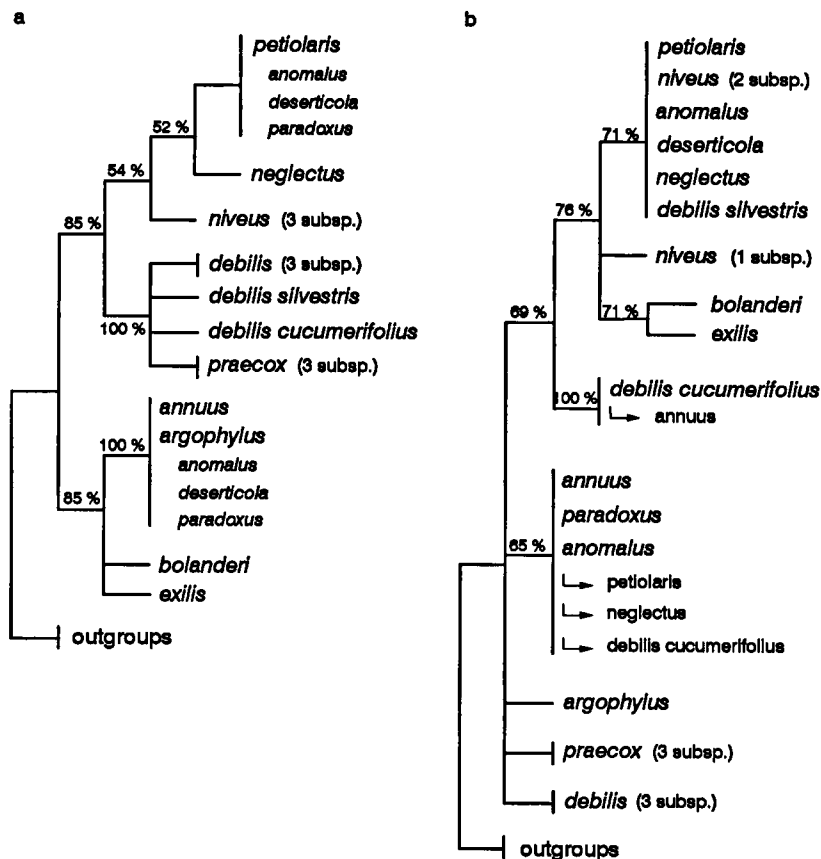
a

```
                                          │ petiolaris
                                          │   anomalus
                                          │   deserticola
                            52 %          │   paradoxus
                   54 %     ┌─────────────┤
                   ┌────────┤             └─ neglectus
           85 %    │        │
           ┌───────┤        └──── niveus (3 subsp.)
           │       │
           │       │        ┌─┤ debilis (3 subsp.)
           │       │        ├── debilis silvestris
           │       └────────┤
           │        100 %   ├── debilis cucumerifolius
           │                └─┤ praecox (3 subsp.)
           │
    ┌──────┤                 │ annuus
    │      │                 │ argophylus
    │      │        100 %    │ anomalus
    │      │       ┌─────────┤ deserticola
    │      │  85 % │         │ paradoxus
    │      └───────┤
    │              ├─── bolanderi
    │              └─── exilis
    │
    └─┤ outgroups
```

b

```
                                      │ petiolaris
                                      │ niveus (2 subsp.)
                                      │ anomalus
                            71 %      │ deserticola
                            ┌─────────┤ neglectus
                   76 %     │         │ debilis silvestris
                   ┌────────┤
                   │        └──── niveus (1 subsp.)
           69 %    │
           ┌───────┤                  71 %  ┌── bolanderi
           │       │                  ┌─────┤
           │       │                  └───── exilis
           │       │
           │       │  100 %│ debilis cucumerifolius
           │       └───────┤
           │               └── annuus
           │
           │              │ annuus
           │              │ paradoxus
           │        65 %  │ anomalus
           │       ┌──────┤ └─ petiolaris
           │       │      │ └─ neglectus
    ┌──────┤       │      │ └─ debilis cucumerifolius
    │      │       │
    │      └───────┤
    │              ├─── argophylus
    │              │
    │              ├─┤ praecox (3 subsp.)
    │              │
    │              └─┤ debilis (3 subsp.)
    │
    └─┤ outgroups
```

Fig. 2. Consensus trees based on nDNA (a) and cpDNA (b) variation in the genus *Helianthus* (adapted from Rieseberg 1991; Rieseberg *et al.* 1991). Percentages indicate the fraction of trees showing the specific branch. Arrows indicate introgression of the particular cpDNA type.

Combined approach

A combination of phenetic and phylogenetic studies can also be useful in unravelling relationships in crop–weed complexes. Two examples will be highlighted. A dendrogram based on isozyme differences and a phylogram of cpDNA data of *Sorghum bicolor* will be compared (Aldrich & Doebley 1992). In this species three subspecies were recognized: *S. bicolor* ssp. *bicolor* (domesticated sorghum), *S. bicolor* ssp. *arundinaceum* (wild relative) and *S. bicolor* ssp. *drummondii* (intermediate). All domesticated races in the study of Aldrich & Doebley (1992) were located in one cluster, while several of these cultivars show a wild type cpDNA (Fig. 3). Several wild populations possess a cpDNA of the domesticated *S. bicolor* ssp. *bicolor*. Sorghum is treated as the model for crop–weed complexes (Harlan 1992). Disruptive selection between domesticated and wild representatives is assumed to clarify the morphological differences (De Wet 1978) and genetic integrity (Aldrich & Doebley 1992) of the subspecies, but intermediate 'shattercanes' which mimic the crop except for their free-shattering rachis do exist (Harlan 1992). Bidirectional introgression can also be concluded from the comparison of the isozyme-based dendrogram (Fig. 4a) and cpDNA based phylogram (Fig. 4b) of *Zea* (Doebley 1990a,b). The two most common types of cpDNA in *Z. mays* ssp. *mays*
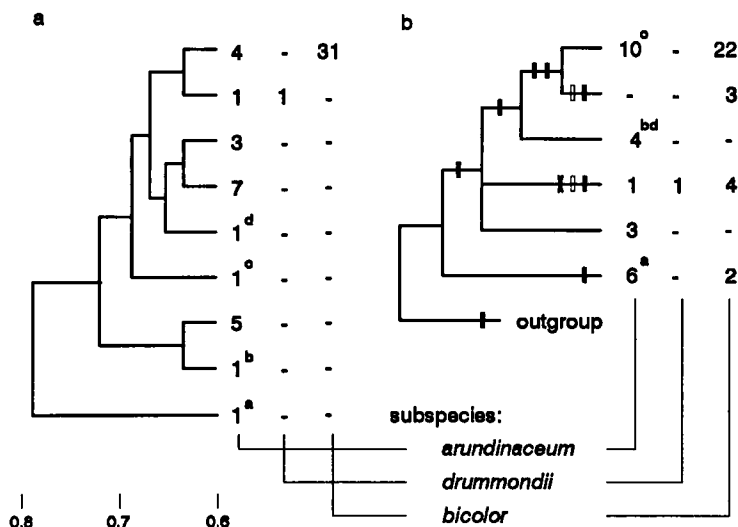
Fig. 3. Dendrogram based on isozyme variation (a) and most parsimonious tree of cpDNA variation (b) of three subspecies of *Sorghum bicolor* (adapted from Aldrich & Doebley 1992). Numbers show the number of accessions for each subspecies at each branch. Indices indicate the same accession in both trees. Solid bars: apomorphisms, open bars: parallelisms, cross: reversal.

were also found in representatives of the other subspecies of *Z. mays* (annual, weedy teosintes). On the other hand, some races of maize possess the cpDNA type of other subspecies (Fig. 4b). Notwithstanding these findings, the nuclear genetic background revealed by isozyme variation does not reflect these differences (Fig. 4a), which indicates introgression events.

