Chapter 1
Allium

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1.1 Introduction

The word "*Allium*" comes from the Greek word "aloe," which means to avoid, and was given to the genus because of the characteristic offensive smell of its members. The genus *Allium* is one of the largest plant genera and includes about 780 species. Cultivation of *Allium* species is reportedly very old and as extensive as civilization itself (Block 2010). The wealth of *Allium* species was mentioned in the ancient civilizations both as flavorful foods and healing herbs.

Allium is a genus within the family Alliaceae and belongs to the order Asparagales of the monocot division. Asparagales and the Poales (which includes the grasses) are two well-supported monophyletic orders within the monocots (Rudall et al. 1997). The genus *Allium* is mainly restricted to the regions that are seasonally dry, with centers of diversity in Soutwest/Central Asia, eastern Asia, and in North America. Members of the genus *Allium* include many economically important crops such as onions (*Allium cepa*), shallots (*Allium oschaninii*), leeks (*Allium ampeloprasum* var. *porrum*), scallions (*Allium ascalonicum*), garlic (*Allium sativum*), chives (*Allium schoenoprasum*), Japanese bunching onions (*A. fistulosum*), rakkyo (*A. chinense*) and Chinese chives (*A. tuberosum*). Others such as *A. karataviense* and *A. christophii* are cultivated as ornamentals (Huxley et al. 1992).

Different communities use several wild *Allium* species for different purposes while breeders use them as sources of economically important traits for improving the cultivated species. Many wild *Allium* species are believed to have significant potential contribution to the *Allium* breeding community and to the global food and health needs. Despite the importance of these species, there are very few studies and research investments on them. The taxonomy is not extensive and conservation efforts have been limited. The limited extent of genomic tools within the genus as a whole has further limited research focus to cultivated species. We provide here a brief review on wild *Allium* species including basic botany, conservation initiatives, contribution toward the development of cytogenetic stocks, genetic tools, and improvement of the cultivated species. The potential for more domestication and commercialization of wild *Allium* species as a source of income, nutrition, and medicinal remedy are also mentioned.

1.2 Basic Botany of the Species

The taxonomy of *Allium* has been described as complicated with a great number of synonyms and intrageneric groupings (Klaas 1998). The genus comprises either short- or long-lived perennials (Brewster 1998) with characteristic storage organs (Fritsch and Friesen 2002). The typical storage organs are rhizomes, roots, or bulbs.

The bulbs are generally enclosed in membranous tunics, free or almost free tepals, and often in a subgynobasic style (Friesen et al. 2006). The bulbs can be large and single, or small, forming clusters (Le Guen-

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Le Saos et al. 2002) and range in size from 2–3 mm to 8–10 cm in diameter.

The leaves are tubular (as in onions) or flat arising from the underground stem with long sheathing base, which can give the appearance of a stem (Block 2010). Many *Allium* species have basal leaves that wither away from the tips downward before or while the plant is flowering (http://www.absoluteastronomy.com/topics/Allium). The inflorescence can be fasciculate, umbel or head like, few to many, and loose to dense flowers have been reported (Fritsch and Friesen 2002). Flowering time varies with various *Allium* species. Flowering has been recorded in spring, summer, or autumn (Brewster 1998). A majority of *Allium* species are outbreeders, but the occurrence of both outbreeding and inbreeding forms in the same species has been reported (Brat 1965).

Allium species contain nectaries, which are located between the base of the ovary and the flattened widened base of the inner whorl of stamen and filaments (Peumans et al. 1997). The ovaries are largely trilocular and the styles are single and slender (Fritsch and Friesen 2002). The seeds can be angular or globular (Fritsch and Friesen 2002). Polyembryony (the development of multiple seedlings from a single seed) has been observed in several *Allium* species within the subgenus *Rhizirideum* (Specht et al. 2001).

1.3 Conservation Initiatives

As in many other crop species, there is evidence of genetic erosion in *Allium* species (Mingochi and Swai 1994). Goodding's onion (*Allium gooddingii*), a delicate perennial with reddish-purple flowers and a pungent onion aroma, was listed as a candidate for federal endangered/threatened status (http://www.fws.gov/southwest/es/Arizona/Goodings.htm*). Allium roseum* var. *odoratissimum*, which is harvested from roadsides during spring in Tunisia, is marketed very cheaply creating the risk of genetic erosion. *Allium roylei,* one of the most important sources of disease resistance genes in the genus *Allium* (Kofoet et al. 1990), is also a threatened species (Araki et al. 2010) and an urgent plea for its conservation has been made (Kohli and Gohil 2009). The need for protection of *A. gooddingii* was recognized in 1998 by the Forest Service and the Environmental Protection Agency of the United States of America, which helped considerably toward the protection of this species against erosion (USFWS 2000). Ghrabi (2010) describes the need to protect and domesticate *A. roseum* as an urgent necessity.

Global networks have, therefore, been formed to coordinate the collection, conservation, and utilization of the genetic resources within the genus *Allium.* Examples include the European Cooperative Program for Plant Genetic Resources (ECPGR) *Allium* Working Group, the United Kingdom Natural Resources Institute Onion Newsletter for the Tropics network, and the *Allium* Improvement Newsletter (Astley 1994). The *Allium* working group (http://www.ecpgr.cgiar.org/Workgroups/Allium/Allium.htm) established in 1982 in Europe is one of the original six working groups constituted during the first phase of ECPGR. The work of the ECPGR *Allium* working group benefited significantly from the work program of the European Genetic Resources *Allium* project (ended 31 Mar 2000), and the research projects FAIR (1996–2001) and "Garlic and Health" (1998–2003). In the framework of the European Genetic Resources 20 Project, over 200 accessions of wild taxa belonging to 35 species were collected and preserved in Greek gene Bank, Greece (Samaras 2001).

