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Onion *Allium cepa* L.

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Allium is a monocotyledonous genus which has been assigned to the Amaryllidaceae, Liliaceae, and a distinct family, the Alliaceae. It is diverse taxon of over 500 species, including the cultivated bulb onion (*A. cepa* L.), chive (*A. schoenoprasum* L.), Japanese bunching onion (*A. fistulosum* L.), garlic (*A. sativum* L.) and leek (*A. ampeloprasum* L. var. *porrum*, syn. *A. porrum* G. Don). The alliums have been cultivated for food, medicine or religious purposes since prehistoric times.[76] Their distinctive flavor and odor occur when plant tissue is bruised, cut or macerated and the enzyme alliinase hydrolyzes s-alk(en)yl cysteine sulfoxide precursors to yield volatile sulfur compounds.[28] These flavor compounds are widely appreciated by many cultures as an important component of their foods. In addition, the alliums possess many medicinal uses, such as lowering of sugar and lipid levels and platelet aggregation or enhanced fibrinolysis in the blood.[2]

The bulb onion is the most economically important cultivated *Allium* species with a total world production in 1989 of approximately 27 million tonnes.[30] The importance of the bulb onion in the diet of a wide range of cultures is reflected by the greatest overall production occurs in the most populous countries: in 1989, China (3.8 million tonnes), India, Indonesia and the USSR (2.5 million tonnes each), and the USA (2.2 million tonnes) were the leading producers.[30] Onion is a major commodity of international trade; imports in 1987 by Germany, France, the UK and the USA were valued at US $265 million.[94] Annually, the US onion crop is the third most valuable commercial vegetable ($426 million in 1988), following only tomato and lettuce.[104]

Cytology

The greatest number of *Allium* species are found in North Africa and Eurasia; over 90% have a basic chromosome number of 8, including all of the widely cultivated alliums.[106] More than 95% of the North American *Allium* species have a basic chromosome number of 7.[106] *Allium cepa* is diploid ($2n = 2x = 16$) with eight large pairs of chromosomes, seven metacentric or submetacentric and one satellited subtelocentric chromosome with the nucleolus organizer region.[102] Onion is an excellent cytological model system because the relatively large chromosomes spread easily for observation and cytogenetic studies. Heterochromatic DNA can be differentiated from euchromatic DNA by Giemsa C-banding, G-banding, Q-banding and fluorescence.[29, 60, 107] Karyotypic analyses of the genus *Allium* have been undertaken to assess the phylogenies of potentially closely related species. Within *A. cepa*, very little variability was observed in the overall symmetry of the chromosomes.[106] However, the size of teleomorphic heterochromatin was variable and may be useful in studies of systematics and evolution.[21] Karyotypic differences demonstrated that the top-setting onion *Allium* × *proliferum* (Moench) Schrad. is an interspecific hybrid between *A. cepa* and *A. fistulosum*.[100]

Genetics

Current understanding of onion genetics is very rudimentary. Only 18 morphological or disease resistance loci have been described,[95] including the color of anthers,[53] foliage[6, 53] and seed coats;[14] dwarf scape;[42] restoration of cytoplasmic male sterility;[52, 101] and resistance to pink root,[84] *Fusarium* basal rot[105] and ozone damage.[26] Four of the 18 known markers are deleterious chlorophyll mutants.[53] There is only one published report of genetic linkage in onion, between yellow seedlings and glossy foliage.[53] Recent advances in the identification and mapping of biochemical markers, e.g. isozymes and restriction fragment length polymorphisms, will probably expand the genetic map and provide basic information on the phylogeny, genetics and breeding of onion.

Numerous authors have studied the inheritance of onion bulb color and five major genes (*I*, *C*, *R*, *G* and *L*) have been named. Rieman[97] described the *I* locus at which a dominant allele ($I-$) inhibits the production of color and the bulbs are white. The expression of red, yellow, or chartreuse pigments requires that the plant be homozygous recessive at the *I* locus. The *C* locus conditions the production of colored bulbs; all *iicc* bulbs are white. Plants with a dominant allele at the *C* locus and homozygous recessive (*rr*) at the *R* locus are yellow to brown in color. Red bulbs are conditioned by dominant alleles at both the *C* and *R* loci ($iiC-R-$).[8] A dominant allele at the *G* locus conditions a golden color without pink; chartreuse bulbs were proposed to be homozygous recessive at the *G* locus.[22] Jones and Peterson[58] described complementary factors conditioning a light-red bulb in progeny from a cross of two yellow bulbs. El-Shafie and Davis[22] named an additional locus, *L*, which conditions the red pigment when the plant has the genotype $iiC-rrG-L-$. In addition, numerous genes intensifying bulb color exist. Even though the inheritance of bulb color is conditioned by several genes, breeders can easily select for the desired type. However, recessive types may continually show up during maintenance of populations, e.g. the inbred MSU 5718 segregates chartreuse bulbs at low frequency.

