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Breeding Field Vegetables

N. L. Innes[1]

Introduction

In reviewing the breeding of field vegetables, one is faced with the dilemma of defining "vegetable" crops. In botanical terms the edible part of the tomato plant Lycopersicon esculentum Mill. is a fruit, yet in most places tomatoes are regarded as vegetables. In the United Kingdom the potato, Solanum tuberosum L., is an important component of the human diet, and most consumers look upon this crop as a vegetable even though it is not listed as such in official statistics. The same can be said of the sweet potato, Ipomoea batatas (L.) Lam., which was identified by AVRDC (5) as one of the six most important vegetable crops for the Asian farmer but is listed by the IBPGR (85) under "root and tuber" crops.

Vegetables are usually an ancillary ingredient of dietary intake, but constitute the main part of the diet in a number of countries. This is especially true in those areas where the protein level of some vegetables is high, and for the very poor of the world whose access to other foods may be limited. Perhaps Grubben's definition of (tropical) vegetables (69) offers a reasonable compromise: "Vegetables . . . provide a source of food, often low in calories and dry matter content, which are consumed in addition to a starchy basic food in order to make it more palatable. Vegetables add protective nutrients, especially vitamins and minerals to the diet." What is not in doubt is the important role of vegetables in achieving a balanced diet.

Given Grubben's definition as reasonable, there still remains the problem of differentiating between the so-called "tropical" and "temperate" vegetables. A number of traditionally temperate crops

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such as carrots can be grown in upland regions in the tropics (11), and others, like cauliflower, have exhibited sufficient variability to permit selection for adaptation to hotter areas of the world (175). Equally, directed breeding has led to the successful adaptation in Europe of the central and south American *Phaseolus vulgaris* (L.) bean as a green vegetable (90), and a modification in growing techniques has resulted in the successful introduction into Europe of the Japanese bulb onion (*Allium cepa* L.) with a daylength requirement for bulbing of 13 to 14 hours compared with 16 hours for the traditional European onion (155).

Although a geographical definition of "tropical" is possible (Grubben (69) has produced a long list of tropical vegetable crops), the division of crops into tropical and temperate seems largely artificial at a time when breeders are striving - with success - to adapt "exotic" temperate and tropical crops to their own environments. Furthermore, genetic principles and breeding techniques are similar for all crops, no matter where they are grown. I therefore propose to avoid the problems of definition by outlining broad objectives in vegetable breeding and discussing some of the ways in which these objectives have been or are being achieved in a range of vegetables, especially through the use of exotic germplasm. In addition, I shall try to predict where present fundamental research and technological developments are likely to make an impact in the future.

Among vegetables there is a wide range of natural breeding systems, including inbreeders and outbreeders, as well as those which are partial inbreeders and partial outbreeders. There are insect- and wind-pollinated forms, and, for those crops in which sex forms vary, there are monoecious and dioecious types. While breeding methods vary according to the natural breeding system of a crop, in any breeding program the breeder requires genetically variable material with which to work. Given suitable selection and evaluation techniques, as well as a knowledge of the natural breeding system so that appropriate breeding strategies may be followed, improved varieties can be developed. Inevitably, there is a need for these varieties to be adapted to the environment for which they were designed, or better still, to be widely adapted to a range of environments. Among the requirements of "adaptation" are plant resistance to pests, diseases, physiological disorders, and the so-called environmental and stress factors such as heat, cold, drought, saline soil, and pollutants.

In addition, there is the important issue of seed maintenance and multiplication so that the grower can rely on a regular supply of high quality seed that is true to type (52).

Although reviews have been published on the use of plant introductions for improving vegetable varieties (138), breeding for improved nutritional value (63,184), plant resistance to diseases (160,190,191), resistance to insects (102,172), breeding for tolerance to environmental stress (173), the use of interspecific crosses in vegetable breeding (145), and general breeding of vegetables (12,26,89,139,194), these have dealt mainly with temperate crops. Two exceptions are Choudhury's review on hybrid breeding (19) and Swarup's booklet on breeding cross-pollinated vegetables in India (174). These aside, however, the general trend is hardly surprising, as vegetables in the tropics have, until recently, tended to be given relatively low priority in the planning of research and development at the national and international levels, partly because of the large number of crops involved. That AVRDC is now celebrating its tenth anniversary is undoubtedly a credit to those who planned and financed the Center. However, while breakthroughs have been made in its programs, ten years is a relatively short period in the breeding of improved varieties. I anticipate that AVRDC will make an even greater contribution to the breeding of vegetables over the next decade, especially at the international level, through its enlightened policy of release of basic breeding materials. The recent release in Taiwan of processing tomato "Tainan Selection No. 2" and of the mungbean "Shanhua" in Korea bears testimony to AVRDC's successful breeding efforts.

Resistance to Diseases, Pests, and Physiological Disorders

Diseases:

There is little doubt that breeding for resistance to diseases is one of the major success stories of plant breeding, even though problems continue to exist. The need for plant resistance to insect pests and nematodes is at least as great as that for resistance to diseases. Progress in the former areas, however, has been much more difficult to achieve.