The case of *Allium cepa* (onion; section *Cepa*) is worth mentioning because introgression between distantly related species has been found, although onion is not considered part of a crop–weed complex. Phylograms based on nDNA, 'supranuclear' (i.e. encoded by nuclear genes) and cpDNA variation have been compared with each other and with phenetic analyses such as PCA of morphological variation and cluster analysis of crossability results (Van Raamsdonk & De Vries 1992; Van Raamsdonk *et al.* 1992; Havey 1992; Van Raamsdonk & Sandbrink 1995). The crossability dendrogram and the cpDNA phylogram appeared to be identical. The species *A. roylei* (section *Rhizirideum*) takes a position in the cpDNA phylogram closer to *A. cepa* and its progenitor *A. vavilovii* than in the nDNA phylogram, which is assumed to be caused by introgression.

It is important to realize in this combined approach that a dendrogram (phenetic analysis) does not include an outgroup or, in other words, a dendrogram is not rooted. Therefore, no direct conclusion about incongruency can be drawn from the different positions of the *Sorghum* populations indicated in Fig. 3 by means of the indices [a], [b], [c] and [d]. Similarly, *Zea mays* ssp. *huehuetenangensis* should not be considered outgroup in the dendrogram of Fig. 4a. Further analysis has to be carried out in order to reveal the reason of the presumed inconsistencies between dendrograms and phylogenetic trees.

CROP EXAMPLES

Pickersgill (1981) listed crops and their weedy and wild relatives of the genera *Beta*, *Capsicum*, *Chenopodium*, *Daucus*, *Hordeum*, *Raphanus*, *Sorghum* and *Zea* as examples of
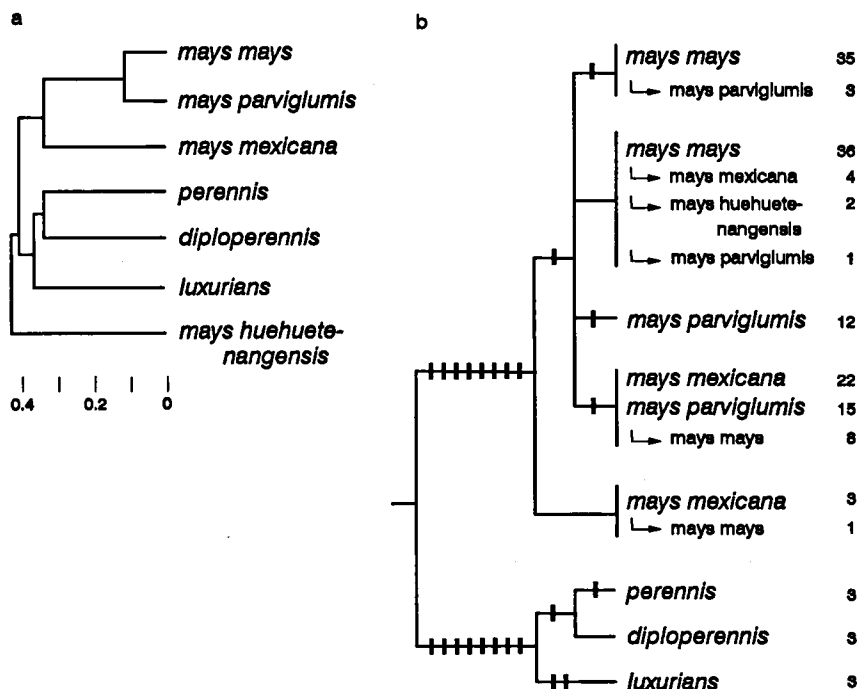
Fig. 4. Dendrogram based on isozyme variation (a) and most parsimonious tree of cpDNA variation (b) of species of the genus *Zea* (adapted from Doebley 1990). Arrows indicate introgression of the particular cpDNA type. Numbers show the number of accessions at each branch. Solid bars: apomorphisms.

crop–weed complexes. Most crops of these examples appeared to be diploids. Van Raamsdonk (1995b) added *Avena* and *Saccharum* as polyploid examples. The crops belonging to *Saccharum* consist of a variety of euploid and aneuploid chromosome numbers, while introgression between domesticated and wild races has been documented. In the following paragraphs we will discuss cases belonging to the groups of legumes, ornamentals and woody plants, which are not all clearly recognized as examples of crop–weed complexes, but which show various levels of gene flow.

Legumes

Most legumes are self-pollinating and weedy intermediates between crop and wild representatives were generally not found (Van Raamsdonk 1995b). Exceptions are the crops belonging to the genus *Phaseolus* (Van der Maesen & Somaatmadja 1989; Gepts 1993) and *Medicago* (Small 1984), which can be outbreeders to a large extent.

In the genus *Phaseolus*, the species *P. vulgaris* (common bean), *P. coccineus* (runner bean) and *P. acutifolius* (tepary bean) are closely related, while *P. lunatus* (Lima bean) is more distantly related (Evans 1976). After cluster analysis of cpDNA variation the species *P. vulgaris*, *P. polyanthus* and *P. costaricensis* appeared to form one main cluster and two subspecies of *P. coccineus* another main cluster. *P. lunatus* and *P. glabellus* were each placed in a cluster at a greater distance (Schmit *et al.* 1993). The data of Schmit *et al.* (1993) were analysed with a phylogenetic method by the present authors (DOLLO parsimony, heuristic search using PAUP, Swofford 1991; Fig. 5) in order to allow more precise comments about ancestry. Two of four escaped *P. polyanthus* populations were
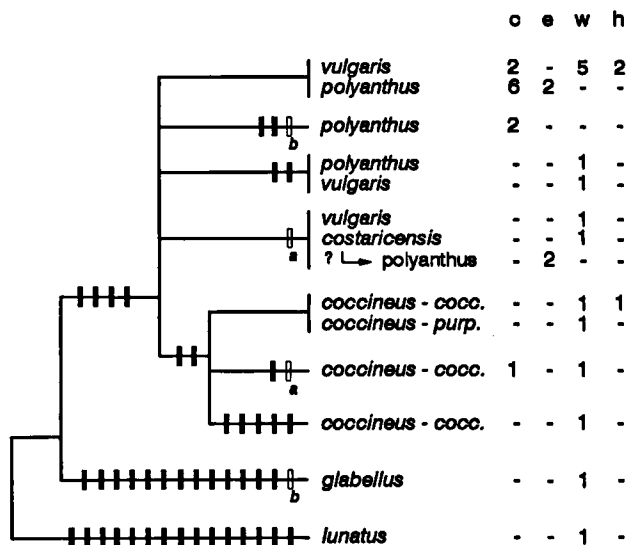
© 1996 Royal Botanical Society of The Netherlands, *Acta Bot. Neerl.* **45**, 135–155

	o	e	w	h
vulgaris	2	-	5	2
polyanthus	6	2	-	-
polyanthus	2	-	-	-
polyanthus	-	-	1	-
vulgaris	-	-	1	-
vulgaris	-	-	1	-
costaricensis	-	-	1	-
? polyanthus	-	2	-	-
coccineus - cocc.	-	-	1	1
coccineus - purp.	-	-	1	-
coccineus - cocc.	1	-	1	-
coccineus - cocc.	-	-	1	-
glabellus	-	-	1	-
lunatus	-	-	1	-

Fig. 5. Most parsimonious tree of cpDNA variation of domesticated (c), escaped (e) and wild (w) accessions and hybrids (h; indicated by the name of the mother) of species of *Phaseolus* (data taken from Schmit *et al.* 1993). Numbers show the number of accessions for each species at each branch. Indices indicate homology of apomorphisms. Solid bars: apomorphisms.

placed in the group with most cultivated accessions of the same species; the other two escaped populations were placed in another group with two wild populations, one each of *P. vulgaris* and of *P. costaricensis* (Fig. 5). It is premature to draw a final conclusion as to whether any introgression from another species to the escaped populations has taken place, since the specific status of *P. polyanthus* is in discussion. Wild accessions of *P. polyanthus* were recently collected. This species has been originally described as *P. coccineus* ssp. *polyanthus*, but Smartt (1990) recognized its close resemblance to *P. vulgaris*. *P. polyanthus* remained at the specific level after rDNA analysis (Jacob *et al.* 1995). The three species *P. vulgaris*, *P. polyanthus* and *P. coccineus* are interfertile to a certain extent. The interspecific hybrid *P. vulgaris* × *P. coccineus* was achieved by Mendel (quoted in Smartt 1990) but not found in nature. Natural hybrids between *P. polyanthus* on one hand and either *P. vulgaris* or *P. coccineus* on the other hand were reported (Debouck 1992). Further analysis of cpDNA variation of *P. coccineus* s.l. and *P. vulgaris* (Llaca *et al.* 1994) revealed substantial polymorphisms within *P. coccineus*. The position of *P. glabellus* distant from *P. coccineus* is confirmed (Llaca *et al.* 1994; Jacob *et al.* 1995). The cpDNA type of *P. polyanthus* (Llaca *et al.* 1994: *P. coccineus* ssp. *darwinianus*) appeared to be more similar to that of *P. vulgaris* than to that of *P. coccineus* ssp. *coccineus*. Llaca *et al.* (1994) reported an incongruency between phylogenies based on nDNA and cpDNA regarding the position of *P. polyanthus*. Their results concerning cpDNA variation could support the assumption of a hybrid origin of *P. polyanthus* with *P. vulgaris* as maternal parent followed by backcrosses to *P. coccineus* ssp. *coccineus* to restore the *P. coccineus* nuclear genetic background of *P. polyanthus* (Llaca *et al.* 1994). Postulation of introgressive hybridization and cpDNA capture may increase the urge of further study of gene flow in *Phaseolus*.