Breeding Objectives

Onion breeders must focus their efforts on traits important to the production of high-quality seed and bulbs. Bulb traits include size, shape, color of skin and flesh, single centers, skin retention, firmness, dormancy, pungency and concentration of soluble solids (traits discussed in the section on quality). Production of commercially acceptable bulbs is dependent on resistance to diseases, pests and

bolting (flowering during bulb production). The production of high-quality seed requires vigorous bulbs, uniform flowering, straight seed stalks, pollinating insects and proper conditions to dry and clean the seed.

The onion bulb is composed of storage leaf bases attached to the basal plate (stem). Bulbing is initiated by a combination of day length and temperature,[68] i.e. the critical day length required for bulbing may be shorter at higher temperatures. Currah and Proctor[13] reported that temperature is more important than day length for bulbing at lower latitudes because there is little annual difference in day length. Onion breeders must recognize that bulbing is environmentally dependent and that cultivars adapted to one region may not produce desirable bulbs at a second location. Unadapted material may reach the critical day length for bulbing too early and produce small bulbs. Conversely, material requiring long days to bulb may never mature properly under short days. Well-matured bulbs with tight necks store better and are less likely to develop storage rots. Tight outer dry skins protect the bulb and reduce the numbers of bald onions after storage. In order to keep onions true to type, breeders constantly select for the desired bulb type. Without selection, bulbs have a tendency to develop multiple centers and become softer and flatter.[41]

Seed yield is a major trait that has received little research attention. Many publicly released inbreds in the USA are poor seeders and production of two-way hybrids is difficult. It is not clear if the poor seed yield is due to the reduced vigor of inbred lines or if the pollinating bees do not visit male sterile lines. Hagler *et al.*[38] reported significant differences between onion cultivars for sugar content in the nectar. They also observed that cultivars with low sucrose content in the nectar received fewer bee visitations than cultivars with high sucrose concentration, although no statistical tests were reported. Nye *et al.*[86] found significant differences among and between sterile and fertile inbred lines for numbers of bee visitations. It would appear that variability exists for the attractiveness of onion flowers to pollinators, but no research has documented a genetic basis.

Germplasm Resources

In spite of its economic significance, very little is known about the phylogeny of various types of onion (long versus short day, seed versus vegetative propagation). No single progenitor is known and the phylogenetic relationships among onion and wild *Allium* species are unclear. Vavilov assigned the center of origin of *A. cepa* to central Asia, comprising Pakistan, Afghanistan, Tadzhikistan and Uzbekistan.[45] Vvedensky[108] classified the bulb onion into section Cepa (Mill.) Prokh. with *A. galanthum* Kar. et Kir., *A. oschaninii* O. Fedtsch, *A. pskemense* B. Fedtsch., and *A. vavilovii* M. Pop. et Vved. The grouping of the bulb onion with these wild species has been supported by geography,[40] serology of seed proteins,[95] Giemsa C-banding and karyotypes,[21, 99, 107] and the banding patterns of esterases.[36, 37] The wealth of genetic variability in wild and other cultivated alliums, e.g. disease and pest resistances, has not been extensively exploited for the improvement of the bulb onion. Research must evaluate the crossability of the cultivated alliums with each other and their wild relatives. *Allium galanthum* and *A. pskemense* show low cross-fertility with *A. cepa*.[71, 77, 98] McCollum[71] reported complete sterility in hybrids between *A. oschaninii* and *A. cepa*. Although *A. cepa* and these wild *Allium* species may have arisen from a common progenitor, the sterility exhibited by interspecific hybrids indicates that their use in the genetic improvement of the bulb onion will be difficult.