Procedures for resistance breeding have involved the development of suitable screening techniques, the search for sources of heritable resistance, and the transfer of resistance to advanced breeding materials which sometimes involves a program of backcrossing to adapted varieties or breeding lines. Germplasm of foreign origin, sometimes of closely related (wild) species, has therefore been of considerable importance to the breeder working with plant resistance. One of the first examples of the utilization of genetic resources in directed resistance breeding was the transfer of resistance to Fusarium wilt (Fusarium oxysporum Schl. f. sp. niveum (E. F. Smith) Snyder and Hansen) from semi-wild, non-edible citron to watermelon in 1911 resulting in the variety "Conqueror" (131). The literature contains many examples of the use of exotic germplasm to breed disease resistant vegetables (138,190).

The problems of resistance breeding arise mainly from the fact that, in addition to genetic variability for plant resistance in the host, there is also genetic variability for pathogenicity in the pathogen or pest. Moreover, there are instances where genetic resistance may be impaired by a change in environmental conditions, especially temperature. Interestingly, Orton (131) noted that although "Conqueror" was resistant to Fusarium in

South Carolina, where it was bred, and in a number of other states including Iowa, it was susceptible in Oregon.

An area of great importance to the breeder is an understanding of the complex relationships involving host, pathogen or pest, and the environment. The gene-for-gene concept proposed by Flor (57) in the flax/rust relationship did much to further such an understanding. A number of other relationships covering host-parasite combinations have been listed by Day (37).

It has been suggested that not all variation in resistance and pathogenicity follows this gene-for-gene pattern, and van der Plank (185,186,187) differentiated two types of relationships between host and pathogen - vertical and horizontal. The former was based on the gene-for-gene relationship and was initially considered to be a more stable system than horizontal resistance. Robinson (150,151) has supported and expanded on the concepts proposed by van der Plank, but others such as Parlevliet and Zadoks (133) and Nelson (118) have disputed that such a distinction can be made. Numerous other terms have been used to describe different features of the host-parasite relationship (152), among which race-specific (or specific) and race non-specific (or general) resistance have become widely used (159). The importance of time as a dimension in the stability of resistance was appreciated by Johnson and Law (95) who coined the term "durable resistance," meaning simply that the effectiveness of the resistance would last regardless of its genetic basis, race-specificity, or expression. This concept was further discussed by Johnson (94).

Detailed genetic studies have in a number of cases enabled vegetable breeders to plan more effective breeding strategies. In lettuce, race-specific type plant resistance has not provided a lasting solution to downy mildew (<u>Bremis lactucae</u> Regel). Until it was appreciated that there existed a gene-for-gene situation for plant resistance/pathogenicity (32), it was believed that by accumulating or "pyramiding" race-specific genes it might be possible to defeat the flexibility of the fungus. While pyramiding sometimes provided a temporary respite, it was unlikely to provide a lasting solution (33) as the fungus proved capable of breaking down the resistance within a relatively short time after the release of a new (race-specific) resistant variety (31). A search for new resistance in wild species of <u>Lactuca</u> related to the cultivated <u>L. sativa</u> L. provided useful sources in <u>L. serriola</u> L. and <u>L. saligna</u> L. (93,121). It is impossible, however, to forecast whether such resistance will be durable, as it may eventually suffer the same fate as so many of the seedling resistance genes on which lettuce breeders originally based their hopes. A more difficult approach, but one which may provide more lasting resistance, is that of using so-called "field" resistance (34). This type of resistance usually allows the fungus to invade the plant, but symptoms are reduced, as is the rate that the disease spreads. Assessment of the resistance requires large, replicated "spreader" trials in the field using material already known to lack race-specific resistance. Field resistance was found in the crisp varieties "Grand Rapids" and "Iceberg," and heritability studies indicated that it is transferrable in breeding work (120).

In the search at Wellesbourne for more lasting resistance to downy mildew of lettuce, over 500 accessions of L. sativa L. and wild species of Lactuca have been tested from a "world" collection of over 1000 accessions assembled for this purpose.

Breeding for durable resistance to bean common mosaic virus (BCMV) in Phaseolus vulgaris L. beans has been made possible by an understanding of complex host-pathogen-environment relationships. Drijfhout (47) showed that a number of recessive genes confer resistance to BCMV and the resistance conferred by these genes can be overcome by "matching" pathogenicity genes in the virus. One recessive gene, bc-u, which confers no resistance on its own, is required for the expression of a series of strain-specific recessive genes occurring at three loci. A temperature-sensitive gene, I, derived originally from "Corbett Refugee" (1), confers localized hypersensitive resistance at temperatures less than 30°C. Above this temperature, a systemic necrotic "black-rot" reaction typifies the presence of this gene (68). Some virus strains will render the I gene ineffective and induce systemic necrosis in varieties homozygous for I at temperatures > 26°C (47,82,83).

To ensure resistance durability, the accumulation of genes for many components of resistance, such as reduced inoculum efficiency, delayed germination time of the pathogen, reduced sporulation, and reduced lesion development, is highly desirable. In practical terms, the current approach used by AVRDC and most other international institutes of using field trials in areas where a disease is prevalent, or of enhancing disease spread and expression by the use of spreader trials, has much to recommend it. Repetition of such trials in various seasons and regions, especially in different countries, is likely to ensure that any material that withstands high selection pressures has a durable type of resistance. The search for multiple disease resistance through simultaneous and sequential screening also shows considerable promise.