Medicago sativa ssp. *sativa* (alfalfa) is a tetraploid domesticated representative of the *M. sativa* polyploid complex. It is assumed to be an autoploid derivative of ssp. *coerulea*
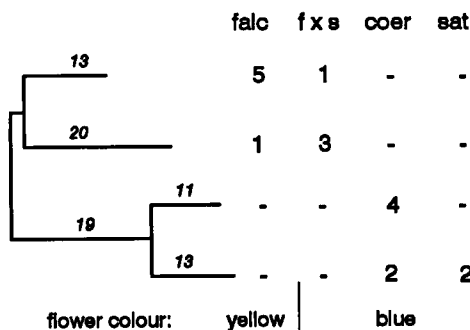
```
                    falc   f x s   coer   sat

        13                  5      1       -      -

        20                  1      3       -      -

                 11
                            -      -       4      -
        19
                 13
                            -      -       2      2

flower colour:        yellow  |   blue
```

Fig. 6. Most parsimonious tree of nDNA variation of diploid forms of the *Medicago sativa* complex (summarized from data of Brummer *et al.* 1991). Numbers at branches show the amount of RFLPs, numbers in columns show the number of accessions for each subspecies at each branch. Abbreviations: falc: ssp. *falcata*, f × s: *falcata*-like plants with blue coloured flowers, coer: ssp. *coerulea*, sat: artificially induced diploids of tetraploid ssp. *sativa*.

(wild diploid; Langer 1995) for the tetrasomic inheritance of a range of characters (Bolton 1962) and for its production of quadrivalents in meiosis (Cauderon 1986; McCoy & Bingham 1991: 0.6–1.7^{IV}). This ancestry is confirmed after molecular analysis (Fig. 6; Brummer *et al.* 1991). Both subspecies have blue flowers and coiled pods. *M. sativa* ssp. *falcata* (di- and tetraploid) with yellow flowers and straight or sickle-shaped pods consists of wild and domesticated forms. Hybrid swarms and backcross hybrids occur in nature between domesticated ssp. *sativa* and wild ssp. *falcata* at both ploidy levels in a variety of intermediate forms (Small 1984). These forms, including *M.* × *varia* can show reduced fertility (Stace 1975), although identical pollen fertility and seed set has been found in *M. sativa* ssp. *falcata* and in *M.* × *varia* (Ohlendorf 1960). Reciprocal spontaneous introgression, i.e. from wild yellow-flowering to domesticated purple-flowering populations, was not traced in Turkey after checking flower colour in numerous occasions (Small 1984). Notwithstanding these observations, it is assumed that the winter hardiness of ssp. *sativa* was introduced from wild ssp. *falcata* in Germany and France during the 16th century (Lesins 1976; Small 1984). Preference of insect pollinators and a partially effective self-incompatibility system (Barnes 1980) may cause the varying nature of these data. It can be concluded that the wild and domesticated forms of the *M. sativa* complex are interfertile to a certain extent, but that the levels of actual gene flow are still to be determined. Variation at the molecular level may be high. Considerable nDNA variation was traced in three tetraploid accessions and one artificially induced diploid accession of ssp. *sativa* (Brummer *et al.* 1991). Johnson & Palmer (1989) found cpDNA heterogeneity within individuals of *M. sativa* and *M. scutellata*. A predominant paternal inheritance of plastids was found (Schumann & Hancock 1989). Although flower colour indicated some introgression in otherwise *falcata*-like accessions, this introgression was not supported by molecular data (Fig. 6). We were not able to retrieve a publication on molecular evidence of introgression.

Whereas artificial hybridization in *Cajanus* (pigeonpea and its wild relatives) is possible in many combinations, the existence of crop–weed complexes has not been established. However, natural hybrids do exist (Van der Maesen 1986: 33). Seeds collected from *C. cajanifolius* (the purported ancestor of pigeonpea *C. cajan*) and *C. sericeus* grew into obvious hybrids, the paternal species being unknown as several species flowered at the same time in a germplasm collection planting. From the islands
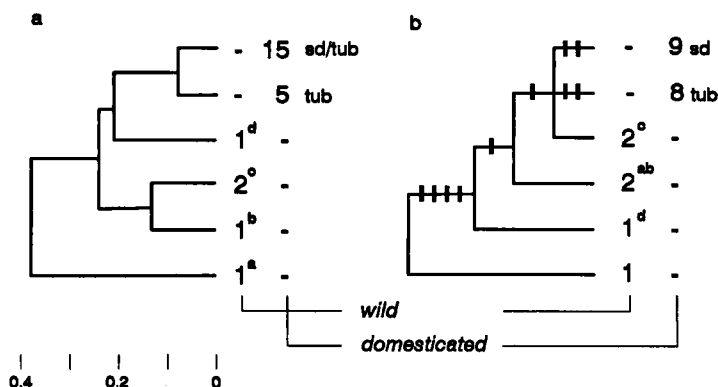
Fig. 7. Dendrogram based on isozyme variation (a) and most parsimonious tree of cpDNA variation (b) of wild and domesticated races of *Sphenostylis stenocarpa* (adapted from Potter & Doyle 1992). Numbers show the number of accessions for each subspecies at each branch. Indices indicate the same accession in both trees. Solid bars: apomorphisms, sd: seed producing races, tub: tuber producing races.

of Réunion and Guam plants were collected, most probably resulting from *C. cajan* × *C. scarabaeoides* natural crosses. The latter is the only wild species present there. *C. scarabaeoides* shows a wide distribution and artificial crosses with pigeonpea produced similar hybrids (Van der Maesen 1986).

Of *Cicer arietinum* (chickpea) several annual wild relatives occur in SE Turkey where the crop is widely grown. The presumed immediate ancestor *C. reticulatum* and the related *C. echinospermum* grow in the vicinity of the crop. Meiotic studies revealed that normal bivalent formation exists in hybrids between *C. arietinum* and *C. reticulatum* (8^{II}), while in hybrids between each of these two species and *C. echinospermum* one quadrivalent ($6^{II}+1^{IV}$) has been found (Ladizinsky & Adler 1976). So far no introgression has been identified in nature, but is apparently possible.

The example of *Sphenostylis stenocarpa* (yam bean) is chosen because both a dendrogram of isozyme differences as well as a phylogram of cpDNA variation of largely the same accessions is available (Potter & Doyle 1992). Yam bean is grown for two purposes, i.e. for its edible tubers (Central Africa) and its seeds (West Africa). Seed- as well as tuber-producing races are located in the same cluster after isozyme analysis (Fig. 7a). These types of yam bean are well separated based on cpDNA type (Fig. 7b). It could be assumed from the different geographic areas where the two types were domesticated that two independent domestication events took place. This assumption is supported by the presented trees (Potter & Doyle 1992). It is also clear from the presented analyses that yam bean does not belong to a crop–weed complex.