As onion cultivation spread to new climates and environments, populations were selected differing in shape, color, flavor and storage ability. It is unclear whether this variability reflects a diverse genetic background or human selection maximizing the differences for bulb type within a restricted background. Germplasm collections of onion are maintained in many countries, including the USA, the European Community, Japan and Israel. The goal of these collections is to preserve genetic diversity in the cultivated onion. It is important to characterize this diversity, understand which sources of germplasm are truly divergent from widely cultivated types, and reduce redundancy in the collections. Astley[1] described three classes of *Allium* germplasm: advanced cultivars, primitive cultivars and landraces, and wild species. To the onion breeder, the primary source of genetic variability is the working collection. This material is highly adapted and most likely to produce commercially acceptable types. Unadapted landraces and wild species represent more diverse germplasm, which often requires a great deal of effort to produce competitive populations or lines. Unadapted material is most often used as a source of a specific trait, such as disease resistance.

Reproductive Biology

For seed production, onion bulbs are grown under conditions conducive to proper bulbing. At maturity, the foliage of the plant collapses and dries. Occasionally, the onions may be undercut to hasten maturity. After bulbing, the onion requires a cool dormant period to induce the formation of floral initials. The length of time required under 15 °C to induce flowering is different for various onion populations. A majority of bulbs stored at 7 – 10 °C for 60 – 100 days will flower. However, highly dormant material may not be induced to flower after months of storage below 10 °C.

Hundreds of perfect flowers are present in each onion umbel. The flowers consist of a single superior pistil with six locules, therefore producing a maximum of six seeds per capsule. Outcrossing is encouraged by protandry. The inner whorl of three stamens are the first to shed pollen, followed by the outer whorl of three. Self-pollination is possible because the individual flowers of the onion umbel mature at different times.[12] Therefore, receptive stigmas will be present when pollen is being shed by flowers in the same umbel.

Manual emasculation and pollination of onion are tedious. Although the stamens are easily removed from a single flower, the size, number and continuous maturity of the many small flowers per umbel make hand pollination unattractive. As a result, onion breeders have developed techniques to manipulate insect pollinators. House flies or blowflies are commonly used for self-pollinations or intercrosses of less than five plants.[55] In the USDA onion breeding program, onion inflorescences are covered with small cages constructed from three metal rings supported by metal strips. The cages are covered with pillow tubing, 50 cm wide, made from a 65% polyester, 35% cotton blend. A small plastic tube is inserted in the top of the cage for introducing the fly pupae and the pillow tubing is tied shut. The cages are

draped over the plants and tied tightly under the flowers with small paper-coated wires. The cage must be tied tightly enough that fly pupae do not fall out of the bottom. The bags are attached to wire supports at the top and bottom of the cage to avoid movement in the wind. After addition of the pupae, a cork is placed in the tube. Flies will emerge from the pupae and pollinate as they visit the flowers searching for nectar. Fly pupae can be raised or obtained from commercial sources.

Production of open-pollinated (OP) populations and experimental hybrids is completed in large mesh cages using bees. Mother bulbs are grown, harvested, cured, vernalized, selected for desirable traits, and planted in rows. Wilson[114] reported that transverse cutting of stored bulbs induced a greater number to flower. In the USDA onion breeding program, the top one-third to one-half of the bulb is cut to stimulate even bolting. After the scapes have emerged, the plots are covered with a mesh cage and bees introduced. For field production of seed, convention dictates that over 4 km should separate seed-production fields of different colored onions (N. Molenaar, personal communication). For hybrid seed production, a ratio of eight seed-parent rows (see below for description of cytoplasmic male sterility) to two pollen-parent rows is commonly used. A problem with seed-to-seed production of hybrids is the simultaneous flowering of inbred lines. To a certain extent, flowering can be manipulated by changing the planting date of inbreds. However, for large-scale production, harvesting and planting of mother bulbs is too expensive and seed-to-seed production is required. Desirable inbreds can be subjected to selection to shift the flowering date to flower simultaneously with the other inbred. Breeders will often select for upright, straight scapes which help to reduce losses of mature seed. Researchers have also noted differences in the seed from self-pollination of individual plants.[54] No information is available on the basis of these differences in seeding ability. Morse (cited in Jones[47]) reported that yellow and brown cultivars are the heaviest seeders of the OP cultivars of that time.