Pests:

The techniques used for breeding resistance to insects (38) are similar to those used in breeding for resistance to diseases. However, entomologists usually classify plant resistance into three main categories: Non-preference, whereby a plant is unattractive to an insect for shelter, food, or egg laying; antibiosis, whereby a plant adversely affects the growth and multiplication of an insect; and tolerance, whereby a plant withstands insect attack more effectively than a susceptible plant. Resistance to a particular pest may be due to one or a combination of these types of resistance.

Although much has been published on plant resistance to insect pests, including reviews on resistance in vegetables by Stoner (172), Kennedy (102), Tingey (182), and Ellis and Kemptom (51), the success rate in terms of commercial varieties that are resistant to insects is relatively low.

When Stoner published his review in 1970 only one variety with resistance to insects, the potato "Sequoia" with resistance to flea beetles and leaf hoppers, had been released. In 1974, Dunn and Kemptom (49) reported on resistance to root aphids in the lettuce varieties "Avoncrisp" and "Avondefiance," and, for the 1966-77 period in North America, Kennedy (102) listed the release of one sweet potato variety resistant to flea beetle, one tomato variety resistant to *Tetranychus urticae* Koch, and two turnip varieties resistant to turnip aphid, as well as a number of useful breeding lines with resistance to other insects.

The dwindling efficacy of existing insecticides, the prohibitive cost of developing and marketing insecticides, and concern for the effects of pesticide residues have increased the need for varieties resistant to insects. Another aspect of resistance breeding that merits attention is the use of low levels of plant resistance to reduce the number of chemical applications. One example is the control of the carrot fly whereby partial plant resistance and insecticides may be used in a complementary fashion (179).

Physiological Disorders:

The causes of physiological disorders in vegetables such as hollow stem in calabrese (35), internal browning in Brussels sprouts (54), tipburn in lettuce (21,154) and Chinese cabbage (176), pepper spot in white cabbage (23), and blossom end-rot in tomato (67) are not fully understood, although some are related to calcium and/or boron nutrition.

Environmental factors also affect the expression of physiological disorders and an accelerated rate of growth may help to induce them. Genetic variability for tolerance or susceptibility to these disorders is known, and there are varietal differences in susceptibility. However, positive breeding for tolerance is difficult because there are no reliable methods for selection. The general area of physiological disorders is one in which increased collaborative efforts between breeders, soil scientists, and physiologists should be beneficial in providing suitable screening tests.

Genetic variation for efficiency of micronutrient utilization occurs in many plant species, and examples for vegetable crops have been given by Gabelman and Gerloff (62). The variation shown by plants in their tolerance to herbicides (55,110) may allow for the selection of vegetable varieties that are better adapted to growing regimes with chemical weed control.

Concern has been expressed about the possible carcinogenic effects of high nitrate levels in vegetables, although the evidence to suggest that cancer is caused by ingested nitrate is sparse (59). Nevertheless, some scientists consider it important to breed low nitrate accumulating varieties (113), and such breeding has been initiated in a number of western European countries.

Tolerance to Environmental Factors

In addition to pests and diseases, abiotic factors such as salinity, extremes of temperature, and air pollution often adversely affect crop quality and yield. Most of the work done in breeding vegetables tolerant to environmental stresses has concentrated on tomato (171,173). Villareal and Lai (188,189) have described a search for sources of heat tolerance in *Lycopersicon* spp. to breed varieties better adapted to the tropics. Their criterion were the ability to set fruit at night temperatures in excess of 20°C. A total of 4,752 accessions from 79 countries were screened in field and glasshouse tests, and provided 39 heat tolerant accessions from 15 countries. This would indicate the possible diversity of heat tolerant genes. Most of these accessions were from *L. esculentum* Mill. and *L. pimpinellifolium* Mill. and had medium to small sized fruits. This work also showed that for hot, wet tropical conditions, screening for tolerance to high night temperatures should also be allied to tests for tolerance to excessive moisture in the soil and in the atmosphere. Kuo, Chen, Chou, Tsai, and Tsay (104) demonstrated that since poor fruit set in tomatoes at high temperatures is due to a number of causes affecting a complex of physiological processes, there is a need for close collaboration between breeders and physiologists if varieties are to be bred that are well adapted to a wide range of tropical conditions. The approach used by AVRDC (6) is to combine into one genotype a number of attributes from several sources, including the production of viable pollen at high temperatures, the effective transfer of pollen to the stigma, germination and growth of pollen in the style, style viability, and fertilization.

In seeking to breed heat tolerant Chinese cabbage at AVRDC, Opeña and Lo (129) first built up a large and diverse germplasm collection and then, in part, used artificial vernalization on seedlings to help identify heat tolerant material through its predilection to bolting (7). They found that heat sensitivity was controlled by an incompletely dominant gene (128). Subsequent studies have emphasized the important role of water relations in heat tolerant Chinese cabbage, and indicated that measurement of stable parameters such as sap electrical conductivity may provide simpler techniques for screening for heat tolerance (105). Despite having screened a wide gene pool for heat tolerance, Opeña and Lo (130) found that heat tolerant material was low yielding and disease susceptible. Moreover, this material was genetically similar and exhibited little response to selection for improved agronomic characters. They therefore concluded that there was a need to broaden the genetic base in the breeding of high yielding, disease resistant, heat tolerant varieties.