In India, the National Bureau of Plant Genetic Resources (NBPGR) conducted extensive plant exploration in different *Allium*-growing states resulting in the collection of over 2,200 accessions of *Allium* species including wild relatives such as *A. ampeloprasum, A. auriculatum, A. ascalonicum, A. carolinianum, A. chinensis, A. wallachi, A. tuberosum,* and *A. rubellum* (Singh and Rana 1994). NBPGR also introduced over 1,100 accessions of *Allium* germplasm from over 40 countries (Singh and Rana 1994). In Tunisia, the Medenine Institut des Regions Arides has recently developed a research program to protect, conserve, and domesticate *A. roseum* (http://www.uicnmed.org/nabp/database/HTM/PDF/p5.pdf).

Given the outbreeding nature of most *Allium* species, cryopreservation has been suggested as a viable method of conservation (Volk et al. 2004) but this will need to be combined with traditional field maintenance, pollen storage, and in vitro culture (Working Group on Allium 2009). Cryopreservation should be done carefully due to the high risk of contamination and virus infection.

1.4 Role in Elucidation of Origin and Evolution of Cultivated *Allium* Species

The genus *Allium* is one of the largest genera of perennial bulbous plants on earth. The use of internal transcribed spacer (ITS) region of ribosomal DNA recently classified the genus into 780 species, 56 sections, and 15 subgenera (Friesen et al. 2006). Earlier molecular comparisons recognized 67 sections and 14 subgenera (Fritsch and Friesen 2002). The fact that so many species exist suggests that a lot of evolutionary differentiation has occurred (Stevenson et al. 1999).

Both morphological and molecular data have been used to study evolution of the genus *Allium*. Wendelbo (1969) initially suggested that all other groups in *Allium* might be derived from rhizomatous species without bulbs. Rhizomes are a distinct feature within the subgenus *Rhizirideum*. More recent reports indicate that rhizomes have evolved from an ancestral bulbous life form that was subsequently lost at least twice independently (Ricroch et al. 2005). Other *Allium* species (*A. caeruleum, A. proliferium, A. vineale, A. carinatum,* and *A. scorodoprasum*) have been grouped as viviparous due to the development of topsets instead of flowers or intermingle with flowers in the florescence (Kamenetsky and Rabinowitch 2001).

More molecular studies of the genus have given insight into evolution of the cultivated *Allium* species. Amplified fragment length polymorphism (AFLP) studies in garlic clustered garlic clones very closely with *A. longicuspis* suggesting that the two species are not genetically distinct (Ipek and Simon 2001). *A. longicuspis* and *A. tuncelianum* are genetically identical to garlic and therefore, were earlier suggested as possible ancestors of garlic (Block 2010). However, DNA analysis indicated that neither *A. longicuspis* nor *A. tuncelianum* are ancestor species of garlic (Block 2010).

In the subgenus *Cepa*, section *Cepa*, the closest wild relative of *A. cepa* and *A. fistulosum* has been identified as *A. vavilovii* and *A. attaicium*, respectively (Klaas and Friesen 2002). *A. oschaninii,* on the other hand, appears to be a sister group to *A. cepa*/*A. vavilovii* evolutionary line (Friesen and Klaas 1998). *A. ampeloprasum* is thought to be the ancestor species of leek and kurrat (*A. ampeloprasum* var. *kurrat*) (Block 2010).

The use of nuclear ribosomal DNA [ITS and external transcribed spacer (ETS)] has been suggested to provide sufficient resolution for investigating evolutionary relationships within *Allium* (Nguyen et al. 2008). Nguyen et al. (2008) used combined sequences from 39 native Californian *Allium* species with 154 ITS sequences available on GenBank to develop a global *Allium* phylogeny with the simultaneous goals of investigating the evolutionary history of *Allium* in the Californian center of diversity and exploring patterns of adaptation to serpentine soils (Nguyen et al. 2008). The ITS region alone was sufficient to resolve the deeper relationships in North American species.

1.5 Role in Development of Cytogenetic Stocks and Their Utility

Allium species show variation in several cytogenetic characters such as basic chromosome number, ploidy level, and genome size. *Allium* species are identified by their symmetrical and uniform karyotypes, which can often make chromosome identification difficult (Stevenson et al. 1999). The somatic chromosome number ranges from $2n = 16\text{–}40$ with basic chromosome numbers of $x = 7, 8,$ and 9 (Karpaviciene 2007).

The ploidy level varies from $2x$ to $16x$ (De Sarker et al. 1997; Klaas 1998; Bennett et al. 2000) while the 2C DNA amounts per genome ranges from 16.93 to 63.57 pg (Ricrocha and Brown 1997). In a study of 25 *Allium* species, Jones and Rees (1968) found considerable differences among 2C-values measured by Feulgen densitometry. Ohri et al. (1998) confirmed this in a survey of 86 *Allium* species (representing all six subgenera), measured in 4C nuclei by Feulgen densitometry. The same conclusions were drawn from the study of genome size in 28 *Allium* species (Baranyi and Greilhuber 1999).

To study chromosome organization within *Allium* species, an integrated map of *Allium cepa* × (*A. roylei* × *A. fistulosum*) was used (Khrustaleva et al. 2005), which showed that *Allium* species recombination predominantly occurs in the proximal half of chromosome arms. Cytological analysis in populations of *A. roylei* has reportedly revealed presence of complex chromosomal configurations during male meiosis and chromosomal heteromorphicity in somatic metaphase spreads (Kohli and Gohil 2009). Unstable

B-chromosomes have also been reported in some European populations of *A. schoenoprasum* (Stevens and Bougourd 1994).

Overall, very little cytogenetic work has been done in wild *Allium* species. The most notable is the use of *A. galanthum* cytoplasm to develop cytoplasmic male sterile (CMS) substitution lines of cultivated *Allium* species (Yamashita 2005). More studies are required in this area to improve our understanding of these complex genomes. Significant utilization of wild *Allium* cytogenetic stocks in the breeding of cultivated species will depend a lot on our deep understanding of the specific genomes involved.

