

THE USE OF AN EVOLUTIONARY SCHEME FOR CAULIFLOWERS IN THE SCREENING OF GENETIC RESOURCES

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SUMMARY

A hypothetical scheme is given for the evolution of the different types of cauliflower (*Brassica oleracea* var. *botrytis* L.). This has been useful in identifying sources of reduced susceptibility to cabbage root fly (*Delia radicum* (L.)), and may also be useful in the search for reduced susceptibility to clubroot (*Plasmodiophora brassicae* WORON.). It is argued that knowledge of the phylogeny of types within each crop species is of great importance in the exploitation of genetic resources.

INTRODUCTION

Occasionally, useful major genes are detected in crop species by screening a large number of genotypes. More often, however, the researcher is presented with a continuous range of variation for the character in question. This is particularly true if the phenotypic penetration of the relevant genes is incomplete or inconsistent, or if seed stocks are themselves genotypically variable. In these circumstances placing genotypes into groups may indicate whether differences are genotypically determined, and perhaps if more intensive screening of part of the gene pool is desirable.

The researcher may be able to put genotypes into groups if he can partition his data according to the evolutionary relationships of the genotypes, as this should reflect the adaptation of related genotypes to common environmental factors. Many crop plants, however, remain unclassified either taxonomically or phylogenetically.

An example is the cauliflower (*Brassica oleracea* var. *botrytis* L.), where although different types are recognised for the purposes of registration of cultivars, there is no taxonomic treatment which is based on the evolution of the crop. I have developed a scheme to describe the evolution of cauliflowers, founded largely on personal observation and communication, which has been helpful in identifying useful genetic material. I present it here for use by other cauliflower breeders, and in order to illustrate the use of phylogeny in the exploitation of genetic resources.

EVOLUTION OF CAULIFLOWERS

Evolution from the wild. Theories concerning the origin of the cultivated forms of *B. oleracea* differ as to the wild progenitor, as to a mono-, bi- or poly-phyletic origin from the wild, and as to the central role of kales (var. *acephala* DC.) in the evolution of other types. Recently, however, evidence seems to be accumulating that the cauliflowers, with heads ('curds') composed of apical meristems, and their close relatives, the broccolis (var. *italica* PLENCK.), with heads composed of flower buds, evolved in the eastern Mediterranean; while most other cole crop types were of western European origin (GATES, 1953; HYAMS, 1971; SNOGERUP, 1980). If this is true, then the important trading role of Italy around the time of Christ might have resulted in a range of types from east and west becoming established there and recombining to give the great diversity of types still to be found in that country. This includes the cauliflowers and broccolis, which can be found in every combination of heading (i.e. with a single head) or sprouting (i.e. multiple heading or much branched), annual or biennial, and with white, green or purple heads.

It is likely that cauliflowers are derivatives of the large, diverse and ancient broccoli gene pool, for broccolis are closer genetically to other *B. oleracea* forms than are the cauliflowers (GRAY, 1982).

Evolution of cauliflower from broccoli. Early Greek and Roman authors referred to sprouting forms of cabbage, which were probably primitive sprouting broccolis (e.g. Cato, 234–149 BC, translated by HOOPER & ASH, 1935). Reference to types with a head rather than sprouts commenced with Pliny (23–79 AD, translated by RACKHAM, 1950), and the first distinction between heading and sprouting forms was made by the Spanish Moor Ibn-al-Awan in the 12th century (HYAMS, 1971). The 16th and 17th century European herbalists commented on and drew heading forms (TOXOPEUS, 1979, and personal communication). None of the ancient authors, however, made a clear distinction between plants with curds (i.e. cauliflowers) and with heads of young flower buds (i.e. broccolis), which suggests that this difference did not exist, or was part of the normal variation of the crop and therefore not worthy of mention. Many of the translators of these ancient works were probably unaware of the intergradations between broccolis and cauliflowers, and assumed that any heading type must have been a cauliflower. The question remains open as to when, where, and how often cauliflowers and broccolis diverged into separate crops.

The two main characters which separate most present-day forms of cauliflower and broccoli are the abilities to form a head, and for that head to be a curd rather than young flower buds.