In a search for a cold tolerant *Phaseolus* dry bean (for processing) that would produce economic yields in the United

Kingdom (88), a wide range of germplasm was used, some of which had been identified for cold tolerance in growth cabinets (4) and which gave excellent yields in field trials (76). Progress has been made (22) but, as Hardwick pointed out (74), the difficulties in devising the suitable large-scale screening techniques needed by the plant breeder have prevented a major breakthrough. Cold tolerance, like heat tolerance, is unlikely to depend on a single or simple character but it can be anticipated that multidisciplinary research will eventually lead to vegetable varieties adapted, as with some of the major cereals, to a much wider temperature range.

Response to light and temperature changes can be extremely important in relation to the formation of vegetative organs or in flowering, and manipulation of such responses by breeding is important in adapting crops to new environments or increasing adaptation in an existing environment. Coyne's information on the genetics of flowering response in Phaseolus beans to temperature and photoperiod (24,25) should enable breeders to produce varieties with greater adaptation across a number of latitudes. In onions, the availability of day-neutral plants, which produce bulbs irrespective of the number of hours of light per day, could significantly increase the adaptation of this globally important vegetable (2). Similarly, increased adaptation of vegetable cowpea (114) and soybean (7,157) by the breeding of photo-insensitive varieties would be advantageous in the tropics and subtropics.

Considerable achievements have also been recorded in breeding for general stability (or lack of responsiveness) to ensure that varieties perform well under a wide range of conditions. Systems are now available that allow the breeder to test for general stability, as a result of studies that quantified differential response of varieties to different environments (50,56,60,77,136, 197) as well as studies in response to selection for sensitivity to environmental variables (99). Although statisticians have disagreed about the validity of joint-regression analyses (and it can be misleading to talk about stability in terms of regression slopes with values greater or less than unity), there is no doubt that joint regression types of analyses are extremely useful and have been successfully applied as aids to breeding Chinese cabbage (7), carrots (46), cauliflower (28,103), and peas (166).

Improved Quality and Nutritional Factors

Although effort is being directed towards breeding nutritionally improved vegetables, there is still a marked conservatism in consumer preferences in different countries and localities. Cosmetic appeal is clearly one of the consumer's overriding considerations. The tomato variety "Caro-Red," for example, was bred for high provitamin A from crosses with a green fruited wild *L. hirsutum* Humb. and Bonpl. from South America but failed to appeal to consumers because of its orange-colored fruit (184). Nevertheless, a number of advances in quality traits have been achieved in a range of vegetables (26), and collaboration with nutritionists is bound to lead to progress (63) as, for example, in breeding for desirable patterns of glucosinolates in Chinese cabbage (195).

Among the problems faced by breeders are those of finding or creating environments in which genetically controlled defects will be readily expressed so that effective selection can be made. Dowker, Fennell, Jackson, and Phelps (41,42,46) overcame this problem in carrots after a series of experiments to measure the magnitude of genotype x environment interactions on blemished roots. Dowker proposed that management of "within-site" environmental treatments by different sowing dates could substitute for the more costly use of different sites, and that low density plots would be the best discriminating environment against split and purple-topped roots. Using this approach, a number of new potential varieties of Chantenay-type carrots have been bred with high resistance to splitting and good internal core color (45).

Crisp and Gray used a different approach with cauliflower (29) to breed against the curd defects of bracting and anthocyanin pigmentation (pinking). These defects are selected against by using a two-tier system comprising field selection followed by tissue culture of selected curds. The use of this system provides a second chance for defects to be expressed and has made possible the development of new varieties with excellent quality curds.

It is encouraging that the AVRDC Nutrition, Environment, and Management Program (NEM) seeks to enhance the nutritional quality of vegetable crops through a multidisciplinary approach that includes testing for genotypic differences in such diverse characters as the quality of soybean curd, protein quality of mungbean, and the protein/carbohydrate balance in sweet potato (7).

Mechanical Harvesting

In countries where labor costs are high or labor is in short supply, mechanical harvesting of vegetables has received considerable attention. The collaborative work of tomato breeder G. D. Hanna, agricultural engineer Coby Lorenzon, and their co-workers in the USA is a classic example of what can be achieved through interdisciplinary research using a wide gene pool. Hanna, with Gentile, Smith, Lippert, Davies, and McCoy (71,72) successfully bred commercial tomato varieties suited to mechanical harvesting. These varieties have a determinate habit with firm, tough skinned fruits that ripen evenly and remain unblemished on the plant for a period after ripening. They are also resistant to *Fusarium* and *Verticillium* wilt. The availability of "jointless" genes (145) may make possible further advances, although Stevens (170) reported that jointless lines had a slight yield disadvantage compared with their "normal" counterparts.