1.6 Role in Classical and Molecular Genetics

Allium genetics is poorly understood mainly due to the large genomes of the *Allium* species. There have been almost no classical genetic studies and the use of molecular tools has only been recently initiated. The few genetic studies in *Allium* species have focused on specific traits of economic importance such as bulb color, flavor, and disease and pest resistance.

Lack of genetic variability within some cultivated *Allium* species necessitates the use of closely related germplasm for the development of linkage maps. In the section *Cepa*, for example, *A. roylei* has been crossed with *A. cepa* and *A. fistulosum* to develop a linkage map. *A. roylei* shows a unique position in the taxonomy of the genus *Allium* (Fritsch and Friesen 2002). The nuclear DNA profile of *A. roylei* is related to the species of *Cepa* and *Phyllodolon* though its chloroplast DNA profile is related to the section *Schoenoprasum* (van Raamsdonk et al. 2000). *A. roylei* crosses easily with *A. cepa* and *A. fistulosum*. Crosses between *A. roylei* and *A. cepa* yield fertile hybrids.

The first *Allium* linkage map based on an F_2 population of an interspecific cross between *A. cepa* and *A. roylei* used AFLP markers (van Heusden et al. 2000a). This map was later used to locate a resistance locus for downy mildew (*Peronospora destructor*) to the distal end of chromosome 3 (van Heusden et al. 2000b). Downy mildew is a common and serious disease in onions, which results in major yield losses. Kofoet et al. (1990) reported that resistance to downy mildew in A. *roylei* was controlled by a single dominant gene named *Pd1*. The location of the resistance gene was confirmed using genomic in situ hybridization (GISH) and this resistance was successfully introduced into a bulb onion cultivar by the use of conventional back-crossing (Scholten et al. 2007).

Studies of resistance to anthracnose (*Colletotrichum gloesporioides* Penz) among *A. cepa* and *A. roylei* (Galvan et al. 1997) revealed that the resistance of *A. roylei* to the Brazilian anthracnose isolate is dominantly inherited. The same study also suggested that the resistance was most likely determined by more than one gene (Galvan et al. 1997).

Another important trait in *Allium* species is bulb color, which has been widely studied. The pigments responsible for bulb color are flavonoids. Flavonoids are common plant secondary metabolites that have been shown to function as antioxidant agents (Sengupta et al. 2004). Flavonoids are involved in UV protection, plant–microbe interactions, fertility, and pigmentation (Shirley 1996). Inheritance of bulb color has been shown to be very complex (Masuzaki et al. 2006), involving five major genes (Davis and El-Shafie 1967). *I* and *C* are the genes concerned with the expression of the pigmentation. *C* of the basic color factor is likely a regulatory gene controlling chalcone synthase (CHS) gene transcription (Kim et al. 2005). *I* is also presumed to be a regulatory gene as it inhibits pigment formation regardless of the other dominant genes (Kim et al. 2004). CHS is presumably located on chromosome 5A (Masuzaki et al. 2006) of *A. cepa*.

Although these genes have been studied in cultivated *Allium* species, it is expected that the flavonoid synthesis pathway in wild *Allium* species would contain similar genes making such reports applicable in the wild species.

1.7 Role of Wild *Allium* Species in Crop Improvement

Wild *Allium* species act as a reservoir of important traits that can be used to broaden the genetic base of the cultivated *Allium* species. However, the relatively long juvenile phase in most cultivated species and severe inbreeding depression have further hindered the use of wild *Allium* species for the improvement of cultivated *Allium* species. There are a few reports of interspecific gene introgression through classical breeding most of which have been done within the section *Cepa*.

Genes for resistance to downy mildew and Botrytis leaf blight (*Botrytis squamosa*) have been transferred from *A. roylei* (Kofoet et al. 1990; de Vries and Wietsma 1992) to *A. cepa*. *A. roylei* has also been used as a bridging species to stably introgress disease resistance genes from *A. fistulosum* into *A. cepa*. *A. fistulosum* harbors a number of genes for resistance to diseases and pests (Rabinowitch 1997). Although *A. fistulosum* and *A. cepa* are grouped under the same section, *Cepa*, the genome of *A. cepa* has a 28% higher DNA content than *A. fistulosum* (Labani and Elkington 1987) making crosses between the two species non-viable. Using the bridge-cross approach, *A. fistulosum* was stably integrated into *A. cepa* genome and unique populations were developed in which the important resistance genes segregated (Khrustaleva and Kik 2000).

Breeding for increased flavonoid content has become a major objective within *Allium* as people pay more attention to health-promoting compounds. In onions, flavonoid content has been the subject of many studies (Masuzaki et al. 2006; Kim et al. 2009a). Given the importance of flavonoids for human consumption, it is important to find ways of developing *Allium* cultivars that accumulate flavonoids to a larger extent (Masuzaki et al. 2006) and the wild germplasm presents a viable option. *Allium ursinum* (wild garlic) and *A. victorialis* have been reported to contain novel flavonoids (Andersen and Fossen 1995; Wu et al. 2009) that could be introgressed into garlic (*A. sativum*). Although garlic breeding in the past was limited to clonal selection of wild varieties or spontaneous mutants, routine seed production has been developed (Simon and Jenderek 2004) making it possible to introgress genes from closely related species using conventional means.

Higher fructan content is another trait of interest in *Allium* that could be improved using wild species. Fructans are a significant source of soluble dietary fiber (Kleessen et al. 1997). Fructan consumption has been correlated with lower rates of colorectal cancers (Roberfroid and Delzenne 1998). Analyses have reported that accumulation of fructans is associated with greater thiosulfinate concentrations (Havey et al. 2004). Thiosulfinates have incredible health benefits and have been shown to be abundant especially in *A. tuberosum* L. (Kim et al. 2008). More screening of the wild germplasm using traditional and molecular means could reveal more novel sources for the improvement of fructan content in the cultivated species.