Ornamentals and woody plants

A vast range of ornamentals, including cut flowers, flower bulbs and shrubs, is cultivated for their beautifully coloured and shaped flowers (Anderson 1952; Darlington 1973). The domestication of plants with this feature is in fact based on the situation that natural co-evolution has resulted in attractive floral parts and frequently visiting pollinators. Examples of economically important, insect pollinated ornamentals are *Rosa* (beetles), *Chrysanthemum* (beetles, wasps, flies), *Tulipa* (bees, flies), *Lilium* (butterflies), *Dianthus* (butterflies), *Aster* (bees, butterflies), *Alstroemeria* (butterflies), *Anthurium* (flies), *Narcissus* (either bumble-bees or butterflies), *Dracaena* (hawkmoths)

and *Begonia* section *Tetraphila* (bees; Meeuse 1961; Proctor & Yeo 1973; Bos 1984; Arends 1992; De Vries *et al.* 1992). Cross-pollination is promoted by several mechanisms, such as monoecious flowers (*Begonia*) and proterandry (*Dianthus, Gladiolus*). In a number of ornamentals successful reproductive isolation is apparently achieved by external, pre-zygotic barriers since wild occurring hybrids are very rarely found, although these crop plants are crossable with wild relatives under artificial circumstances (Rees 1992). Therefore, for instance, *Lilium* section *Sinomartagon* (Van Creij *et al.* 1990; Van Holthoon & Posthuma 1995) and *Tulipa* (Van Eijk *et al.* 1991; Van Raamsdonk *et al.* 1995a) cannot be indicated as crop–weed complexes, contrary to ornamentals such as *Narcissus*, where natural hybridization is frequently found (De Vries *et al.* 1992; Rees 1992). Besides these bulbous crops, some remarks will be made on woody plants.

The domesticated apple belongs to the species *Malus domestica*. In a broader species concept *M. domestica* is part of the collective species *M. pumila* together with *M. sylvestris* (wild crab apple) and *M. pumila* s.s., including var. *paradisiaca* (paradise apple). These classifications are artificial to a certain extent, since the species of *Malus* are predominantly self-incompatible and most species can be readily hybridized. A range of species has contributed to the variation in forms either used for fruit production or as ornamental (compilospecies; Watkins 1976; Way *et al.* 1991). Prehistoric findings of presumed wild apples from the fourth and fifth millennium BC contained fruits of 2–2·5 cm in carbonized form, which means a fresh fruit size of approximately 2·6–3·3 cm (C. C. Bakels, Leiden, personal communication). Naturalized stands of apple along the inner border of the dunes in the Netherlands are frequent. Plants of these stands produce fruits of 4–5 cm in size. This can be due to introgression of alleles responsible for allometric growth from domesticated to already naturalized populations. However, many of these stands will have originated from apple cores thrown away more recently (Visser 1989). Differences in fruit size may also be caused by the fact that the modern cultivars are clearly genetically different from wild or primitive apple trees, and by changes in nutrition and water supply during several millennia (J. Janse, personal communication).

The genus *Vitis* (grape) consists of more than 60 species, which can presumably be better indicated as ecospecies, since hardly any hybridization barriers exist in the genus. Domestication started with the utilization of *V. vinifera* (Alleweldt *et al.* 1991; Olmo 1995). A shift from allogamy to autogamy was achieved due to breeding efforts. Wild species and some primitive cultivars are dioecious and, hence, cross-pollinated by bees and wind, while more modern cultivars are hermaphrodite and self-pollinating. Because of intensive hybridization the entire genus can be designated as one complex. Although some modern cultivars contain genetic information introduced from other species, quality improvement is generally obtained only after backcrossing to *V. vinifera* (Olmo 1995). In the genus *Philadelphus*, of which representatives are used as ornamentals, interspecific hybridization played an important role in the production of new cultivars. The collected cultivars and artificial hybrids cannot be indicated as compilospecies in the strict sense, since the hybrid forms were until recently arranged in nothotaxa rather than in a collective 'species' (Hoffman 1996). There are several naturally occurring species of presumed hybrid origin (e.g. *P. floridus, P. laxiflorus, P. maculatus, P. insignis*) and a hybrid origin cannot be ruled out for species which are geographically and morphologically intermediate between two other, related species (e.g. *P. confusus, P. delavayi*; Hu 1954–1956). The occurrence of natural hybrids in the mentioned genera

indicates that introgression can play a role in the relationship between the domesticated representatives and their wild relatives, as is the case in complete crop–weed complexes. However, it is to be expected that weedy populations of woody crops can establish only with great difficulty because of the long juvenile phase.

As pointed out for compilospecies (Harlan & De Wet 1963), many present-day forms of ornamentals consist of genetic information obtained from a range of relatives due to frequent hybridization and backcrossing (Rees 1992). Ancestral species cannot easily be indicated, if at all, as is possible in most agricultural crops and vegetables (Van Raamsdonk 1995b). The domestication scenario of compilospecies is additional to the four crop domestication models already described (Van Raamsdonk 1995b). It can be referred to as the *Tulip model*, since tulip is one of the most important cut flowers and bulbous plants on a world scale. Ornamentals or fruit crops of which the domestication history can be described according to the *Tulip model* are *Rosa, Chrysanthemum, Tulipa, Lilium, Alstroemeria, Aster, Kalanchoe* and *Malus* (Darlington 1973; Saakov 1976; Kroon *et al.* 1989; Van Creij *et al.* 1990; Van Eijk *et al.* 1991; De Vries *et al.* 1992; Hetterscheid & Van den Berg, 1996). In some ornamentals polyploidy plays a certain role, whether naturally occurring (*Rosa, Tulipa, Lilium, Malus*) or artificially induced (e.g. *Lilium*, Van Tuyl 1990; *Malus*, Watkins 1976). In *Chrysanthemum* the entire complex is of polyploid origin, which is in itself an aspect of the so-called *Cotton model* (cf. *Avena*; Van Raamsdonk 1995b). Another aspect of crops which are domesticated as described by the *Tulip model* is the large variation. In *Tulipa*, for example, the variation found in flavonoids (Van Raamsdonk 1993b) and in morphology (Van Raamsdonk & De Vries 1996) exceeds that of the wild relatives. This situation is in contrast to that of a range of other crops (Ladizinsky 1985; Doebley 1989; Van Raamsdonk *et al.* 1989). Reduced diversity is reported in some of the previously discussed crops such as *Lactuca* (Kesseli & Michelmore 1986), *Capsicum* (McLeod *et al.* 1983), *Zea mays* (Smith *et al.* 1985), *Phaseolus vulgaris* (Gepts 1993) and *Medicago sativa* (Quiros 1983).

TAXONOMY OF DOMESTICATED PLANTS

The classification of domesticated plants is currently in a process of reconsideration (Hetterscheid & Brandenburg 1995; Hetterscheid *et al.* 1996). The term 'domesticated' is used throughout our paper instead of 'cultivated', since 'cultivated' points to all plants which are grown intentionally in man-made habitats, bred for certain purposes ('domesticated') or not. Domesticated plants are altered genetically in comparison to their wild relatives, although relationships by means of various levels of gene flow exist between domesticated plants and wild relatives, as is illustrated by the forementioned examples of crop–weed complexes. The intrinsic relationship between domesticated and wild plants is also illustrated by the ongoing discussion on biosafety of transgenic plants (Raybould & Gray 1993; Williamson 1993; Regal 1994; Gliddon 1994; Fredshavn *et al.* 1995; Van Raamsdonk *et al.* 1995b). In this discussion focus is primarily on crops which belong to crop–weed complexes or have at least some level of introgression from the crop to wild relatives (Van Raamsdonk 1995a). A containment of domesticated plants as a result of strict separation between domesticated and wild plants would, if present, solve the biosafety problems of transgenic plants for the greater part. In addition, domesticated plants escaping from cultivation or running wild, the commercial produc- tion and trade of wild plants, and the cultivation of plants that are noxious weeds in
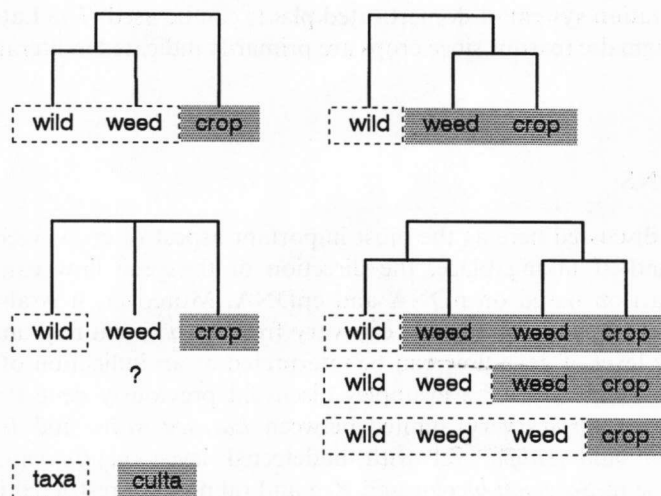
Fig. 8. Several models for the span of application of the taxon concept (botanical classification) and the culton concept (classification of domesticated plants). Length of forks indicates relative resemblance.

other parts of the world, add to the problem of the twilight zone between wild and domesticated plants (Van Raamsdonk 1986, 1990; Harlan 1992; Gregorius & Steiner 1993; Bartsch et al. 1993).