Observations of populations derived from crosses made between sprouting and heading forms of both broccolis and cauliflowers suggest that the heading versus sprouting character is controlled by several genes (P. CRISP, unpublished data); a conclusion supported by the occurrence of a wide range of intermediate types and cultivars.

The curding character is, however, probably under major gene control. The evidence is of two kinds:

EVOLUTION OF CAULIFLOWER

Table 1. Segregation for curd formation in self pollinated progenies of F₈ or F₉ plants of broccoli phenotype derived from broccoli X cauliflower.

Progeny	Number of plants of phenotype		Significance of difference from a single recessive allele for curding (χ^2 test) P =
	broccoli	cauliflower	
A	31	12	0.5-0.7
B	39	12	0.8-0.9
C	46	9	0.1-0.2
D	25	12	0.2-0.3
Total	141	45	0.7-0.8

1. The curd is believed to be a precociously developed floral button, made up of apical meristems, over 90% of which abort with the onset of flowering (CRISP & WALKER, 1974). The excess tissue, and the egress of pathogens afforded by aborting tissue give the cauliflower a reduced chance of survival, and a low reproductive capacity in comparison with the broccoli. Its survival depends heavily on selection by man in favour of the cauliflower phenotype.

It is, therefore, difficult to envisage the curd evolving slowly over many generations; it is more likely that a sudden genetic event gave the ancient horticulturalists the cauliflower phenotype, which they immediately recognised as useful, and selected for seed production. This infers that a relatively simple genetic factor was involved – perhaps even a single major gene mutation.

2. Crosses between broccoli and cauliflower do not generally give recognisable Mendelian ratios for crop type in the F₂ (P. CRISP, unpublished data), which taken with poor curding ability expressed by the F₁'s and F₂'s from wide crosses within cauliflower (CRISP & GRAY, 1978; GRAY & CRISP, 1979) may infer polygenic control of the ability to curd.

However, CRISP et al. (1975) reported a single gene mutation in cauliflower which gave very small curds on vegetatively normal plants, giving, in effect, cauliflower plants with the reproductive fitness of broccoli. Curding was dominant to non-curding. This may have represented a back-mutation to an ancestral allele.

Although the broccoli × cauliflower populations referred to above gave no simple Mendelian ratios in early generations, selfs of F₈ and F₉ individuals grown in the field in 1981 at Wellesbourne showed clear indications of a single gene difference between the formation of a curd or a broccoli head (Table 1). In contrast, here the curding allele was recessive.

Further investigation is needed to see if the same or different genes are involved, and it is possible that modifier genes have a fundamental effect.

If, however, the hypothesis of major genes controlling curding is correct it would explain the great diversity seen in the cauliflower – which from the historical evidence may be no older than kohlrabi and Brussels sprouts, two other *B. oleracea* crops of far less diversity. One or a few major genes for curding present or repeatedly re-introduced in the ancient, variable, broccoli gene pool could have resulted in the generation of many fundamentally different cauliflower genotypes.

Evolution of ancient cauliflower types. The ancient Roman name for broccoli was 'cyma' (ROBINSON, 1905). 'Broccoli' is probably a more recent term derived from the Latin 'brachium' meaning branching (BOSWELL, 1949) and is applied in Italy to a wide range of sprouting brassicas, including turnips. 'Cauliflower', as in other languages ('Blumenkohl', 'bloemkool', 'cavolo-fiore'), translates as the flowering cole; and it seems likely that these are recent rather than ancient words. In Italy the term 'broccoli' is frequently used for forms of cauliflower with green or purple heads.

The modern names, although confusing, are of interest for until a few years ago in Britain they were reserved for two quite distinct types of cauliflower. The term 'heading broccoli' was used for autumn-maturing cultivars grown from seed of Italy, and for types maturing during the winter and spring which were bred in maritime regions of North-west Europe from material of Italian origin (HORNE, 1954). 'Cauliflower' was used for the annual forms of the crop imported as seed or breeding stock from north-west European countries – Denmark, Germany, Belgium and France. In recent years the distinction between these two types had diminished as, respectively, earlier and later maturing types have been selected giving an overlap of maturity periods during the autumn period, and also Australian cultivars maturing during the autumn have been introduced. However, it is now established that 'heading broccoli' and the annual 'cauliflower' differ fundamentally in their breeding system (GRAY & CRISP, 1977), and in their response to the environment (CRISP & KESAVAN, 1978). When hybrids are made between the two types the F_1 and large proportions of the F_2 do not display the cauliflower phenotype (CRISP & GRAY, 1978; GRAY & CRISP, 1979), indicating different genetic controls of curd quality, and even of the ability to form a curd.