Wild *Allium* species have played a role in creating and restoring CMS in cultivated *Allium* species. CMS is a maternally inherited condition in which a plant is unable to produce functional pollen (Schnable and Wise 1998). Male sterile plants are essential to exempt breeders from the difficulty of emasculation and results in the production of large numbers of F_1 seeds. Compared with genic male sterility, which is controlled only by nuclear genes, the CMS system allows easy propagation by using the appropriate maintainer line (Yamashita et al. 2010). The cytoplasm of *A. galanthum* Kar. et Kir., a wild species in section *Cepa*, has been used to develop a male sterile line for shallot and bunching onion (Yamashita et al. 1999) thus making it possible to produce hybrid seeds in these species at a commercial scale. *A. roylei* restores CMS (type T) in *A. cepa* (de Vries and Wietsma 1992).

Embryo rescue has been employed where distant crosses do not result in viable offspring. The procedure of embryo culture defines the techniques used to promote development of an immature or weak embryo into a viable plant. Depending on the organ used, embryo rescue is referred to as embryo, ovule, or ovary culture. Interspecific hybrids between *A. fistulosum* L. and *A. macrostemon* Bunge have been developed through ovary culture (Umehara et al. 2006a). *A. macrostemon* is a perennial herb with medicinal properties that propagates vegetatively and grows wild in China, Korea, and Japan (Fritsch and Friesen 2002). Embryo rescue has also been done to improve the aroma profile of onions (Keusgen et al. 2002). Embryo rescue of *Allium* species is usually done on a phytohormone-free medium (Umehara et al. 2006b).

Tsukazaki et al. (2006) proposed a “simple sequence repeats (SSR)-tagged breeding” scheme to enhance the rapidity, ease, and accuracy of variety identification and F_1 purity test in bunching onion. Their breeding scheme could be extended to other *Allium* species and utilized in backcrossing programs. With the current progress in *Allium* transformation (Eady et al. 2005; Kenel et al. 2010), it will be possible to transfer genes of interest from distant wild relatives into cultivated *Allium* species. Despite the few successes in introgression of resistance genes within the section *Cepa*, there are many diseases and pests such as neck rot (*Botrytis allii* Munn.), basal rot (*Fusarium* spp.), black mold (*Aspergillus niger* Tiegheim) for which sources of resistance are yet to be identified (Singh and Rana 1994). There is potential in identifying these genes from the wild germplasm. As domestication of more *Allium* species is still going on, future research will need to focus on optimization of screening, transformation protocols, and development of more molecular markers for the newly domesticated species.

1.8 Genomics Resources

Molecular tools for the improvement of *Allium* species have been lacking and the huge nuclear genomes are the major constraint. The first isolation of SSRs in the genus *Allium* was from bulb onion (*A. cepa*) (Fischer and Bachman 2000) only recently. In wild *Allium* species, the AFLP linkage map developed using F_2 population of an interspecific cross between *A. roylei* and *A. cepa* was the first *Allium* genetic map based on an interspecific cross (van Heusden et al. 2000a, b). However, this effort resulted in two maps; one map based on *A. cepa* markers and the second map based on *A. roylei* markers. The two maps were not integrated and 25% of the markers remained unlinked (van Heusden et al. 2000a, b). More recently, SSR markers have been developed and evaluated in both cultivated (*A. fistulosum, A. cepa*) and wild *Allium* species (*A. roylei, A. vavilovii, A. galanthum, A. altaicum*) (Araki et al. 2010).

A number of expressed sequence tags (ESTs) have been developed for cultivated *Allium* species (Kuhl et al. 2004; Kim et al. 2009b), even though none was detected from the National Center for Biotechnology Information (NCBI) database for wild *Allium* species. ESTs are a useful resource for identifying full-length genes and could be used in wild *Allium* species to identify novel genes. SSRs and single nucleotide polymorphisms (SNPs) derived from ESTs are likely to be transferred to the wild species as they are derived from less variable regions of the genome. There are currently EST-derived SSRs developed from an analysis of a bulb onion cDNA library (Kuhl et al. 2004) that could be tested for transferability in wild *Allium* species of interest. A garlic EST database (Kim et al. 2009b) is also available for the development and testing of more markers in interesting closely related wild species.

There are no known reports of bacterial artificial chromosomes (BACs) developed for the wild *Allium* species but those developed for onion (Suzuki et al. 2002) and garlic (Lee et al. 2003) will be a starting point toward the identification of candidate genes in wild *Allium* species. Given the close phylogenetic relationship between the Poales (includes the grasses) and Asparagales (Chase et al. 2000), it is highly expected that the advanced genomic resources available within the Poales (complete genomic sequence in *Oryza sativa* L., assembled BAC contigs, comprehensive EST databases) could be used for genetic improvement of Asparagales. However, only scant colinearity has been observed so far at the recombinational level between onion and rice (*O. sativa* L.) (Martin et al. 2005). More analysis within the wild *Allium* species may reveal more significant colinearity and provide insights into the evolution of the *Allium* species.

With the advances recently made in sequencing technologies, more genomic resources will be developed at a faster and cheaper rate than was possible a decade ago. These resources will make it possible to exploit the useful genetic variation available within the wild *Allium* species.

1.9 Scope for Domestication and Commercialization

The genus *Allium* comprises about 700 species of which less than 10% are cultivated but reports show evidence that domestication is still going on (Fritsch and Friesen 2002). There are several species of minor importance grown as semi-domesticated types or as wild economic species (Pandey et al. 2005) in India and other parts of the world. Domestication has therefore been done for different purposes.