In all cases of crop–weed complexes it is extremely difficult to draw the line between the class of individuals for which the system of botanical nomenclature and classification should be applied and the class of individuals subjected to a system for classification of cultivated plants. The borderline is subjected to change due to the occurrence of the mentioned twilight zone (e.g. 'dispersal' of plants from one system to the other, intermediacy, etc.), to the span of the species concept used, and to conflicting opinions of botanists. Some decisions on taxonomic borderlines are illustrated in Fig. 8.

It can be important for the study of crop–weed complexes to assess the level in botanical classification where the three parts of a crop–weed complex are to be considered one unit each. Crop and wild relative(s) can be assigned to at the level of the genus (e.g. Narcissus 'Carlton' and N. pseudonarcissus, N. poeticus a.o., respectively), the species (e.g. Cicer arietinum 'Vilmorin' and C. reticulatum, respectively), the subspecies (e.g. Beta vulgaris ssp. vulgaris 'Evita' and B. vulgaris ssp. maritima, respectively), the variety (e.g. Capsicum annuum var. annuum 'Bell' and C. annuum var. aviculare, respectively) or even another level. From the viewpoint of botanical classification this level is largely influenced by the species concept used. The adoption of a narrow species concept, hence a high number of species, results in cases where cultivars cannot be assigned to a species but only to a genus, as advocated by Hetterscheid & Brandenburg (1995). A narrow species concept, however, will also result in a higher frequency of 'interspecific' hybridization and introgression (Van Raamsdonk 1995a), which will greatly increase the problem of defining the borderline between wild and domesticated plants. In our present paper the domesticated or cultigenic parts of the crop–weed complexes are indicated by Latin names. The Latin name is used for the crop as entity, in order to indicate its position in the botanical classification. At infracultigenic levels a

practical classification system of domesticated plants can be used. The Latin names are also used for pragmatic reasons since crops are primarily indicated in literature by Latin suffixes.

CONCLUSIONS

Introgression is discussed here as the most important aspect of crop–weed complexes. The existence and, if taking place, the direction of the gene flow can be inferred from tree-comparison based on nDNA and cpDNA. Moreover, it is also important to know the level of gene flow, which can vary from zero to entirely unrestricted. A zero or very low level of gene flow can be interpreted as an indication of the absence of a crop–weed complex. In the examples discussed previously gene flow is absent in *Sphenostylis stenocarpa*, (very) limited between *Lactuca sativa* and *L. serriola*, in *Phaseolus*, *Lilium* and *Tulipa*, yet with undetected levels in *Cajanus*, *Cicer* and *Medicago*, notable in *Sorghum bicolor* and *Zea* and (almost) unrestricted in *Capsicum*, *Helianthus*, *Vitis* and *Narcissus*. For different reasons the examples of *Lactuca*, *Phaseolus*, *Medicago*, *Cajanus* and *Cicer* are or should be on the borderline of being considered as crop–weed complexes and further study is required. Studies on the relationship between distance and level of pollen flow have been carried out in a range of plants (Hamrick 1987; Ellstrand & Hoffman 1990; Klinger *et al.* 1991; Kohn & Casper 1992; Gregorius & Steiner 1993; Arias & Rieseberg 1994; reviewed in Van Raamsdonk 1995a). The necessary containment distances of seed production fields are smaller in inbreeders than in outbreeders. An interpopulation mating rate of more than 1% has been detected in the wind-pollinated grass species *Agrostis capillaris* at a distance of 8000 m. The level of pollen flow should be incorporated in studies of crop–weed complexes and results can cast new light on the structure of these complexes (Wilson 1990).

It has been made clear in population genetic studies that even a limited gene flow between populations can have a considerable effect on allele frequencies (Dobzhansky *et al.* 1977) but disruptive selection can eliminate this effect for the greater part, as illustrated by the *Sorghum* example.

SUMMARY

Crop–weed complexes consist of crops, modified for human requirements and adapted to man-made habitats, their wild ancestors and other close relatives, and intermediate weeds. A key aspect in these complexes is the possibility of gene flow between any two of the three mentioned elements. Several models of ancestry of crop and weed from their wild ancestor have been postulated. The structure of crop–weed complexes can be studied by using either phylogenetic or phenetic methods, or by using a combined approach. For all methods morphological, electrophoretic and molecular data can be used. These experimental approaches are discussed by means of examples from a range of genera, including *Lactuca*, *Capsicum*, *Helianthus*, *Sorghum*, *Zea* and *Allium*. Further crop examples of which the status as part of a crop–weed complex is not clear are taken from three groups of domesticated plants, i.e. pulses (Leguminosae), ornamentals and woody plants. The domestication scenario of many ornamentals, which consist of

genetic information obtained from a range of different relatives (compilospecies) is referred to as the *Tulip model*. Every level of gene flow can be found between crops and their weedy and wild relatives ranging from absolute reproductive isolation to unrestricted outcrossing.

ACKNOWLEDGEMENTS

REFERENCES

Aldrich, P.R. & Doebley, J. (1992): Restriction fragment variation in the nuclear and chloroplast genomes of cultivated and wild *Sorghum bicolor*. *Theor. Appl. Genet.* **85**: 293–302.

Alleweldt, G., Spiegel-Roy, P. & Reisch, B. (1991): Grapes (*Vitis*). In: Moore, J.N. & Ballington, J.R. (eds): *Genetic Resources of Temperate Fruit and Nut Crops*, pp. 289–327, International Society for Horticultural Science, Wageningen.

Anderson, E. (1952): *Plants, Man and Life*. Little, Brown and Company, Boston.

Arends, J.C. (1992): The biosystematics of *Begonia squamulosa* Hook. f. and affiliated species in section *Tetraphila a*, D.C. Thesis, Agricultural University Wageningen, *Wageningen Agricultural University papers, 91–6*, Wageningen.

Arias, D.M. & Rieseberg, L.H. (1994): Gene flow between cultivated and wild sunflowers. *Theor. Appl. Gen.* **89**: 655–660.

Barnes, D.K. (1980): Alfalfa. In: Fehr, W.R. & Hadley, H.H. (eds): *Hybridization of Crop Plants*, pp. 177–186, American Society of Agronomy and Crop Science Society of America, Madison.

Barrett, S.C.H. (1983): Crop mimicry in weeds. *Econ. Bot.* **37**: 255–282.

Bartsch, D., Sukopp, H. & Sukopp, U. (1993): Introduction of plants with special regard to cultigens running wild. In: Wöhrmann, K. & Tomiuk, J. (eds): *Transgenic Organisms, Risk Assessment of Deliberate Release*, pp. 135–151, Birkhäuser Verlag, Basel.

Baum, B.M. (1986): Computer methods in intraspecific taxonomy of wild and cultivated plants. In: Styles, B.T. (ed.), *Infraspecific Classification of Wild and Cultivated Plants*, pp. 239–254, Clarendon Press, Oxford.

Bolton, J.L. (1962): *Alfalfa. Botany, Cultivation and Utilization*. Leonard Hill Ltd, London; Interscience Publishers Inc., New York.

