Chapter 1
Actinidia

P.M. Datson and A.R. Ferguson

1.1 Introduction

Kiwifruit in comparison with most other crop plants have a very short history of cultivation.

The two commercially important kiwifruit species are *Actinidia deliciosa* and *A. chinensis*. These are sometimes combined as varieties of the same species (Li et al. 2007a, b), but we retain them here as distinct species. *A. deliciosa* was introduced into cultivation toward the end of the nineteenth century (Ferguson and Huang 2007) and the first commercial orchards were established in New Zealand around 1930. *A. chinensis*, a species closely related to *A. deliciosa*, was successfully introduced into cultivation in China as recently as 1961 (Zhang et al. 1983) and it has been grown commercially in other countries and its fruits have been traded internationally for little more than a decade. At present, *A. deliciosa* provides about 85% of the kiwifruit produced commercially worldwide and *A. chinensis* about 15%. A few other *Actinidia* species are also cultivated, *A. arguta*, *A. eriantha*, *A. kolomikta*, and *A. polygama*, but these are of very minor commercial importance.

Almost all current kiwifruit cultivars are either direct selections from the wild or only a few generations removed from the wild (Ferguson and Huang 2007; Ferguson and Seal 2008; Ferguson 2009; Li et al. 2010). All the early New Zealand cultivars of *A. deliciosa*, including the main commercial cultivar 'Hayward', are selections descended from a very small number of seedlings grown from a single seed introduction into New Zealand from China at the beginning of the twentieth century (Ferguson and Bollard 1990). Very few cultivars of *A. deliciosa* have yet emerged from systematic breeding programs and there are only small commercial plantings of them (Testolin and Ferguson 2009). Only one commercially important cultivar of *A. chinensis* has so far resulted from a controlled hybridization. 'Hort16A' came from the cross of a female, the product of open-pollination of seedlings from a seed accession from the wild, and a male raised from seed collected in the wild (Mugglestone et al. 1998; Ferguson et al. 1999).

- Cultivated kiwifruit are, therefore, generally not greatly different from those in the wild. Some wild individuals of *A. deliciosa* and *A. chinensis* contained genes suitable for domestication and selection has involved recognition of plants with fruit having commercial potential. Comparison of the plants that have been selected with those remaining in the wild contributes to our understanding of the kiwifruit we now grow and the potential for their improvement. We describe studies using both cultivated plants and their wild allies on the origin, evolution, phylogenetic relationships, cytogenetics, and the genetic improvement of kiwifruit employing both classical strategies and advanced tools of genomics and biotechnology.

1.2 Basic Botany

1.2.1 The Genus Actinidia

Kiwifruit belong to the genus *Actinidia* Lindl. Currently, 55 species and about 76 taxa are recognized

P.M. Datson (✉)
The New Zealand Institute for Plant & Food Research Ltd. (Plant & Food Research), Private Bag 92 169, Auckland, New Zealand
e-mail: Paul.Datson@plantandfood.co.nz

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within the genus, with the most recent revision (Li et al. 2007a, b, 2009) having relegated about 25% of the species and 40% of all taxa previously described (Ferguson and Huang 2007). Further changes seem inevitable as many taxa are not well known, and transitional forms, sometimes formally described, suggest considerable hybridization between taxa with overlapping geographical distributions (Liang 1983; Ferguson 1990a, b; Chat et al. 2004; Li et al. 2009).

Female flowers of the genus have a characteristic radiating arrangement of styles, like the spokes of the wheel. This is the basis for Lindley's generic name *Actinidia* from aktis (Greek), ray. In China, the name mihoutao [monkey peach] is used for the whole genus and individual species are now distinguished such as zhonghua [Chinese] mihoutao for *A. chinensis* and meiwei [delicious] mihoutao for *A. deliciosa* (Cui et al. 2002; Li et al. 2007a). In older literature, these two species were usually distinguished by the hairs on the fruit, ruanmao for soft-haired [*A. chinensis*] and yingmao [*A. deliciosa*] for stiff-haired. A variety of names were used traditionally, yangtao [sun peach] being one of the most common (Ferguson 1990c). Outside China, "Chinese gooseberry" became the most popular name (or translations such as groseille de Chine) until it was replaced in New Zealand by kiwifruit (Ferguson and Bollard 1990). This is the most widely used name today, even in China, although in Italy, "actinidia" is often used. Kiwifruit is sometimes incorrectly shortened to "kiwi" or wrongly separated into two words.