Breeding Methods

The genetic improvement of the bulb onion is slow because 2 years are required to complete one generation (seed-to-bulb and bulb-to-seed). Because the primary economic product is the bulb, breeders must evaluate for quality in each generation. Shortening of the generation time to 1 year has been achieved,[61] however, no information is available on the tendency of populations selected on an annual cycle to bolt under normal field conditions.

The bulb onion is an outcrossing species that exhibits severe inbreeding depression and historically has been maintained as OP populations. Cultivars and hybrids currently grown in the USA trace back to a few OP populations of unknown origin.[69] Although hybrid onions are widely available, high-quality OP populations of onion with excellent seeding ability represent a significant component of commercial production.[10] The large general combining abilities observed for important bulb quality characteristics (see below) indicate that populations can be improved by recurrent selection. The advantages of progeny testing prior to recombination have been well documented for other outcrossing species.[39] Currah[12] described the improvement of tropical onion cultivars by mass and stratified mass selection. Although mass selection was successful in adapting a diverse population to a specific growing region in Ethiopia, it probably would not produce benefits for traits of low heritability. Dowker *et al.*[20] subjected European onion populations to S_1 and half-sib recurrent selection. Improved bulb quality was reported with no apparent yield reduction. Improved populations can be released as cultivars or subjected to inbreeding to extract inbred lines for hybrid development. Werner *et al.*[113] attempted to use the performance of early generation material to predict the performance of inbred lines derived from a cross between two diverse populations. Within a single season, the yield, quality and maturity of the recombinant inbred lines agreed well with the early generation material; however, genotype × environment interactions obscured the predictability over years or locations.

Jones and Davis[54] inbred six onion populations for up to six generations and observed that loss of vigor was most pronounced in the first generation. Inbreeding for one to two generations often produced uniform lines. Vigor was restored by crossing between inbreds; some hybrid combinations were higher-yielding than the parental populations and more uniform for maturity and for bulb size, shape and color.[54, 59] However, other combinations yielded better than the inbred parents, but less well than the best commercial cultivar. Jones and Davis[54] concluded that uniform, high-yielding hybrids could be generated after inbreeding and selection for two to five generations.

Heterosis and Hybrid Seed Production

Analyses of combining ability between onion inbreds have demonstrated consistent heterosis over the best inbred parent and occasionally over leading commercial OP population. Large general combining abilities (GCA) and specific combining abilities (SCA) have been reported for bulb maturity, yield and its components (rings per bulb, ring thickness), firmness and storage ability.[19, 43, 45, 59] Hosfield *et al.*[44, 45] generated diallel crosses of onion inbreds and observed consistently greater GCA over SCA for bulb yield and weight, earliness, rings per bulb, ring thickness, number of centers and storage loss. The SCA effects were about 10% of the GCA, but significant for 19 out of 24 comparisons. The authors concluded that the significant SCA effects warranted continued development of hybrid onion cultivars. However, only 2 of 36 hybrids outperformed the best inbred parent (B2190). Dowker and Gordon[19] observed that most reports of heterosis in onion compare the hybrid with the inbred parents and not with the best commercial cultivar. Significant heterosis over widely grown OP populations has been reported by Jones and Davis[54] and by Joshi and Tandon.[59]

Most publicly released onion inbreds were developed by selfing individual plants from OP cultivars or recombining previously developed inbreds. The large GCA effects indicate that superior inbreds are more likely to be selected from populations improved by recurrent selection or synthesized by recycling inbreds with good combining ability. However, it is important that inbreds be evaluated over years and locations before recycling into new populations.[44]

The production of hybrid onion seed became economically feasible with the discovery by Jones and Emsweller[56] of cytoplasmic male sterility (CMS). Jones and colleagues were inbreeding plants of the cultivar 'Italian Red' to develop a hybrid

red onion for storage. One plant (13-53) did not set seed after self-pollination and was saved by virtue of bulbils in the inflorescence. Sterility in 'Italian Red' 13-53 was cytoplasmically inherited (CMS-S) with fertility restored by a dominant allele (*Ms*) at a single nuclear restorer locus.[52] Male sterile plants possess the sterile cytoplasm and are homozygous recessive at the restorer locus (S *msms*). Male sterile lines can be maintained by crossing the sterile line with a maintainer line with normal cytoplasm and homozygous recessive at the restorer locus (N *msms*). After successive generations of backcrossing, the sterile line essentially possesses the genotype of the maintainer line. When planted together in isolation, the sterile and maintainer are propagated by harvesting seed separately from each line.