Bos, J.J. (1984): *Dracaena* in West Africa, Thesis, Agricultural University Wageningen, *Wageningen Agricultural University Papers, 84–1*, Wageningen.

Boudry, P., Mörchen, M., Saumitou-Laprade, P., Vernet, Ph. & Van Dijk, H. (1993): The origin and evolution of weed beets: consequences for the breeding and release of herbicide-resistant transgenic sugar beets. *Theor. Appl. Gen.* **87**: 471–478.

Brandenburg, W.A. (1981): Possible relationships between wild and cultivated carrots (*Daucus carota* L.) in the Netherlands. *Kulturpflanze* **29**: 369–375.

Brandenburg, W.A. & Wijnheimer, E.H.M. (1989): De invloed van cultuurpeen op wilde peen in een veldsituatie. In: de Gier, A.M. & van Raamsdonk, L.W.D. (eds), Risico-analyse van transgene planten in de praktijk, *Supplement Prophyta* **43**: 234–235.

Brummer, E.C., Kochert, G. & Bouton, J.H. (1991): RFLP variation in diploid and tetraploid alfalfa. *Theor. Appl. Gen.* **83**: 89–96.

Cauderon, Y. (1986): Cytogenetics in breeding programmes dealing with polyploidy, interspecific hybridization and introgression. In: *Genetic Manipulation in Plant Breeding*, pp. 83–104, Walter de Gruyter & Co., Berlin, New York.

D'Arcy, W.G. & Eshbaugh, W.H. (1974): New world peppers (*Capsicum*—Solanaceae) north of Colombia: a résumé. *Baileya* **19**: 93–105.

Darlington, C.D. (1973): *Chromosome Botany and the Origins of Cultivated Plants*. George Allen & Unwin Ltd, London.

Debouck, D.G. (1992): Views on variability in *Phaseolus* beans. *Ann. Rep. Bean Improv. Coop.* **35**: 9–10.

Debouck, D.G. & Smartt, J. (1995): Beans, *Phaseolus* spp. (Leguminosae-Papilionoideae). In: Smartt, J. & Simmonds, N.W. (eds), *Evolution of Crop Plants*, 2nd edn, pp. 287–294, Longman Scientific & Technical, Harlow.

De Jong, T. (1992): Plant invasions and ecological risks of genetically modified organisms. In: Weverling, J. & Hekstra, G.P. (eds), *Ecological Effects of Genetically Modified Organisms,* pp. 51–57, Netherlands Ecological Society, Arnhem.

Den Nijs, J.C.M. & Wardenaar, E.C.P. (1989): Engels raaigras (*Lolium perenne* L.): literatuuronderzoek. In: de Gier, A.M. & van Raamsdonk, L.W.D. (eds), Risico-analyse van transgene planten in de praktijk. *Supplement Prophyta* **43**: 239–240.

De Vries, F.T., Van der Meijden, R. & Brandenburg, W.A. (1992): Botanical files: a study of the real chances for spontaneous gene flow from cultivated plants to the wild flora of the Netherlands. *Gorteria* Suppl. **1**, Rijksherbarium/Hortus Botanicus, Leiden.

De Vries, I.M. & Van Raamsdonk, L.W.D. (1994): Numerical morphological analysis of lettuce cultivars and species (*Lactuca* sect. *Lactuca,* Asteraceae). *Pl. Syst. Evol.* **193**: 125–141.

De Wet, J.M.J. (1978): Systematics and evolution of *Sorghum* sect. *Sorghum* (Gramineae). *Am. J. Bot.* **65**: 477–484.

De Wet, J.M.J. (1981): Species concepts and systematics of domesticated cereals. *Die Kulturpflanze* **29**: 177–198.

Dobzhansky, Th., Ayala, F.J., Stebbins, G.L. & Valentine, J.W. (1977): *Evolution*. W.H. Freeman and Co., San Francisco.

Doebley, J. (1989): Isozymic evidence and the evolution of crop plants. In: Soltis, D.E. & Soltis, P.S. (eds), *Isozymes in Plant Biology*, pp. 165–191, Dioscorides, Portland.

Doebley, J. (1990a): Molecular evidence and the evolution of maize. *Econ. Bot.* **44** (Suppl.): 6–27.

Doebley, J. (1990b): Molecular evidence for gene flow among *Zea* species. *BioScience* **40**: 443–448.

Ellstrand, N.C. & Hoffman, C.A. (1990): Hybridization as an avenue of escape for engineered genes. Strategies for risk reduction. *Bioscience* **40**: 438–442.

Fredshavn, J.R., Poulsen, G.S., Huybrechts, I. & Rüdelsheim, P. (1995): Competitiveness of transgenic oilseed rape. *Transgenic Res.* **4**: 142–148.

Frietema-de Vries, F.T., Meijden, R. Van der & Brandenburg, W.A. (1994): Botanical files on lettuce (*Lactuca sativa*): on the change for gene flow between wild and cultivated lettuce (*Lactuca sativa* L. including *L. serriola* L., Compositae) and the generalized implications for risk-assessments on genetically modified plants. *Gorteria*, Suppl. **2**, Rijksherbarium/Hortus Botanicus, Leiden.

Gepts, P. (1993): The use of molecular and biochemical markers in crop evolution studies. In: Hecht, M.K., MacIntyre, R.J. & Clegg, M.T. (eds): *Evolutionary Biology*, vol. 27, pp. 51–94, Plenum Press, New York.

Gliddon, C. (1994): The impact of hybrids between genetically modified crop plants and their related species: biological models and theoretical perspectives. *Mol. Ecol.* **3**: 41–44.

Gregorius, H.-R. & Steiner, W. (1993): Gene transfer in plants as a potential agent of introgression. In: Wöhrmann, K. & Tomiuk, J. (eds): *Transgenic Organisms, Risk Assessment of Deliberate Release*, pp. 83–107, Birkhäuser Verlag, Basel.

Hamrick, J.L. (1987): Gene flow and distribution of genetic variation in plant populations. In: Urbanska, K.M. (ed.), *Differentiation Patterns in Higher Plants*, pp. 53–67, Academic Press, London.

Hancock, J.F. (1992): *Plant Evolution and the Origin of Crop Species*. Prentice Hall, New Jersey.

Harlan, J.R. (1992): *Crops and Man*, 2nd edn. American Society of Agronomy, Crop Science Society of America, Madison, WI.

Harlan, J.R. & De Wet, J.M.J. (1963): The compilospecies concept. *Evolution* **17**: 497–501.

Havey, M.J. (1992): Restriction enzyme analysis of the chloroplast and nuclear 45s ribosomal DNA of *Allium* sections *Cepa* and *Phyllodolon* (Alliaceae). *Plant Syst. Evol.* **183**: 17–31.

Heiser, C.B. Jr (1965): Sunflowers, weeds and cultivated plants. In: Baker, H.G. & Stebbins, G.L. (eds), *The Genetics of Colonizing Species*, pp. 375–386, Academic Press, New York.

Heiser, C.B. Jr (1969): The North American sunflowers (*Helianthus*). *Mem. Torrey Bot. Club* **22**: 1–218.

Hetterscheid, W.L.A. & Brandenburg, W.A. (1995): Culton versus taxon: conceptual issues in cultivated plant systematics. *Taxon* **44**: 161–175.

Hetterscheid, W.L.A. & Van den Berg, R.G. (1996): Cultonomy of *Aster* L. *Acta Bot. Neerl.* **45**: 173–182.

Hetterscheid, W.L.A., Van den Berg, R.G. & Brandenburg, W.A. (1996). An annotated history of the principles of cultivated plant classification. *Acta Bot. Neerl.* **45**: 123–134.

Hoffman, M. (1996): Cultivar classification of *Philadelphus* L. (Hydrangeaceae). *Acta Bot. Neerl.* **45**: 199–210.

Hu, S.Y. (1954–1956): A monograph of the genus *Philadelphus. J. Arnold Arbor.* **35**: 275–333; **36**: 52–109, 325–368; **37**: 15–90.

IBPGR (1983): Genetic resources of *Capsicum*. International Board of Plant Genetic Resources, Rome.

Jacob, M., Zink, D. & Nagl, W. (1995): RFLPs of the rRNA genes in the genus *Phaseolus*. *Gen. Res. Crop Evol.* **42**: 97–106.