In recent years pea breeders have made considerable progress in reducing the height of pea varieties to make them more suitable for mechanical harvesting. Nevertheless, both in vining (harvested as a fresh green product for freezing, canning, or direct marketing) and dry peas, problems with excessive amounts of haulm and lodging have encouraged breeders to adapt a more radical approach with so-called "leafless" and "semi-leafless" peas (36, 165). In plants with the "semi-leafless" character, all the leaflets are converted into tendrils but the stipules are greatly reduced in size. According to Snoad and Hedley (167), a "leafless" type with slight increases in stipule size and growth rate is likely to prove a suitable ideotype.

Hybridization

Intraspecific:

Within species hybridization followed by selection remains one of the most powerful tools available to breeders. It often misses special mention in reviews on plant breeding, however, even though backcrossing - usually to adapted local varieties or breeding material - is regularly highlighted. For any crossing program to be successful, useful, heritable variation and the availability of a large gene pool is essential. Most breeders assemble, and while actively engaged in a specific breeding project, maintain a wide range of indigenous and exotic germplasm. The tendency in the past had been either to neglect the maintenance of such germplasm or even to discard material once specific breeding objectives had been attained. Fortunately genetic conservation is now recognized to be as important as utilization.

Also important are the transfer of genes (e.g. dominant S-alleles from agricultural kale to Brussels sprout inbreds (161)) and the useful genetic variability created by hybridization between types within a species. Crisp (27) reported a number of such crosses between types in *Brassica oleracea* L. but commented that none had been commercially successful. More recently, however, Gray and Crisp (66) suggested that advances could be achieved by selecting self-compatible material from annual x biennial hybrid populations of cauliflower. Gray and Crisp also successfully produced excellent self-compatible autumn heading forms from summer (annual) x winter (biennial) crosses (unpublished). Hybridization between *italica* and *botrytis* forms of *B. oleracea* can considerably widen the useful gene pool for cauliflower/calabrese/ broccoli breeders (65), as evidenced by the new calabrese-like plants selected by Crisp, Sanders, and Roberts (30) from crosses between cauliflower and Cape broccoli.

Interspecific and Intergeneric:

Interspecific crossing in vegetable breeding has been applied mainly to the transfer of disease resistance, as in the transfer of bean yellow mosaic virus resistance from *Phaseolus* coccineus L. to P. vulgaris L. beans (8,15,39) and clubroot resistance from turnip Brassica campestris L. to swede B. napus L. (106). Rick (145,147) and Coyne (26) reviewed the contribution from interspecific crossing, where major successes have been achieved in the transfer of Fusarium wilt (13) and tomato root-knot nematode (64) resistance from wild to cultivated tomatoes. The transfer of Erysiphe mildew resistance to Cucurbita maxima Duch. ex Lam. and C. pepo L. from C. lundelliana Bailey is another example (143).

In addition to disease resistance, other useful characters, sometimes novel, may be transferred from, or appear in, crosses to wild species, e.g. the successful transfer of useful genes from the wild Lactuca virosa L. into cultivated lettuce (180) and from wild Lycopersicon species into cultivated tomato (147). The useful gene pool of Cucurbita has also been increased by interspecific crossing in this polymorphic genus (144). Barriers to interspecific hybridization may be overcome by embryo culture or somatic hybridization. The latter will undoubtedly play a much more important role in difficult interspecific crosses such as Brassica oleracea L. x B. campestris (sensu lato), which provided the synthesized leaf vegetable "Hakuran" (119). Within the Brassicae, the transfer of cytoplasmic male sterility from Raphanus sativus L. to Brassica oleracea L. (9) represents a major breakthrough. McNaughton and Ross (115) produced an excellent review of interspecific and intergeneric hybridization in the Brassicae which, though concerned mainly with the improvement of forage crops, also contains useful information for breeders of horticultural brassicas. Namai, Sarashima, and Hosoda's review (117) on interspecific and intergeneric hybridization breeding in Japan is also useful.

Hybrid Varieties

The pioneering work of G. H. Shull on the importance of heterosis (or hybrid vigor) in corn, Zea mays L., led to the development of F_1 hybrids in that crop (168). F_1 hybrid breeding, especially in outbreeders, has now become important in many vegetable crops. Coyne (26) has drawn attention to the predominance of hybrid varieties of sweet corn and squash in the USA and the increasing emphasis on hybrid seed production in cucumber, summer squash, cabbage, broccoli, onion, and carrot.

In vegetables, three basic genetic systems have been used to exploit the expression of heterosis following the hybridization of inbred lines that have been rigorously selected for characters of value and that usually display inbreeding depression. These systems are cytoplasmic male sterility (CMS), self-incompatibility (SI), and the manipulation of sex forms. Additionally, hand-pollination techniques are used, especially where large amounts of seed are set from one pollination, as in eggplant (19) and tomato (146) (the latter provides an unusual example of successful F_1 hybrid breeding in a predominantly inbred crop).

Genetic male sterility has also been used to a limited extent in some vegetable crops (61,196).

Cytoplasmic Male Sterility:

One of the most important discoveries in the breeding of vegetables was cytoplasmic male sterility (CMS) in onions by Jones and Clarke (96). Henry A. Jones found his male sterile plant in a progeny of "Italian Red" grown at Davis, California, providing yet another classic example of the impact of foreign germplasm in plant breeding. The concepts of using cytoplasmic male sterility and interactive nuclear genes are illustrated in Figure 1.