A. komarovianum Vved was recently introduced into cultivation in North Korea as a vegetable (Hanelt 2001). Other wild *Allium* species used as vegetable in different parts of the world include *A. fasciculatum* in Bhutan (Pandey et al. 2008) and *A. roylei* in India (Kohli and Gohil 2009). Najjah et al. (2009) demonstrated the potential of *A. roseum* as an antimicrobial agent against food poisoning bacteria. *A. oschaninii*, *A. pskemense,* and *A. praemixtum* are used in Tajikistan and Uzbekistan as spices. In the western Himalayas, dried leaves of *A. stracheyi* are used for seasoning vegetable curries (Negi and Gaur 1991). *Allium vineale*, a perennial from bulblets emits a strong garlic or onion smell when crushed and has potential for use as spice.

The use of curative members of the genus *Allium* has a long tradition in several Asian populations with deep historical roots (Keusgen et al. 2006). *A. pskemense* and *A. praemixtum* are used in Tajikistan and Uzbekistan for medicinal purposes. In India, *A. wallichii*, *A. ampeloprasum*, *A. griffithianum*, and *A. tuberosum* are used as medicine (Pandey et al. 2008). *A. roylei* is used in India to relieve headache and fed to horses to relieve colic (Kohli and Gohil 2009).

The potential of domestication of *A. mongolicum* in China has been explored for its high nutritious, medicinal, and ecological value (Zi-Zhu et al. 2006). Wild *Allium* species have also received attention as ornamentals due to a wide range of attractive colors and persistence of floral or long vegetative cycle (Pandey et al. 2008). *Allium* species are used in rock gardens, herbaceous beds, perennial borders, as pot plants, as decorative items, and in dry arrangements (Kamenetsky and Fritsch 2002). Processed products of wild species of *A. auriculatum, A. carolinianum, A. griffithianum, A. humile, A. roylei,* and *A. wallichii* are reportedly in great demand (Pandey et al. 2008).

Wild garlic capable of producing seed has played a major role in generation of sexually producing garlic enabling commercial seed production in garlic. As important traits continue to be selected by end users of various wild *Allium* species, more domestication of these important species will need to be done in order to protect them from overexploitation.

1.10 Some Dark Sides and Recommendations for Future Actions

The major problem faced with some wild *Allium* species is their weediness. The most studied weedy *Allium* is *A. vineale* (wild garlic), a perennial bulb flower, native to Europe, North Africa, and western Asia. *A. vineale* has a highly developed system of reproduction (Ronsheim and Bever 2000), which allows it to survive a wide range of environmental conditions as well as various chemical and control measures (Leys and Slife 1986). This species was introduced in Australia and North America, where it has become an invasive species. *A. vineale* is especially a problem among cultivated grasses (Ferguson et al. 1992). Wild garlic is resistant to herbicides due to the structure of its leaves, being vertical, smooth, and waxy (Davies 1992; Block 2010). The use of herbicides is not effective especially because unsprouted underground bulbs may remain dormant and gradually sprout over a 4–5 year period. More knowledge of this species at DNA level would benefit the development of novel control approaches.

The other problem is the strong odor of most species within the genus *Allium* normally produced upon damage of vegetative parts. Although evidence shows that the substances responsible for the odor have health benefits (Rose et al. 2005), stronger and more offensive odors reduce their successful utilization in breeding and consumption. Allelopathic effects have been reported in several *Allium* species both cultivated and wild (Djurdjevic et al. 2003). These plants release allelochemicals by exudation, decomposition, leaching, and vaporization. Such chemicals may be toxic within the rhizosphere (Yu 1999) and have been reported to inhibit germination of some plant species (Djurdjevic et al. 2003).

The ongoing activities relating to collection and conservation of genetic resources of *Allium* will require much more support in the future, if exhaustive collection of all species is to be achieved and genetic erosion avoided. The use of more modern techniques in germplasm enhancement through characterization and conservation will be needed. More genomic resources such as ESTs and molecular markers, as well as transcriptome and/or genome sequence data will be necessary in these species for more efficient utilization of their resources. Breeders will also need to come up with more long-term pre-breeding programs that will be necessary for the transfer of useful traits from the wild to the domesticated species. More investment in biotechnology-related research projects in future will go along way toward the improvement of these species.

References

Andersen OM, Fossen T (1995) Anthocyanins with an unusual acylation pattern from stem of *Allium victorialis*. Phytochemistry 40:1809–1812

Araki N, Masuzaki SI, Tsukazaki H, Yaguchi S, Wako T, Tashiro Y, Yamauchi N, Shigyo M (2010) Development of microsatellite markers in cultivated and wild species of sections Cepa and Phyllodolon in Allium. Euphytica 173:321–328

Astley D (1994) A network approach to the conservation of Allium genetic resources. Int Symp on Alliums for the Tropics, ISHS. Acta Hortic 358:135–142

Baranyi M, Greilhuber J (1999) Genome size in Allium: in quest of reproducible data. Ann Bot 83:687–695

Bennett MD, Bhandol P, Leitch IJ (2000) Nuclear DNA amounts in angiosperms and their modern uses – 807 new estimates. Ann Bot 86:859–909

Block E (2010) Garlic and other Alliums: the lore and the science. Royal Society of Chemistry, Cambridge, UK. ISBN 978-0-85404-190-9

Brat SV (1965) Genetic systems in Allium III. Meiosis and breeding systems. Heredity 20:325–339

Brewster JL (1998) Onions and other Alliums. CABI, Wallingford, UK. ISBN 978-1-84593-399-9

Chase MW, Soltis DE, Soltis PS, Rudall PJ, Fay MF, Hahn WH, Sullivan S, Joseph J, Molvray M, Kores PJ, Givnish TJ, Sytsma KJ, Pires JC (2000) Higher-level systematics of the monocotyledons: an assessment of current knowledge and a new classification. In: Wilson K, Morrison S (eds) Monocots: systematics and evolution, vol 1. CSIRO, Melbourne, Australia, pp 3–16

Davies D (1992) Alliums: the ornamental onions. Timber, Portland, OR, USA. ISBN 0-88192-241-2