Johnson, L.B. & Palmer, J.D. (1989): Heteroplasmy of chloroplasts DNA in *Medicago. Plant Mol. Biol.* **12**: 3–11.

Kesseli, R. & Michelmore, R.W. (1986): Genetic variation and phylogenies detected from isozyme markers in species of *Lactuca*. *J. Hered.* **77**: 324–331.

Kesseli, R., Ochoa, O. & Michelmore, R.W. (1991): Variation at RFLP loci in *Lactuca* spp. and origin of cultivated lettuce (*L. sativa*). *Genome* **34**: 430–436.

Klinger, T., Elam, D.R. & Ellstrand, N.C. (1991): Radish as a model system for the study of engineered gene escape rates via crop–weed mating. *Cons. Biol.* **5**: 531–535.

Kohn, J.R. & Casper, B.B. (1992): Pollen-mediated gene flow in *Cucurbita foetidissima* (Cucurbitaceae). *Am. J. Bot.* **79**: 57–62.

Koopman, W.J.M. & De Jong, J.H. (1996): A numerical analysis of karyotypes and DNA amounts in lettuce cultivations and species (*Lactuca* subsect. *Lactuca*, Compositae). *Acta Bot. Neerl.* **45**: 211–222.

Kroon, G.H., De Jong, J. & Van Raamsdonk, L.W.D. (1989): Evaluation of the genus *Kalanchoe* for breeding of new cutflowers and potplants. *Acta Horticulturae* **252**: 111–116.

Ladizinsky, G. (1979): Seed dispersal in relation to the domestication of Middle East legumes. *Econ. Bot.* **33**: 284–289.

Ladizinsky, G. (1985): Founder effect in crop–plant evolution. *Econ. Bot.* **39**: 191–199.

Ladizinsky, G. & Adler, A. (1976): The origin of the chickpea *Cicer arietinum* L. *Euphytica* **25**: 211–217.

Langer, R.H.M. (1995): Alfalfa, lucerne, *Medicago sativa* (Leguminosae-Papilionoideae). In: Smartt, J. & Simmonds, N.W. (eds), *Evolution of Crop Plants*, 2nd edn, pp. 283–286, Longman Scientific & Technical, Harlow.

Lesins, K. (1976): Alfalfa, lucerne, *Medicago sativa*. In: Simmonds, N.W. (ed.), *Evolution of Crop Plants*, pp. 165–168, Longman, London, New York.

Llaca, V., Delgado Salinas, A. & Gepts, P. (1994): Chloroplast DNA as an evolutionary marker in the *Phaseolus vulgaris* complex. *Theor. Appl. Genet.* **88**: 646–652.

Loos, B.P. (1993): Morphological variation in *Lolium* (Poaceae) as a measure of species relationships. *Pl. Syst. Evol.* **188**: 87–99.

McCoy, T.J. & Bingham, E.T. (1991): Alfalfa cytogenetics. In: Tsuchiya, T. & Gupta, P.K. (eds), *Chromosome Engineering in Plants: Genetics, Breeding, Evolution, Part B*, pp. 399–418, Elsevier, Amsterdam.

McLeod, M.J., Guttman, S.I. & Eshbaugh, W.H. (1982): Early evolution of chili peppers (*Capsicum*). *Econ. Bot.* **36**: 361–368.

McLeod, M.J., Guttman, S.I., Eshbaugh, W.H. & Rayle, R.E. (1983): An electrophoretic study of evolution in *Capsicum* (Solanaceae). *Evolution* **37**: 562–574.

Meeuse, B.J.D. (1961): *The Story of Pollination*. The Ronald Press Company, New York.

Michelmore, R.W., Kesseli, R.V. & Ryder, E.J. (1994): Genetic mapping in lettuce. In: Phillips, R.L. & Vasil, I.K. (eds), *DNA-based Markers in Plants*, pp. 223–239, Kluwer Academic Publishers, Dordrecht.

Ohlendorf, H. (1960): Untersuchungen über den Samenansatz bei *Medicago falcata* und Artbastarden (*Med. falcata* × *Med. sativa*), thesis, Technischen Universität, Berlin.

Olmo, H.P. (1995): Grapes, *Vitis*, *Muscadinia* (Vitaceae). In: Smartt, J. & Simmonds, N.W. (eds), *Evolution of Crop Plants*, 2nd edn, pp. 485–490, Longman Scientific & Technical, Harlow.

Pickersgill, B. (1981): Biosystematics of crop–weed complexes. *Die Kulturpflanze* **29**: 377–388.

Pickersgill, B. (1991): Cytogenetics and evolution of *Capsicum* L. In: Tsuchiya, T. & Gupta, P.K. (eds), *Chromosome Engineering in Plants: Genetics, Breeding, Evolution, Part B*, pp. 139–160, Elsevier, Amsterdam.

Pickersgill, B., Heiser, C.B. & McNeill, J. (1979): Numerical taxonomic studies on variation and domestication in some species of *Capsicum*. In: Hawkes, J.G., Lester, R.N. & Skelding, A.D. (eds), *The Biology and Taxonomy of the Solanaceae*, pp. 679–700, Academic Press, London.

Potter, D. & Doyle, J.J. (1992): Origins of the African yam bean (*Sphenostylis stenocarpa*, Leguminosae): evidence from morphology, isozymes, chloroplast DNA, and linguistics. *Econ. Bot.* **46**: 276–292.

Proctor, M. & Yeo, P. (1973): *The Pollination of Flowers*. Collins, London.

Quiros, C.F. (1983): Alfalfa. In: Tanksley, S. & Orton, T.J. (eds), *Isozymes in Plant Breeding and Genetics*, pp. 253–294, Elsevier, Amsterdam.

Quiros, C.F., Ortega, R., Van Raamsdonk, L.W.D., Herrera-Montoya, M., Cisneros, P., Schmidt, E. & Brush, S.B. (1992): Amplification of potato genetic resources in their center of diversity: the role of natural outcrossing and selection by the Andean farmer. *Gen. Res. Crop Evol.* **39**: 107–113.

Raybould, A.F. & Gray, A.J. (1993): Genetically modified crops and hybridization with wild relatives: a UK perspective. *J. Appl. Biol.* **30**: 199–213.

Rees, A.R. (1992): *Ornamental Bulbs, Corms and Tubers*. CAB International, Wallingford.

Regal, P.J. (1994): Studying and managing the risk of cross-fertilization between transgenic crops and wild relatives. *Mol. Ecol.* **3**: 5–13.

Rieseberg, L.H. (1991): Homoploid reticulate evolution in *Helianthus*: evidence from ribosomal genes. *Am. J. Bot.* **78**: 1218–1237.

Rieseberg, L.H., Beckstrom, S., Liston, A. & Arias, D.M. (1991): Phylogenetic and systematic inferences from chloroplast DNA and isozyme variation in *Helianthus* sect. *Helianthus* (Asteraceae). *Syst. Bot.* **16:** 50–76.

Rieseberg, L.H. & Brunsfeld, S. (1992): Molecular evidence and plant introgression. In: Soltis, P.S., Soltis, D.E. & Doyle, J.J. (eds), *Molecular Systematics of Plants*, pp. 151–176, Chapman & Hall, New York.

Rieseberg, L.H., Choi, H., Chan, R. & Spore, C. (1993): Genomic map of a diploid hybrid species. *Heredity* **70:** 285–293.

Saakov, S.G. (1976): *Wild- und Gartenrosen*. V.E.B. Deutscher Landwirtschaftverlag, Berlin.

Schmit, P., Du Jardin, P., Baudoin, J.P. & Debouck, D.G. (1993): Use of chloroplast DNA polymorphisms for the phylogenetic study of seven *Phaseolus* taxa including *P. vulgaris* and *P. coccineus*. *Theor. Appl. Genet.* **87:** 506–516.

Schumann, C.M. & Hancock, J.F. (1989): Paternal inheritance of plastids in *Medicago sativa. Theor. Appl. Gen.* **78:** 863–866.

Simmonds, N.W. (1979): *Principles of Crop Improvement*. Longman, London, New York.