A little is known of the history of these cauliflower types (or perhaps the heading broccolis which were their immediate predecessors). The annual type was first reported by DODOENS (1559, in GILES, 1941 and 1944), referring to a cauliflower in the Netherlands as *B. cypria*, perhaps indicating an origin in Cyprus. HYAMS (1971) refers to cauliflower being grown in France in the 16th century as 'Cyprus cabbage' and says that it then appeared in England in the 17th century. BOSWELL (1949) stated that cauliflower seed from Cyprus was used to grow the crop in England in 1586. There is no evidence that the annual type of cauliflower ever became established in Britain, for in contrast to several mainland north-west European countries, no native forms of the crop were recorded (ROBINSON, 1905).

The 'heading broccolis' became established in Britain from Italy by the early 18th century, sometimes from lots of seed which gave mixtures of types of both cauliflowers and broccolis (GRAY, 1982). From that beginning a wide range of white curded cultivars was developed (GILES, 1941; GRAY, 1982), which gave the Old English type of cauliflower, with variants throughout the country. Similar developments probably gave further biennial cauliflowers, such as the Roscoff, Angers and St Malo cauliflowers in north-west France, and the Walcheren in the Low Countries.

The historical, etymological and genetic evidence therefore suggests a quite separate origin for the N. European annual and NW European biennial cauliflowers. The biennial type is undoubtedly of Italian origin, and differs from the annual type. But is the latter of separate Italian origin, or was it introduced to northern Europe directly from the eastern Mediterranean?

Recent evolution of cauliflowers. Two further groups of cauliflowers have appeared since the beginning of the 19th century, both of which probably owe their parentage to recombinant types derived from the annuals and biennials described above. British colonialism resulted in European cauliflowers being established as important crops in India and Australia. In India, types were developed adapted to hot, humid conditions, which have now spread throughout tropical regions of the world (CHATTERJEE & SWARUP, 1978); many are characterised by possessing the self-incompatibility of the biennial cauliflower recombined with the annual habit (SWARUP & CHATTERJEE, 1972; GRAY & CRISP, 1977; CHATTERJEE & SWARUP, 1980). In Australia, the recombinant types include a wide range of self-compatible cultivars, many of which mature much later under British conditions than does the ancestral annual type.

Classification of modern cauliflowers. The phylogenetic relationships of cauliflowers are defined in Table 2. There are deficiencies in this scheme. The Australian types cover a wide range of morphologies and maturity times, and some classification within this group could be useful. A further classification of the Italian material is essential. Additionally, the scheme is restricted to the heading forms of cauliflower, those cauliflowers where several curds form on side branches (CRISP et al., 1981) are omitted. Moreover, the broccolis, from which the cauliflowers evolved, and with which they share a gene pool, are also omitted. However, it gives some order where none existed before, and its usefulness in interpretation of results from screening large numbers of accessions for pest and disease resistance is shown below.

I have not detailed morphological differences between the groups, and indeed the anecdotal history of a cultivar may be as important in allocating it to a group as

Table 2. Groups of cauliflowers as determined by their phylogeny

Group name	Characteristics	Common types
Italian	Very diverse, include annuals and biennials and types with peculiar curd conformations and colours	Jezi Naples (= Autumn Giant) Romanesco Flora Blanca
NW European biennials	Derived within the last 300 years from Italian material	Old English Walcheren Roscoff Angers St Malo
N European annuals	Developed in northern Europe for at least 400 years. Origin unknown; perhaps Italian, perhaps eastern Mediterranean	Le Cerf Alpha Mechelse Erfurt Danish
Asian	Recombinants of European annuals and biennials, developed within the last 250 years. Adapted to tropics	Four maturity groups are recognized by Swarup & Chatterjee (1972)
Australian	Recombinants of European annuals and biennials, and perhaps Italian stocks; developed during the last 200 years	Not yet been categorised

are, say, the morphological affinities of its leaves. The characteristics of the various groups are given by FINCH (1955, 1957), JEMMET & FINCH (1959), HOW (1967), and HAINE & HOW (1968).