Davis GN, El-Shafie MW (1967) Inheritance of bulb color in the onion (*Allium cepa* L.). Hilgardia 38:607–622

De Sarker D, Johnson MAT, Reynolds A, Brandham PE (1997) Cytology of the highly polyploid disjunct species, *Allium dregeanum* (Alliaceae), and of some Eurasian relatives. Bot J Linn Soc 124:361–373

De Vries JN, Wietsma WA (1992) *Allium roylei* Stearn restores cytoplasmic male sterility of Rijnsburger onion (*A. cepa* L.). J Genet Breed 46:379–382

Djurdjevic L, Dinic A, Pavlovic P, Mitrovic M, Karadzic B, Tesevic V (2003) Allelopathic potential of *Allium ursinum* L. Biochem Syst Ecol 32:533–544

Eady C, Davis S, Catanach A, Kenel F, Hunger S (2005) *Agrobacterium tumefaciens*–mediated transformation of leek (*Allium porrum*) and garlic (*Allium sativum*). Plant Cell Rep 24:209–215

Ferguson GP, Coats EG, Wilson GB, Shaw DR (1992) Postemergence control of wild garlic (*Allium vineale*) in turfgrass. Weed Technol 6:144–148

Fischer D, Bachman K (2000) Onion microsatellites for germplasm analysis and their use in assessing intra- and interspecific relatedness within the subgenus Rhizirideum. Theor Appl Genet 101:153–164

Friesen N, Klaas M (1998) Origin of some minor vegetatively propagated Allium crops studied with RAPD and GISH. Genet Resour Crop Evol 45:511–523

Friesen N, Fritsch RM, Blattner FR (2006) Phylogeny and new intrageneric classifion of *Allium* L. (Alliaceae) based on nuclear ribosomal DNA ITS sequences. Aliso 22:372–395

Fritsch RM, Friesen N (2002) Evolution, domestication and taxonomy. In: Rabinowitch HD, Currah L (eds) Allium crop science: recent advances. CABI, Wallingford, UK, pp 5–30

Galvan GA, Wietsma WA, Putrasemedja S, Permadi AH, Kik C (1997) Screening for resistance to anthracnose (Colletotrichum gloeosporioides Penz.) in *Allium cepa* and its wild relatives. Euphytica 95:173–178

Ghrabi Z (2010) *Allium roseum* var. odoratissimum: a guide to medicinal plants in North Africa, pp 23–24. http://www.uicnmed.org/nabp/database/HTM/PDF/p5.pdf. Accessed 5 July 2010

Hanelt P (2001) Alliaceae. In: Hanelt P and Institute of Plant Genetics and Crop Plant Research (eds) Mansfelds encyclopedia of agricultural and horticultural crops, vol 4, 3rd edn. Springer, Berlin, Germany, pp 2250–2269

Havey MJ, Galmarini CR, Gökçe AF, Henson C (2004) QTL affecting soluble carbohydrate concentrations in stored onion bulbs and their association with flavor and health-enhancing attributes. Genome 47:463–468

Huxley A, Griffiths M, Levy M (1992) The New Royal Horticultural Society dictionary of gardening. Macmillan, Stockton, London, UK. ISBN 978-0-333-47494-5

Ipek M, Simon P (2001) Genetic diversity in garlic (*Allium sativum* L.) as assessed by AFLPs and isozymes. In: 98th Annual conference & exhibition, American Society of Horticultural Science, P3, 22–25 July 2001

Jones RN, Rees H (1968) Nuclear DNA variation in Allium. Heredity 23:591–605

Kamenetsky R, Fritsch R (2002) Ornamental Alliums. In: Rabinowitch HD, Currah L (eds) Allium crop science: recent advances. CABI, Wallington, UK, pp 459–492

Kamenetsky R, Rabinowitch HD (2001) Floral development in bolting garlic. Sex Plant Reprod 13:235–241

Karpaviciene B (2007) Chromosome numbers of Allium from Lithuania. Ann Bot Fennici 44:345–352

Kenel F, Eady C, Brinch S (2010) Efficient *Agrobacterium tumefaciens*-mediated transformation and regeneration of garlic (*Allium sativum*) immature leaf tissue. Plant Cell Rep 29:223–230

Keusgen M, Schulz H, Glodek J, Krest I, Krüger H, Herchert N, Keller J (2002) Characterization of some Allium hybrids by aroma precursors, aroma profiles, and allinase activity. J Agric Food Chem 10:2884–2890

Keusgen M, Fritsch RM, Hisoriev H, Kurbonova PA, Khassanov FO (2006) Wild Allium species (Alliaceae) used in folk medicine of Tajikistan and Uzbekistan. J Ethnobiol Ethnomed 2:18

Khrustaleva LI, Kik C (2000) Introgression of *Allium fistulosum* into *A. cepa* mediated by *A. roylei*. Theor Appl Genet 100:17–26

Khrustaleva LI, de Melo PE, van Heusden AW, Kik C (2005) The integration of recombination and physical maps in a large-genome monocot using haploid genome analysis in a trihybrid Allium population. Genetics 169:1673–1685

Kim S, Binzel ML, Park S, Yoo K, Pike LM (2004) Inactivation of DFR (Dihydroflavonol 4-reductase) gene transcription results in blockage of anthocyanin production in yellow onions (*Allium cepa*). Mol Breed 14:253–256

Kim S, Yoo K, Pike LM (2005) The basic color factor, the C locus, encodes a regulatory gene controlling transcription of chalcone synthase genes in onions (*Allium cepa)*. Euphytica 142:273–282

Kim SY, Park KW, Kim JY, Shon MY, Yee ST, Kim KH, Rhim JS, Yamada K, Seo KI (2008) Induction of apoptosis by thiosulfinates in primary human prostrate cancer cells. Int J Oncol 32:869–875