The major problem with commercial F_1's is seed production (61), especially with straight hybrids (male sterile inbred x pollinator, Figure la) where the weak inbred nature of the parents leads to low seed yields. This problem is partly overcome by the use of three-way hybrids in which the male sterile parent is itself a vigorous F_1 (Figure 1b). In the early days of F_1 hybrid onions in Europe the uniformity of so called hybrids fell below expectation because pollinators were open-pollinated varieties. As breeding progresses, however, pollinators are more likely to be from half-sib families or even inbreds, thereby improving hybrid uniformity. Nevertheless, Dowker and Gordon (43) have suggested that the advantages of F_1 hybrid row crops such as onions are not as great as many suppose, especially as competition within a closely spaced row nullifies the effects of genetic uniformity.

Hybrid onions began to make their mark commercially in the USA in the 1950s, and by 1979 it was estimated that 50% of the onion crop in the USA was grown from hybrid seed (194). In Europe, however, it is only now that open-pollinated onion varieties are losing ground to hybrids. There is no doubt that in the temperate regions of the world the numbers of hybrid varieties of onions are likely to increase dramatically over the next few years, partly because of the exclusivity that ownership of the parent lines confers upon breeders and seed producers. This is a trend that should be resisted in the developing world, at least until more positive proof is available of the advantages of F_1 hybrid onions in the tropics, and until well organized, efficient seed multiplication schemes have been devised.

Synthetic varieties (44), on which recurrent selection can be imposed during maintenance and seed multiplication, may provide breeders in the developing world with alternatives to F_1 hybrids. A number of breeders are now trying to exploit CMS as an alternative to SI systems to produce F_1 hybrids in *Brassica oleracea* L. (cabbage, Brussels sprouts, cauliflower, broccoli, and calabrese), *Brassica campestris* spp. *pekinensis* Rupr. (Chinese cabbage), and *Raphanus sativus* L. (radish) (10,127,135,158,196). Unfortunately, in temperate regions the association of low temperature chlorosis with CMS transferred from radish to brassica crops has been a serious handicap. As research progresses CMS

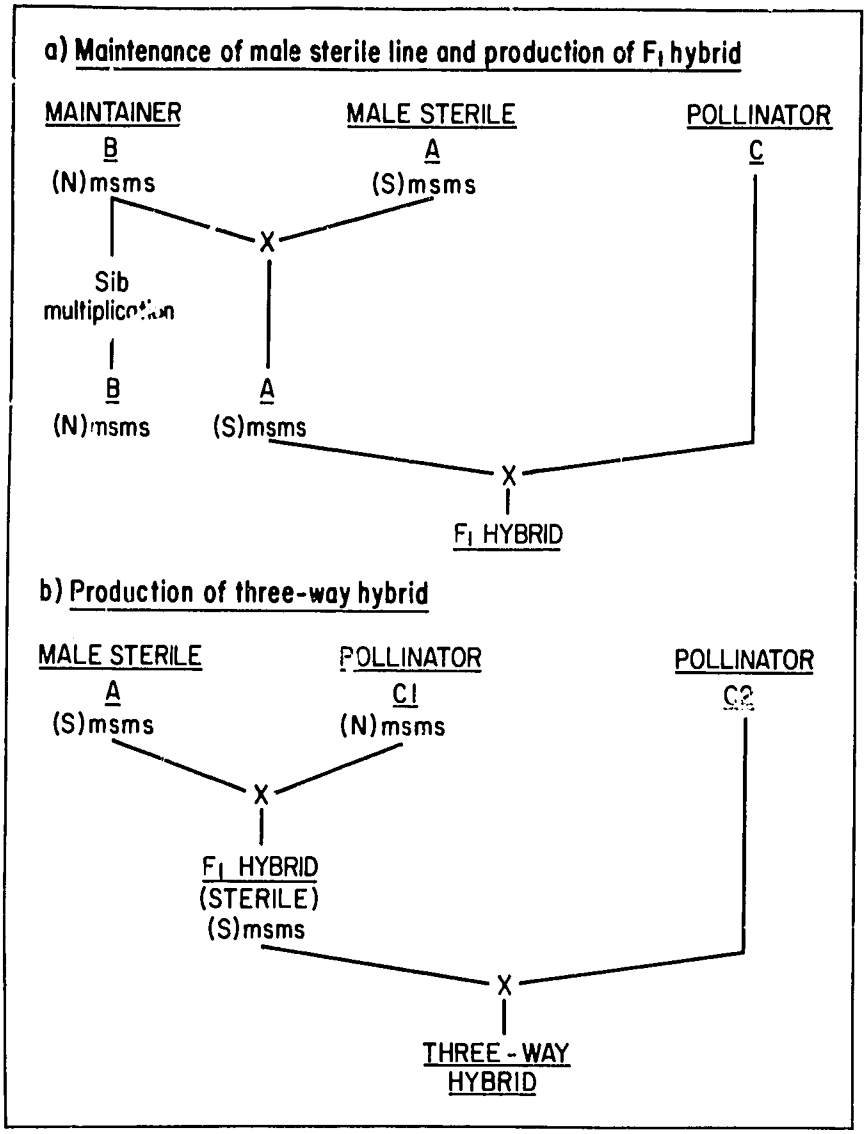

Figure 1: Scheme for seed production of hybrid onions using cytoplasmic male sterility.