SCREENING THE CAULIFLOWER GENE POOL

Susceptibility to cabbage root fly. Cabbage root fly (*Delia radicum* (L.)) is restricted to the holarctic region between 30 and 60°N. Its larvae damage cruciferous roots, and it can be a serious pest on brassica crops. There is no known total resistance in brassicas to the fly, but a combination of reduced susceptibility and insecticide treatments may give effective control (P. R. ELLIS & A. R. THOMPSON, personal communication).

In 1977, 173 cultivars of cauliflower were screened in the field for damage caused by the fly. Significant differences were found between and within the types categorised according to their evolutionary relationships (CRISP et al., 1977).

It is clear that the NW European biennials, which evolved where the fly has its greatest effect, showed the least damage and little variation for this character. The N European annuals also showed little damage, but were more variable, perhaps reflecting their origin outside of the fly's range, or that some developed more recently in continental parts of Europe where the fly is less damaging than in maritime regions. The high variation shown by Italian material may be because of heterogeneity in selection pressure by the fly or because of continuous recombination of genes at the gene centre. The Asian material evolved where the fly has no effect and was correspondingly highly and uniformly damaged. Australian material was variable, perhaps because of its recent origin from diverse parents.

The evolutionary theory, therefore, gave a plausible explanation of these results. It also raised the possibility that the two least attacked groups, the N European annuals and NW European biennials, might possess different genetic controls of this character, for they may have evolved separately for several centuries. Therefore these parts of the gene pool were screened more extensively, and the most promising parents within each of these groups were identified and crossed (ELLIS et al., 1979). The F₁ showed less damage than either parent, and the F₂ segregated for the degree of damage (ELLIS et al., 1981), suggesting that, indeed, annual X biennial recombinants might give reductions in susceptibility.

Susceptibility to clubroot. Clubroot, a root disease of crucifers caused by the obligately biotrophic *Plasmiodiophora brassicae* WORON., is prevalent in temperate regions, but is a world wide problem. Resistance is known in several cruciferous species, but that in *B. oleracea* is mainly restricted to kales and cabbages (CRUTE et al., 1980).

The cauliflower breeder may try to introduce major genes for resistance from related species, which is an expensive operation with a high likelihood of failure. Or he may attempt to transfer the genes from kale and cabbage into cauliflower; but here also there are considerable difficulties in recovering the crop type (WEISAETH, 1974). Instead, we have searched the cauliflower gene pool for partial resistance which can be used directly or recombined within the crop to accumulate minor genes to give less susceptible cultivars.

Using two highly pathogenic collections of *P. brassicae* both coded -/-/31 on the ECD set (BUCZACKI et al., 1975) 327 cultivars of cauliflowers have been screened for resistance in a series of glasshouse tests. There were two replicates of the two pathogen collections, each containing ten plants of each cultivar and the highly susceptible cabbage cultivar Septa, which was used throughout as a control. Full experimental details of these and other tests will be reported separately.

The degree of galling on each plant was scored on a 0 (absent) to 3 (severe) scale. The control, cv. Septa, had a consistently high score and in only one out of 30 tests did it score significantly less (at $P = 0.05$) than the maximum possible. Most other plant lines scored at or near the maximum, and therefore the data were not suitable for analysis of variance. Moreover, only 3% of the cultivars scored less than 2.6, a result which has already led us to suggest that there is no resistance in cauliflower comparable with that in kales or cabbages (CRUTE et al., 1981), and is in agreement with other screenings of cauliflower germplasm (CATOVIC-CATANI & RICH, 1964; CRETE & CHIANG, 1967, 1980; CHIANG & CRETE, 1972; M. GUSTAFSSON, personal communication).