The non-restoring nuclear allele has been found in a variety of OP onion populations.[15, 66] Extraction of maintainer lines from some onion populations, e.g. the American short-day cultivar 'Grano' or the Japanese cultivar 'Sapporo-Ki', has been difficult due to the high frequency of the restorer allele. Male sterility is stably expressed,[78] although some male fertility may be present at high temperatures.[4] Significant progress in the development of onion hybrids has been realized and most commercially grown eastern storage onions in the USA are hybrids. Selection exercised during inbreeding has resulted in improved inbreds with disease resistance, e.g. to pink root and *Fusarium* basal rot, and the uniform maturity of hybrids also helps to avoid diseases associated with late-maturing plants, e.g. neck rot (*Botrytis allii*) and sour scale (*Pseudomonas alliicola*).[33] Due to low seed yield, many hybrid onion cultivars in the USA are generated by three-way crosses, i.e. the commercially marketed hybrid results from crossing a sterile F_1 seed parent (A × B) with a third inbred line.

Other sources of CMS in the bulb onion have been described; Berninger[7] discovered sterility (CMS-T) in the French cultivar 'Jaune Paille des Vertus'. Schweisguth[101] identified three independently segregating nuclear restorer loci. Fertility is restored by a dominant allele at one locus ($A-$) or at both of two complementary loci ($B-C-$). The complex inheritance and common occurrence of the restorer alleles make CMS-T cytoplasm more difficult to use successfully. Although sterility has been described in other onion populations,[10] it has not been characterized and the relationship to S or T cytoplasms are unclear.

Breeding for Disease Resistance

The major diseases of onion include pink root (*Pyrenochaeta terrestris*), *Fusarium* basal rot (*Fusarium oxysporum* f. sp. *cepae*), leaf blight (*Botrytis squamosa*), neck rot (*Botrytis allii*), white rot (*Sclerotium cepivorum*), smut (*Urocystis magica*), downy mildew (*Peronospora destructor*), purple blotch (*Alternaria porri*), black mold (*Aspergillus niger*), *Stemphyllium* blight (*Stemphyllium vesicarium*), smudge (*Collectotrichum circinas*), bacterial rots (*Erwinia carotovora* and *Pseudomonas alliicola*), nematodes (*Ditylenchus dipsaci* and *Meloidogyne hapla*), and yellow dwarf virus. The socioeconomic climate in many countries is against the use of pesticides and genetic resistance is becoming more desirable. Sources of onion germplasm showing resistance to ozone damage,[26] purple blotch,[illegible] downy mildew,[111] *Botrytis* neck rot[79, 80] and white rot[105] have been reported. Resistance to pink root is inherited as a recessive allele at a single locus[57, 54] and has been incorporated into many commercial cultivars, although stable expression has been problematic in some environments.[91] Cultivars showing adequate levels of resistance to *Fusarium* basal rot have also been developed[33] and resistance is conditioned by a single dominant gene.[103] Warid and Tims[111] scored an F_2 family under natural downy mildew inoculum and reported that dominant alleles at two genes conditioned resistance. Jones *et al.*[50] observed that the plant 'Italian Red' 13-53 was highly resistant to downy mildew but, to the knowledge of this author, the resistance has never been incorporated into a leading commercial cultivar. Many of the storage diseases of onion, e.g. neck rot or bacterial rots, are controlled by planting pathogen-free seed, applying chemicals, or properly curing and storing bulbs.

The two major insect pests of onion are thrips (*Thrips tabaci*) and maggot (*Delia antiqua*). Resistance to onion maggot has not been reported in *A. cepa*. Thrips routinely cause economically important losses by damaging the leaves during bulb production. Jones *et al.*[49] reported resistance to thrips in the cultivar 'White Persian'. The basis of this resistance appears to be reduced waxiness (glossy) of the foliage. Molenaar[81] described two genes controlling wax production; recessive alleles at one locus condition glossy foliage and at the second condition glossy scapes. The expression of a glossy scape occurs only when glossy foliage is present. The USDA has released four glossy inbreds (B9885, B9897, B11278, and B11377) useful in the production of glossy hybrids.