(N) represents normal cytoplasm, (S) sterile cytoplasm, and msms nuclear male sterility. Interaction between (N) and msms gives fertile plants and (S) msms gives male sterile plants. The symbols A, B, and C are used to describe male-sterile, maintainer, and pollinator parents.

could play a more important part in the breeding of hybrid brassicas.

Self-Incompatibility:

The use of self-incompatibility as a tool in the breeding of hybrid brassica crops is now well established (27,92) despite the problems, especially those of cost, in maintaining parental inbreds and in obtaining F_1 hybrid seed lots that are relatively free from "sibs." The historical development and use of this system has been reviewed by Hinata and Nishio (78,79).

The principle is that inbred lines homozygous for a given S-allele (the gene controlling self-incompatibility) (109,124,125) are produced by self-pollinating in the bud stage when the self-incompatibility mechanism is not operating (134) or artificial aids, such as treatment with CO_2, are used to stimulate selfing of the open flower (91,108,116). Recently, Smith and Mee (163) obtained good sets of selfed seed on SI lines of Brussels sprouts using blowflies enclosed with the plants in cellophane bags.

Hybrid seed is usually produced from seeding together two parental inbreds that are mutually cross-compatible. Rigorous selection for parents with stable self-incompatibility in a range of environmental conditions has greatly improved the reliability of this system (123). In hybrid brassica seed production, blowflies appear to be more reliable pollinators than honeybees (53), but add to the cost of seed production because of the need to confine them on seeding crops. Modifications to improve seed set over the traditional F_1 hybrid with two parents include double cross hybrids (A x B) x (C x D) and three parent crosses (A x B) x C.

While the use of CMS may eventually replace SI in the breeding and seed production of brassica hybrids, it is likely that the latter method will be preferred by most brassica breeders for a number of years to come.

Manipulation of Sex Expression:

Manipulation of sex expression in spinach (192), cucumber (137), and asparagus (73,112,164) has provided major breakthroughs in the breeding of F_1 hybrids in these crops.

At Versailles, Thevenin and Dore (177,178) have successfully employed tissue culture techniques to clone parental inbreds of asparagus and have created homozygous parents by searching for haploids and then doubling their chromosome numbers.

Inbreds Versus Hybrids:

A number of geneticists, including Jinks (97), have raised doubts about the need for F_1 hybrids. Unless it can be shown that heterosis is due to overdominance, genetic justification for this breeding practice is scarce. Jinks has proposed that dispersion of dominant genes is the major cause of heterosis and that reported cases of apparent overdominance can be attributed to non-allelic interaction and linkage biases. Pure breeding self-compatible or self-fertile lines of crops (e.g. horticultural brassicas, onions, and carrots) that are sufficiently vigorous for use as commercial varieties may be possible. Studies such as those described by Smith (162) on Brussels sprouts, in which attempts are made using single seed descent to produce vigorous inbreds as good as or better than F_1 hybrids, are playing an important part in combining the best from theoretical genetics and applied plant breeding.

Genetic Conservation

The need for genetic variability in all breeding programs is evident. Breeders throughout the world attempt to assemble as wide a relevant gene base as possible. Peterson (138) summarized the extensive use of plant introductions for vegetable breeding in the USA and stressed the important role played by the Plant Introduction (PI) Stations. It is one thing, however, for an individual breeder or group of breeders to assemble useful genetic variation, but another to ensure that such material is preserved, described, and made readily available to breeders everywhere.

Fortunately methods are now available to store seed in a viable condition over a lengthy period of time. Long-term storage of seed has helped stem the erosion of genetic resources (58) caused by the rapid disappearance of land races and old varieties and by the destruction of natural habitats of important wild relatives of crop species. Seed stores maintained at low temperatures and low humidity (149) now form the core of national and international gene banks. The conservation of global genetic resources is, however, a task beyond most individual countries' means. Thus, in 1974 the International Board for Plant Genetic Resources (IBPGR) was formed by the Consultative Group on International Agricultural Research with a mandate to promote and coordinate work on the collection and preservation of germplasm, and the data storage and retrieval systems that are a key to the efficiency of gene banks. Although the IBPGR initially concentrated on cereal crops, in recent years it has increased its efforts on vegetables and has published, or intends to publish, reports on the genetic resources of amaranth, cruciferous crops, tomato, *Allium*, *Capsicum*, okra, eggplant, and Cucurbitaceae (86). In addition, there is a worldwide list of vegetable germplasm collections, including smaller ones and those belonging to private companies (183). The collaborative role of research stations is exemplified by the joint work of AVRDC and the National Vegetable Research Station, Wellesbourne (NVRS), with AVRDC serving as a main center for conservation of Chinese cabbage and NVRS providing facilities for storing a duplicate seed collection.