Each cultivar was then assessed by comparing it with the control cv. Septa. If one or more of the four plots (2 replicates X 2 pathogen collections) gave mean scores of 2.5 or less then this was significantly less galled than cv. Septa ($P = 0.05$). The results are given in Table 3, as the % of cultivars in each cauliflower group less galled than cv. Septa. There is a clear indication that the Australian cultivars were nearly all highly susceptible, in contrast to their putative parents. The pathogen causes few problems in the hot dry climate of Australia, and it is possible that lack of selection pressure allied with recombination of different genetic types has resulted in the dispersal or loss of genes reducing susceptibility. In contrast, clubroot is of some significance in parts of Asia (YOSHIKAWA & BUCZACKI, 1978) and selection pressure by the pathogen may have continued after recombination of different cauliflower genotypes. However, the comparatively low proportion of Asian and N European annual cultivars showing low susceptibility may reflect a fairly low selection pressure, respectively, recently in Asia, and historically, if the N European annuals did indeed originate in the eastern Mediterranean. Alternatively, the disease may have reached northern Europe and Asia recently (WATSON & BAKER, 1969).

Of more interest to the breeder are the results for the NW European biennials and the Italian cultivars. Closer inspection of the NW European biennials showed considerable differences between types of cultivars (Table 4). It is difficult to speculate why these should differ so markedly, if selection pressure is the sole criterion, for clubroot

Table 3. Clubroot damage on 327 cultivars of cauliflower.

Group	Number of cultivars screened	% significantly ($P = 0.05$) less damaged than cv. Septa
Italian	133	26
NW European biennials	63	21
Asian	33	15
N European annuals	36	14
Australian	45	2

Table 4. Clubroot damage on 63 cultivars of NW European biennial cauliflowers.

Type	Number of cultivars screened	% significantly ($P = 0.05$) less damaged than cv. Septa
Roscoff	26	46
Old English	21	5
Walcheren	3	0
Angers	13	0

is a ubiquitous disease throughout maritime north-west Europe and has been for about two centuries (WATSON & BAKER, 1969). An alternative explanation is that this represents the chance introduction of genes with their Italian ancestors. If so, then a more intensive analysis of Italian material should prove useful; and, indeed, the Italian material showed the highest proportion of less damaged cultivars (Table 3). WATSON & BAKER (1969) suggested that clubroot originated in the western Mediterranean region. They also suggested, without evidence, that useful, new resistance may still occur in wild species, a finding not substantiated by M. GUSTAFSSON (personal communication). The putative evolution of cauliflower taken with these results could, however, give some support to WATSON'S & BAKER'S claim, but with the modification that resistance, or low susceptibility, may exist in primitive cultivars rather than wild species in the Italian region.

DISCUSSION

The elucidation of phylogenies for crop species is likely to call on disciplines outside of those usually employed by taxonomists. Where *Brassica* is concerned, conventional methods have defined the relationships within the genus and with related genera (reviewed by PRAKASH & HINATA, 1980). Studies of the transition from wild to cultivated types are, however, limited, for these depend to a large extent on historical accounts, and as SNOGERUP (1980) has stated, the study of ancient authors is a specialised field. My account of the evolution of cauliflowers would undoubtedly benefit from a close inspection of ancient Greek, Roman, Arab and Jewish writings, of Mediaeval herbalist literature, and even of old paintings of vegetables.

Additionally, it seems probable that a phylogeny of this type can only satisfactorily be defined by a person with a knowledge of the crop, for much of the evidence must be anecdotal, and therefore suspect. Even the 'experimental taxonomy' advocated by SMARTT (1981) for crop species may be insufficient for this purpose, for, as with any retrospective view of evolution, weight may be given to characters which are taxonomically good, but evolutionarily irrelevant. It is, therefore, not surprising that the only other attempts to define evolutionary relationships within *Brassica* crops have been by breeders with long experience of particular crop types: TOXOPEUS (1974, 1979), dealing mainly with oil seed and forage species; and LI (1980, 1981) with forms of *B. campestris* L. and *B. juncea* L.

As crop plant genetic conservation and the manipulation of data concerning this resource become more organised on a world-wide scale (IBPGR, 1981), then it is increasingly important that phylogenies within crops are defined; not only to ensure

that the complete range of each crop is adequately collected, but also, as the results in this paper demonstrate, so that sources of useful dispersed genes can be identified. It is logical, therefore, to suggest that part of the effort in genetic conservation should be directed towards encouraging persons with knowledge of particular crops to record their experiences. The marketing, technological and legislative forces which have such an effect on the cultivars now grown are modern phenomena, and seedsmen, commercial growers, and even amateur gardeners whose experiences go back over 30 years are likely to offer useful information.

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