Cultivated and wild alliums possess many disease resistances potentially useful in the genetic improvement of the bulb onion, e.g. white-rot resistance in *A. ampeloprasum*;[9] downy mildew resistance in *A. roylei*;[64] and resistance to pink root,[93] smut[110] and onion maggot[23] in *A. fistulosum*. Fertile hybrids between *A. roylei* and *A. cepa* and successful transfer of downy mildew resistance have been accomplished.[65] Hybrids between *A. cepa* and *A. fistulosum* have long been known,[24] but the F_1 always shows extremely low fertility due to poor chromosomal pairing.[25, 67] The low degree of fertility exhibited by the hybrids between *A. cepa* and other *Allium* species restricts that successful introgression of disease resistances.

Breeding for Quality

Important bulb quality traits include size, shape, color, pungency, firmness, dormancy and amount of soluble solids (carbohydrate concentration). Bulbs of various shapes and colors are preferred by consumers in different parts of the world. Bulbs may be white, red, brown or yellow; round, piriform or flat; and soft or firm. Dormancy is important because onions are often stored and marketed when prices are higher. Higher soluble solids are important to the dehydrating industry producing onion chips or powder used as seasonings. The amounts of s-alkyl cysteine sulfoxide precursors and the enzyme alliinase contribute to the yield of volatile sulfur compounds that constitute the pungency of the onion bulb. Consumers in the USA often prefer a less pungent onion, whereas many tropical onions are prized for their strongly pungent flesh.

Most bulb quality characteristics have a genetic base and can be manipulated by onion breeders. Nakamura,[83] McCollum,[73, 74, 75] and Dowker and Fennell[18] estimated the heritabilities of bulb size and shape in different populations of onion. Although their estimates pertain only to the populations studied, agreement among

these independent studies indicates that the estimates may be true for onion in general. All three studies determined that the diameter and weight of onion bulbs show low heritabilities. Bulb height and shape index (calculated as height over diameter) showed relatively large genetic components. Therefore, breeders can expect response to selection for bulb height, but not for bulb size. These estimates are supported by practical observations; 'Italian Red Torpedo', a piriform onion, was selected from the flat cultivar 'California Early Red'.[74] It may be that the onion bulb will reach a certain height and continue to increase in diameter. The extent to which the environment is conducive to diameter increase would determine the shape of the bulb. If there is little time for the bulb diameter to increase, the bulb will be piriform; if the diameter of the bulb increases for a longer time, the bulb will appear flat.

Onion populations show marked differences in storage ability,[70] firmness,[27] pungency[92] and moisture content.[51] The environment can have a large effect on pungency and storage ability. Pitenius and Knott[92] observed that temperature and type of soil affect pungency. A common observation is that bulbs subjected to stress during the growing season are more likely to sprout in storage. Nevertheless, these traits also have a genetic base.[45, 87, 112] Phenotypic correlations between large size, softness, low pungency and poor storage ability have been widely recognized.[5, 31, 43, 45] In the USA, yellow short-day onions are characterized by large, soft, non-pungent bulbs, low solids and poor storage ability. These onions must be marketed soon after harvest or kept in refrigerated storage. Long-day eastern storage onions are generally smaller, firmer and more pungent; they have higher solids, and show better storage ability. The only reported genotypic correlation is between high solids and small bulb size.[73] These phenotypic correlations could be explained by water retention of onion at maturity. A large, less pungent, soft onion may retain more water at maturity, diluting the alkyl sulfides responsible for pungency. This onion would therefore be softer and more likely to sprout during storage. Eastern storage onions may retain less water at maturity resulting in firmer flesh, a higher concentration of solids and pungency compounds per unit dry weight, and longer storage. However, phenotypic correlations do not necessarily mean that the traits are conditioned by the same genes, and experiments must test this hypothesis. An interesting observation is that 'Sweet Sandwich', a three-way hybrid developed by the USDA, is a firm, well-storing and significantly less pungent onion.[88]