While moves to ensure conservation of valuable germplasm have undoubtedly been at least partially successful, there is little room for complacency. A great deal of genetic material still requires collection, multiplication, characterization, evaluation, and storage. Moreover, data storage and retrieval systems must be devised to make known to potential users the useful characters of genetic material. For open-pollinated species, the optimum method of seed multiplication is still under debate, and it seems certain that logistic problems in handling large populations will result in compromise. Although a number of data storage and retrieval systems have been tried experimentally (75,80,81,84), a universally acceptable system has yet to be devised. Thus, although interactive systems are highly desirable, it seems probable that in the foreseeable future breeders will have to depend on individual gene banks producing printouts with information on their own collections. Fortunately, there is increasing standardization of descriptor lists for a wide range of crops through the aegis of the IBPGR.

Future Prospects

Over the past decade, plant tissue culture techniques have been widely used in plant propagation and the elimination of pathogens (181), and are now being used increasingly as aids in plant breeding (17,122,140).

At a time when we regularly hear terms like biotechnology and genetic engineering, it is tempting to think that the use of new techniques in genetics and cell biology will revolutionize plant breeding. These techniques have an important role in the applied biological sciences (16), and their possible application in plant breeding has been reviewed by Riley (148), Sprague, Alexander, and Dudley (169), and Ingle (87). Nevertheless, it is perhaps premature to assume that the transfer of nitrogen fixing (Nif) genes from Klebsiella pneumoniae (Schroetar) Trevisan to Escherichia coli (Migula) Castellani and Chalmers (40) will lead to their transfer to higher plants. More immediate success is likely to be achieved in leguminous crops such as peas and beans through the improvement of existing associations between plants and nitrogen fixing organisms such as Rhizobium spp.

Anther or pollen culture, somatic cloning, and protoplast fusion should play an increasingly important part in vegetable breeding. The aseptic culture of hybrid embryos has already contributed to overcoming difficult gene transfers from one species or genus to another, and protoplast fusion techniques (20) are making possible a number of hitherto unattainable interspecific and intergeneric crosses. The major breakthrough by Power, Berry, Chapman, and Cocking (141) in achieving somatic hybrids of two Petunia species with different chromosome numbers, P. parodii Steere with 2n = 14 and P. parviflora Jusseau with 2n = 18, is extremely encouraging for breeders trying to transfer genes in interspecific or intergeneric crosses such as Petroselinum hortense Hoffm. (parsley) x Daucus carota spp. sativus Hoffm. (carrot) (48). In the transfer of useful genes, an alternative and more rapid method than either traditional sexual hybridization or somatic hybridization, both of which are likely to necessitate recurrent backcrossing, may be the use of irradiated pollen to transfer characteristics from a paternal source into a maternal genotype, as reported by Pandey (132) and Jinks, Caligari, and Ingram (98) in their experiments with irradiated pollen in Nicotiana. Using this method, attempts are now being made at NVRS, Wellesbourne to transfer genes for resistance to clubroot from turnip (Brassica campestris L. var. rapa Thell) into the horticultural forms of B. oleracea L. (P. Crisp, unpublished).

Protoplast culture may also contribute to vegetable breeding by allowing the selection of cells tolerant to various agents incorporated in a growth medium. For example, maize plants have been produced that are resistant to the fungal disease known as "Southern Corn Blight", after selection of cells that are tolerant to the toxin produced by the blight fungus (14). Protoplast cloning in potatoes by Secor and Shepard (156) and Gunn (70) has provided an unexpectedly wide range of variation among protoclones developed from the same variety. Although it is not known exactly why such variability arises, the technique may open the way for correcting specific weaknesses in varieties that are otherwise acceptable, and may be applicable to vegetable crops other than potatoes (107).

Whether or not inbreds or hybrids will predominate as commercial varieties, the synthesis of so-called instant inbreds by pollen or anther culture to produce haploid plants that are converted into homozygous diploids (111) could considerably shorten the time span of breeding programs, especially in biennial crops. This is a technique that has been successfully used in rape (B. napus L. var oleifera (E and G)) breeding (100,193) and is showing promise in horticultural B. oleracea L. (126).

Studies on the molecular basis of cytoplasmic male sterility, such as those on maize (101) and sugar beet (142), may help to make it possible to manipulate CMS systems to the benefit of breeders and seed producers of F_1 hybrids using chemicals to make normal cytoplasm male sterile and vice versa.

Genetic manipulation at the cell level is undoubtedly attractive to the plant breeder but, as has been emphasized by Arnold (3), most breeders are concerned with balanced complexes of genes, and the value of the transfer of a specific piece of DNA from one plant type to another is likely to be limited to certain clearly defined and specialized cases. Moreover, as stressed by Sprague, Alexander, and Dudley (169), field evaluation of a breeder's lines and potential varieties continues to be the most time consuming and expensive step in breeding programs. Perhaps the role of biotechnology in plant breeding is best summarized by Ruttan and Sundquist: "Contrary to the contention of some, the emerging biotechnologies are not a substitute for conventional plant breeding but are expected to generate improved plant capabilities which will then be incorporated into conventional breeding programs" (153). Although biotechnology does offer exciting new possibilities for vegetables, it can be anticipated that for the next ten to twenty years most improved varieties will be developed from traditional breeding programs and will have resistance to pests, diseases, and physiological disorders as well as better adaptability to environmental stress.

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