Kim S, Baek D, Cho DY, Lee ET, Yoon MK (2009a) Identification of two novel inactive DFR-A alleles responsible for failure to produce anthocyanin and development of a simple PCR-based molecular marker for bulb color selection in onion (*Allium cepa* L.). Theor Appl Genet 118:1391–1399

Kim DW, Jung TS, Nam SH, Kwon HR, Kim A, Chae SH, Choi SH, Kim DW, Kim RN, Park HS (2009b) GarlicESTdb: an online database and mining tool for garlic EST sequences. BMC Plant Biol 9:61

Klaas M (1998) Applications and impact of molecular markers on evolutionary and diversity studies in the genus *Allium*. Plant Breed 117:297–308

Klaas M, Friesen N (2002) Molecular markers in Allium. In: Rabinowitch HD, Currah L (eds) Allium crop science – recent advances. CABI, Wallingford, UK, pp 159–185

Kleessen B, Sykura B, Zunft H, Blaut M (1997) Effects of inulin and lactose on fecal microflora, microbial activity, and bowel habit in elderly constipated persons. Am J Clin Nutr 65:1397–1402

Kofoet A, Kik C, Wietsma WA, de Vries JN (1990) Inheritance of resistance to downy mildew (Peronospora destructor (Berk.) Casp.) from *Allium roylei* Stearn in the backcross *Allium cepa* L. (A. roy- lei x A. cepa). Plant Breed 105:144–149

Kohli B, Gohil RN (2009) Need to conserve *Allium roylei* Stearn: a potential gene reservoir. Genet Resour Crop Evol 56:891–893

Kuhl JC, Cheung F, Yuan Q, Martin W, Zewdie Y, McCallum J, Catanach A, Rutherford P, Sink KC, Jenderek M, Prince JP, Town CD, Havey MJ (2004) A unique set of 11,008 onion expressed sequence tags reveals expressed sequence and genomic differences between the monocot orders Asparagales and Poales. Plant Cell 16:114–125

Labani R, Elkington T (1987) Nuclear DNA variation in the genus *Allium* L. (Liliaceae). Heredity 59:119–128

Le Guen-Le Saos F, Hourmant A, Esnault F, Chauvin JE (2002) In vitro bulb development in shallot (*Allium cepa* L. aggregatum group): effects of anti-gibberellins, sucrose and light. Ann Bot 89:419–425

Lee HR, Eon EM, Lim YP, Bang JW, Lee DH (2003) Construction of a garlic BAC library and the chromosomal assignment of BAC clones using the FISH technique. Genome 46:514–520

Leys A, Slife FW (1986) The response of wild garlic (*Allium vineale*) to the timing of spray applications of chlorsulfuron. Weed Sci 34:718–723

Martin WJ, McCallum J, Shigyo M, Jakse J, Kuhl JC, Yamane N, Pither-Joyce M, Gokce AF, Sink KC, Town CD, Havey MJ (2005) Genetic mapping of expressed sequences in onion and in silico comparisons with rice show scant colinearity. Mol Genet Genom 274:197–204

Masuzaki S, Shigyo M, Yamauchi N (2006) Direct comparison between genomic constitution and flavonoid contents in Allium multiple alien addition lines reveals chromosomal locations of genes related to biosynthesis from dihydrokaempferol to quercetin glucosides in scaly leaf of shallot (*Allium cepa* L.). Theor Appl Genet 112:607–617

Mingochi DS, Swai REA (1994) Role of the Southern Africa development community in the conservation of Allium genetic resources. In: International symposium on Alliums for the tropics, ISHS. Acta Hortic 358:161–164. http://www.actahort.org/books/358/358_25.htm

Najjah H, Ammar E, Neffati M (2009) Antimicrobial activities of *Allium roseum* L., a wild edible species in North Africa. J Food Agric Environ 7:150–154

Negi KS, Gaur RD (1991) Little known endemic wild Allium species in the Uttar Pradesh hills. Mt Res Dev 11:162–164

Nguyen NH, Driscolla HE, Specht CD (2008) A molecular phylogeny of the wild onions (Allium; Alliaceae) with a focus on the western North American center of diversity. Mol Phylogenet Evol 47:1157–1172

Ohri D, Fritsch RM, Hanelt P (1998) Evolution of genome size in Allium (Alliaceae). Plant Syst Evol 210:57–86

Pandey A, Pandey R, Negi KS (2005) Wild Allium species in India: biodiversity distribution and systematic studies. In: National Conference on Allium (Abstr), Banaras Hindu University, Varanasi, UP, India, 24–25 Feb 2005, 44 p

Pandey A, Pandey R, Negi KS, Radhamani J (2008) Realizing value of genetic resources of Allium in India. Genet Resour Crop Evol 55:985–994

Peumans WJ, Smeets K, Van Nerum K, Van Leuven F, Van Damme EJM (1997) Lectin and alliinase are the predominant proteins in nectar from leek (*Allium porrum* L.) flowers. Planta 201:298–302

Rabinowitch HD (1997) Breeding alliaceous crops for pest resistance. Acta Hortic 433:223–246

Ricroch A, Yockteng R, Brown SC, Nadot S (2005) Evolution of genome size across some cultivated Allium species. Genome 48:511–520

Ricrocha A, Brown SC (1997) Junk DNA: the role and the evolution of non-coding sequences – DNA base composition of Allium genomes with different chromosome numbers. Gene 205:255–260

Roberfroid MB, Delzenne NM (1998) Dietary fructans. Annu Rev Nutr 18:117–143

Ronsheim ML, Bever JD (2000) Genetic variation and evolutionary trade-offs for sexual and asexual reproductive modes in *Allium vineale* (liliaceae). Am J Bot 87:1769–1777

Rose P, Whiteman M, Mooreb PK, Zhun Zhu Y (2005) Bioactive S-alk(en)yl cysteine sulfoxide metabolites in the genus Allium: the chemistry of potential therapeutic agents. Nat Prod Rep 22:351–368