Biotechnology

The long generation time of onion makes the application of biotechnology to its genetic improvement very attractive. Successful micropropagation, callus culture and embryo rescue of *Allium* species have been reported[55] and are potentially useful tools in onion breeding. Embryo rescue offers the possibility of increasing the number of interspecific hybrids,[16, 34, 89] but introgression of beneficial genes may be severely restricted by low fertility. Meristem tip culture can be used to free vegetatively propagated shallot from virus infection.[109] *In vitro* evaluations for resistance to pink root or *Fusarium* basal rot of onion have been proposed by treating cultured cells with toxins produced by these fungi.[3, 35] Culture of the inflorescence or basal plate can be used to propagate male sterile plants without a maintainer line.[32, 90] Vegetatively propagated female parents of the hybrid would be transplanted directly in the field for pollination. The use of this technology will depend directly on the cost of propagating the female versus the increased revenue generated by hybrid seed. Another potentially useful application of tissue culture is the extraction of haploid plants by ovule culture. Muren[82] reported a high frequency of haploids from culture of unpollinated onion ovules. In contrast, poor recovery of haploids was observed by Keller.[62] Haploid plants can spontaneously double (or be induced to do so), generating completely homozygous plants. If these double haploid plants can be maintained by seed, the process will yield numerous inbred lines avoiding the '2 years per generation' cycle. Assuming that this technology will be generally applicable to diverse populations, inbred lines could be quickly extracted and tested in hybrid combinations.

Recent advances in the identification and mapping of biochemical markers, e.g. isozymes and restriction fragment length polymorphisms, are likely to expand the rudimentary genetic map of onion and provide basic information on phylogeny, genetics and breeding. Because of this crop's long generation time and the high cost of harvesting and storing bulbs, the genetic improvement of onion would benefit from genetic markers linked to desirable traits. These markers would allow for precise identification of plants with the desired genetic constitution at an earlier stage of development. Markers linked to the genes conditioning traits such as high solids, low pungency or long dormancy would reduce the number of evaluations completed on each bulb or family. A breeder would evaluate for the genotypes at the marker loci instead of completing numerous independent evaluations.

Onion is a monocotyledonous plant and transformation with commonly used *Agrobacterium* vectors may be difficult. Jakowska[46] observed that abnormal outgrowths were associated with infection of onion bulbs with *Agrobacterium tumefaciens*. Dommisse *et al.*[17] reported successful transformation of onion by *A. rhizogenes* for the nopaline marker gene. Transformation offers great potential to onion breeding because of the long generation time and strict quality standards. However, its successful application will depend on the availability of cloned genes.

Future Prospects

The economic importance, widespread use and potential health benefits of onion are an impetus to continued research on the phylogeny, breeding and genetics of this important vegetable. High-quality OP cultivars represent a significant proportion of world production, both now and in the future. Mass or recurrent selection will continue to improve OP populations for quality, uniformity, and resistance to diseases and bolting. However, the greater uniformity and significant heterosis expressed by hybrids will remain as a stimulus to their continued development. Exploitation of male sterility will be a primary factor in the economic production of hybrid seed.

Onion would benefit from increased resistance to diseases and pests. Identification of new sources of resistance and incorporation into elite cultivars could result in greater yield stability and significant reductions in pesticide use. In addition, market trends will require onion breeders to develop new cultivars with specific characteristics to meet processing requirements (large rings for breading, or high levels of dry matter for dehydration) or changes in consumer preferences, e.g. lower pungency preferred in the USA; in subtropical and tropical production areas, highly pungent onions with long dormancy are demanded.

The documented health benefits of *Allium* species may increase consumption. Although the bases of these benefits are unclear, continued research should elucidate the responsible compounds and their genetic bases, and whether recurrent selection can increase the benefits to humans of *Allium* consumption.

In the future, biotechnology will play a more significant role in the development of superior cultivars and hybrids. Micropropagation or cell culture of male sterile plants would aid the development of hybrids from populations with a high frequency of the nuclear restorer. Other sources of cytoplasmic male sterility may become available. Transformation of *Allium* may become an important breeding tool, assuming the availability of cloned genes.

A better understanding of the phylogenetic relationships between onion and its wild relatives is a necessary research goal. Although interspecific hybridizations have been reported, little information is available on successful introgression of desired traits. Identification and characterization of the progenitors of the bulb onion are desirable, especially given that the habitat of some wild *Allium* species is threatened.[41] Once identified, wild *Allium* species closely related to the cultivated forms must be collected and maintained in germplasm collections. This secondary gene pool may be a source of unique traits, such as disease resistances, important in the development of new cultivars and hybrids.

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