Small, E. (1978): A numerical taxonomic analysis of the *Daucus carota* complex. *Can. J. Bot.* **56:** 248–276.

Small, E. (1984): Hybridization in the domesticated weed–wild complex. In: Grant, W.F. (ed.), *Plant Biosystematics*, pp. 195–210, Academic Press, Toronto.

Smartt, J. (1990): *Grain Legumes: Evolution and Genetic Resources*. Cambridge University Press, Cambridge.

Smith, J.S.C., Goodman, M.M. & Stuber, C. (1985): Relationship between maize and teosinthe of Mexico and Guatamala: numerical analysis of allozyme data. *Econ. Bot.* **39:** 12–24.

Smith, P.G. & Heiser, C.B. (1957): Taxonomy of *Capsicum sinense* Jacq. and the geographic distribution of the cultivated *Capsicum* species. *Bull. Torrey Bot. Club* **84:** 413–420.

Soltis, D.E., Soltis, P.S. & Milligan, B.G. (1992): Intraspecific chloroplast DNA variation: systematic and phylogenetic implications. In: Soltis, P.S., Soltis, D.E. & Doyle, J.J. (eds), *Molecular Systematics of Plants*, pp. 117–150, Chapman & Hall, New York.

Stace, C.A. (ed.) (1975): *Hybridization and the Flora of the British Isles*. Academic Press, London, New York.

Stuessy, T.F. (1990): *Plant Taxonomy*. Columbia University Press, New York.

Swofford, D. (1991): PAUP: Phylogenetic Analysis Using Parsimony, version 3.0. University of Michigan, Ann Arbor.

Van Creij, M.G.M., Van Raamsdonk, L.W.D. & Van Tuyl, J.M. (1990): Results of pollination and embryo-rescue methods in wide interspecific hybridization in *Lilium. Lily Yearbook* **43:** 28–37.

Van den Berg, R.G., Groendijk-Wilders, N. & Kardolus, J.P. (1996): The wild ancestors of cultivated potato: the *brevicaule* complex. *Acta Bot. Neerl.* **45:** 157–172.

Van der Maesen, L.J.G. (1986): *Cajanus* DC. and *Atylosia* W. & A. (Leguminosae). *Agricultural University of Wageningen Papers* **85–4,** Wageningen.

Van der Maesen, L.J.G. (1994): Systematics of crop–weed complexes. *Acta Bot. Neerl.* **43:** 78–79.

Van der Maesen, L.J.G. & Somaatmadja, S. (eds) (1989): *Pulses*. Plant Resources of South-East Asia no 1. Pudoc, Wageningen.

Van Eijk, J.P., Van Raamsdonk, L.W.D., Eikelboom, W. & Bino, R.J. (1991): Interspecific crosses between *Tulipa gesneriana* cultivars and wild *Tulipa* species: a survey. *Sexual Pl. Reprod.* **4:** 1–5.

Van Holthoon, F. & Posthuma, K. (1995): *Lilium*: de sectie *Sinomartagon*, Doctorate report, Department of Plant Taxonomy, Agricultural University, Wageningen.

Van Raamsdonk, L.W.D. (1986): The grey area between black and white: the choice between botanical code and cultivated code. *Acta Horticulturae* **182:** 153–158.

Van Raamsdonk, L.W.D. (1990): Biosystematics of cultivated plants and their wild relatives. In: Kawano, S. (ed.), *Biological Approaches and Evolutionary Trends in Plants*, pp. 51–66. *Proceedings of the Fourth International Symposium on Plant Biosystematics*. Academic Press, London.

Van Raamsdonk, L.W.D. (1993a): Wild and cultivated plants: the parallelism between evolution and domestication. *Evol. Trends Pl.* **7:** 73–84.

Van Raamsdonk, L.W.D. (1993b): Flower pigment composition in *Tulipa. Gen. Res. Crop Evol.* **40:** 49–54.

Van Raamsdonk, L.W.D. (1995a): The effect of domestication on plant evolution. *Acta Bot. Neerl.* **44:** 421–438.

Van Raamsdonk, L.W.D. (1995b): The cytological and genetical mechanisms of plant domestication exemplified by four crop models. *Bot. Rev.* **61:** 367–399.

Van Raamsdonk, L.W.D., Den Nijs, A.P.M. & Jongerius, M.R. (1989): Meiotic analysis of *Cucumis* hybrids and an evolutionary evaluation of the genus *Cucumis* (Cucurbitaceae). *Pl. Syst. Evol.* **163:** 133–146.

Van Raamsdonk, L.W.D. & De Vries, T. (1992): Biosystematic studies in *Allium* L. section *Cepa. Bot. J. Linn. Soc.* **109:** 131–143.

Van Raamsdonk, L.W.D. & De Vries, T. (1996): Cultivar classification in *Tulipa* (Tulipaceae). *Acta Bot. Neerl.* **45**: 183–198.

Van Raamsdonk, L.W.D. & Sandbrink, J.M. (1995): Phylogenies inferred from morphological, nuclear DNA, chloroplast DNA and crossability data in *Allium* section *Cepa* are not congruent due to different effects of introgression. *Acta Bot. Neerl.* **44**: 85.

Van Raamsdonk, L.W.D., Van Eijk, J.P. & Eikelboom, W. (1995a): The analysis of cross-ability between species of *Tulipa* subgenus *Tulipa*. *Bot. J. Linn. Soc.* **117**: 147–158.

Van Raamsdonk, L.W.D., Schouten, H.J. & Smulders, M.J.M. (1995b): A literature survey for the development and validation of a simulation model on introgression and establishment of domestication genes. In: *Proceedings of the Workshop on Unanswered Safety Questions When Employing GMOs*, pp. 59–65, Coordination Commission Risk Assessment Research, Utrecht.

Van Raamsdonk, L.W.D., Wietsma, W.A. & De Vries, J.N. (1992): Crossing experiments in *Allium* L. section *Cepa*. *Bot. J. Linn. Soc.* **109**: 293–303.

Van Tuyl, J.M. (1990): Survey research on mitotic and meiotic polyploidization at CPRO-DLO. *Lily Yearbook* **43**: 10–18.

Vermeulen, A., Desprez, B., Lancelin, D. & Bannerot, H. (1994): Relationship among *Cichorium* species and related genera as determined by analysis of mitochondrial RFLPs. *Theor. Appl. Gen.* **88**: 159–166.

Visser, T. (1989): Distribution pattern and scab resistance of volunteer apple seedlings in the Dutch isle of Schiermonnikoog. *Euphytica* **40**: 265–270.

Watkins, R. (1976): Apple and pear, *Malus* and *Pyrus* spp. (Rosaceae). In: Simmonds, N.W. (ed.), *Evolution of Crop Plants*, pp. 247–250, Longman, London, New York.

Way, R.D., Aldwinckle, H.S., Lamb, R.C., Rejman, A., Sansavini, S., Shen, T., Watkins, R., Westwood, M.N. & Yoshida, Y. (1991): Apples (*Malus*). In: Moore, J.N. & Ballington, J.R. (eds), *Genetic Resources of Temperate Fruit and Nut Crops*, pp. 289–327, International Society for Horticultural Science, Wageningen.

Whitkus, R., Doebley, J. & Wendel, J.F. (1994): Nuclear DNA markers in systematics and evolution. In: Phillips, R.L. & Vasil, I.K. (eds), *DNA-based Markers in Plants*, pp. 116–141, Kluwer Academic Publishers, Dordrecht.

Wijnheimer, E.H.M., Brandenburg, W.A. & Ter Borg, S.J. (1989): Interactions between wild and cultivated carrots (*Daucus carota* L.) in the Netherlands. *Euphytica* **40**: 147–154.

Williamson, M. (1993): Risks from the release of GMOs: ecological and evolutionary considerations. *Evol. Trends Pl., Environ. Update* **1**: 5–9.

Wilson, H.D. (1990): Gene flow in squash species. Domesticated *Cucurbita* species may not represent closed genetic systems. *Bioscience* **40**: 449–455.

Zijlstra, S., Purimahua, C. & Lindhout, W.H. (1991): Pollen tube growth in interspecific crosses between *Capsicum* species. *HortScience* **26**: 585–586.