Rudall P, Furness C, Chase M, Fay M (1997) Microsporogeneisis and pollen sulcus type in Asparagales (Lilianae). Can J Bot 75:408–430

Samaras S (2001) European collections of vegetatively propoagated Allium. A report on the current status of the greek Allium wild taxa, ECPGR, 20–21 May 2001, 44 p

Schnable PS, Wise RP (1998) The molecular basis of cytoplasmic male sterility and fertility restoration. Trends Plant Sci 3:175–180

Scholten OE, van Heusden AW, Khrustaleva LI, Burger-Meijer K, Mank RA, Antonise RGC, Harrewijn JL, Van Haecke W, Oost EH, Peters RJ, Kik C (2007) The long and winding road leading to the successful introgression of downy mildew resistance into onion. Euphytica 156:345–353

Sengupta A, Ghosh S, Bhattacharjee S (2004) Allium vegetables in cancer prevention: An Overview. Asian Pac J Cancer Prevent 5:237–245

Shirley BW (1996) Flavonoid biosynthesis: 'new' functions for an 'old' pathway. Trends Plant Sci 1:377–382

Simon PW, Jenderek MM (2004) Flowering, seed production and the genesis of garlic breeding. Plant Breed Rev 23:211–244

Singh BP, Rana RS (1994) Collection and conservation of Allium genetic resources: an Indian perspective. Acta Hortic 358:181–190

Specht CE, Meister A, Keller ERJ, Korzun L, Börner A (2001) Polyembryony in species of the genus *Allium*. Euphytica 121:37–44

Stevens JP, Bougourd SM (1994) Unstable B-chromosomes in a European population of Allium schoenoprasum L. (Liliaceae). Biol J Linn Soc 52:357–363

Stevenson M, Armstrong SJ, Jones GH, Ford-Lloyd BV (1999) Distribution of a 375 bp repeat sequence in Allium (Alliaceae) as revealed by FISH. Plant Syst Evol 217:31–42

Suzuki G, Do GS, Mukai Y (2002) Efficient storage and screening system for onion BAC clones. Breed Sci 52:157–159

Tsukazaki H, Fukuoka H, Song YS, Yamashita KI, Wako T, Kujima A (2006) Considerable heterogeneity in commercial F1 varieties of bunching onion (*Allium fistulosum*) and proposal of breeding scheme for conferring variety traceability using SSR markers. Breed Sci 56:321–326

Umehara M, Sueyoshi T, Shimomura K, Nakaha T (2006a) Production of interspecific hybrids between *Allium fistulosum* L. and *A. macrostemon* Bunge through ovary culture. Plant Cell Tiss Org Cult 87:297–304

Umehara M, Sueyoshi T, Shimomura K, Iwai M, Shigyo M, Hirashima K, Nakahara T (2006b) Interspecific hybrids between *Allium fistulosum* and *Allium schoenoprasum* reveal carotene-rich phenotype. Euphytica 148:295–301

USFWS (2000) Notice of reclassification of nine candidate taxa. Fed Regist 64(204):63044–63047

van Heusden AW, van Ooijen JW, van Vrielink Ginkel R, Verbeek WHJ, Wietsma WA, Kik C (2000a) A genetic map of an interspecific cross in Allium based on amplified fragment length polymorphism (AFLP) markers. Theor Appl Genet 100:118–126

van Heusden AW, Shigyo M, Tashiro Y, van Vrielink Ginkel R, Kik C (2000b) AFLP linkage group assignment to the chromosomes of *Allium cepa* L. via monosomic addition lines. Theor Appl Genet 100:480–486

van Raamsdonk LWD, van Vrielink Ginkel M, Kik C (2000) Phylogeny reconstruction and hybrid analysis in Allium subgenus Rhizirideum. Theor Appl Genet 100: 1000–1009

Volk GM, Maness N, Rotindo K (2004) Cryopreservation of garlic (*Allium sativum* L.) using plant vitrification solution 2. Cryoletters 25:219–226

Wendelbo P (1969) New subgenera, sections and species of Allium. Bot Notiser 122:25

Working Group on Allium (2009) In: Astley D, Bas N, Branca F, Daunay MC, Díez MJ, Keller J, van Dooijeweert W, van Treuren R, Maggioni L, Lipman E (eds) Report of a vegetables network. Reports by the Working Groups' rapporteurs on issues discussed during the parallel meetings. 2nd Meeting, 26–28 June 2007, Olomouc, Czech Republic, Bioversity International, Rome, Italy. ISBN 978-92-9043-792-5

Wu H, Dushenkov S, Ho C-T, Sang S (2009) Novel acetylated flavonoid glycosides from the leaves of Allium Ursinum. Food Chem 115:592–595

Yamashita K (2005) Breeding of Allium cultivated species using cytoplasm engineering technique. Rearing of male sterile line using the cytoplasm of wild species. Agric Hortic 80:7–14

Yamashita K, Arita H, Tashiro Y (1999) Cytoplasm of a wild species, *Allium galanthum* Kar. et Kir., is useful for developing the male sterile line of *A. fistulosum* L. J Jpn Soc Hortic Sci 68:788–797

Yamashita K, Tsukazaki H, Kojima A, Ohara T, Wako T (2010) Inheritance mode of male sterility in bunching onion (*Allium fistulosum* L.) accessions. Euphytica 173:357–367

Yu JQ (1999) Allelopathic suppression of Pseudomonas solanacearum infection of tomato (Lycopersicon esculentum) in a tomato-Chinese Chive (*Allium tuberosum*) intercropping System. J Chem Ecol 25:2409–2417

Zi-zhu Y, Shi-zeng L, Ai-de L, Shu-juan SA (2006) Tentative exploring to the developing value of wild vegetable resources – *Allium mongolicum*. J Gansu For Sci Technol. doi:cnki:ISSN:1006-0960.0.20