1.2.2 Geographic Distribution

Nearly all *Actinidia* species (52 of 55) and taxa (73 of 76) occur in China (Li et al. 2007a) and some extend to adjoining countries, but only three species occur exclusively outside China: *A. strigosa* from Nepal, *A. petelotii* from Vietnam, and *A. hypoleuca* from Japan. The genus has a wide geographic distribution in eastern Asia, from just south of the Equator, to as far north as latitude 50°, with most taxa occurring in south-central and south-west China between the Yangzi (Chang Jiang) and Pearl (Zhu Jiang) Rivers, in a belt between approximately 25 and 30°N (Fig. 1.1). Most *Actinidia* grow best in warm, moist, and sheltered environments; cold, dry conditions are unsuitable. Hence, the northernmost boundary of the area of greatest abundance corresponds to the Qin Ling Mountains in southern Shaanxi, the western boundary, the lower mountains of the eastern border of the Tibetan plateau, the Hengduan Shan (Hengduan Mountains) to the west of Yunnan and Sichuan, and the southernmost, the isotherm that corresponds to a mean annual temperature between 20°C and 22°C (Ferguson and Huang 2007). This area is considered to be the center of diversity of *Actinidia* as well as the center of current evolution (Liang 1983). Taxa tend to vary little in their relative vertical distributions, but the altitude at which a particular *Actinidia* taxon occurs is not absolute but decreases with increasing latitude (Ferguson and Huang 2007). Thus, taxa that grow high in the mountains of southern China can be found at sea level in Siberia.

1.2.3 Vegetative Morphology

All *Actinidia* are climbing plants and under most conditions are deciduous. Vines can be extraordinarily robust and vigorous, capable of smothering large trees (Li 1952), but high in the mountains or in cold, northernmost regions, plants may be reduced to scrambling thickets rather like brambles (Berestova 1970). In cultivation, vine vigor will depend on local growing conditions and genotype, but commercial vines are usually very vigorous and require strong and expensive support structures.

Actinidia species are often very variable in vegetative structures. Even individual plants can show variation in the leaves produced at different times of year or on different types of wood (Dunn 1911). This can cause confusion when single specimens are used to describe taxa. Differences in vegetative morphology between staminate and pistillate plants can also be misleading (Cuong et al. 2007). Widespread species have often been divided into morphologically distinct varieties, which sometimes, but not always, occupy discrete geographical areas. Broader taxonomic concepts with more intrataxal variation seem more realistic, and further collections, especially of taxa based on only a few specimens, are needed (Li et al. 2009).

Key	Taxa
F	1-5
E	6-10
D	11-15
C	16-20
B	21-30
A	31-40

Countries	Taxa
Bhutan	2
Cambodia	1
India	2
Indonesia	1
Japan	5
Korea	4
Laos	1
Malaysia	1
Myanmar	2
Nepal	2
Russia	3
Thailand	2
Vietnam	6

Fig. 1.1 Geographic distribution of *Actinidia* taxa

1.2.4 Flower Morphology and Sex Determination

All *Actinidia* species appear to be dioecious, although functional dioecy has been confirmed in only *A. deliciosa* and *A. polygama* (McNeilage 1991a; Kawagoe and Suzuki 2004). *Actinidia* are cryptically dioecious: female plants produce morphologically perfect flowers with well-developed pistils and stamens, but their stamens produce non-viable pollen; flowers of male plants have small, rudimentary ovaries without viable ovules, but their stamens release viable pollen (Rizet 1945; Schmid 1978; White 1990) (see Fig. 1.2). Failure of pollen maturation or of pistil growth occurs late in flower bud development (Brundell 1975; Schmid 1978; Messina 1993). Dioecy creates problems in commercial cultivation: part of the orchard area (usually about 10%) must be dedicated to pollenizer vines, male and female vines must flower at the same time, and there must be efficient transfer of pollen as fruit size in kiwifruit is largely dependent on the number of seed set. Orchard layout must also encourage honeybee activity to facilitate pollination. Some of these problems are overcome by mechanical pollination of fruiting vines by harvested pollen; a better solution might be the development of hermaphrodite, self-setting vines.

Fig. 1.2 Flowers of female (*left*) and male (*right*) *Actinidia eriantha*

There is an active-Y sex determination system (X_nX/X_nY) in *Actinidia* with the plants that contain

Y-chromosomes being male (Testolin et al. 1995; Harvey et al. 1997b; Fraser et al. 2009). Sex determination in *Actinidia* is probably controlled by two genes: one suppressing pistil development in staminate flowers, and the other stopping pollen development in pistillate flowers (Harvey et al. 1997a). It is likely that the sex chromosomes of extant *Actinidia* have a single origin that pre-dates the radiation of the group (Harvey et al. 1997a; Yan et al. 1997b; Testolin et al. 1999). Disomic sex segregation seems to operate at the different ploidy levels (Testolin et al. 1995).

The large number of *Actinidia* species that contain related sex chromosomes is a valuable tool for studying sex chromosome evolution in plants as it should allow for comparative analysis of the process of sex chromosome evolution across a wide range of related species.

Gender changes are possible. A bud mutation in a mature male vine caused a gender change from male to female (Testolin et al. 2004). Gender inconstancy has also been observed in individuals of *A. arguta*, *A. chinensis*, *A. deliciosa*, and *A. eriantha* (Messina et al. 1990; Tang and Jiang 1995; Testolin et al. 1999; Mizugami et al. 2007). Fruiting ("inconstant" or andromonoecious) males occasionally occur: these have labile sex expression with occasional bisexual flowers occurring among staminate flowers (Hirsch et al. 1990; McNeilage 1991a, b). Hermaphrodite plants of *A. deliciosa* have been produced from crosses involving inconstant males (McNeilage and Steinhagen 1998; McNeilage et al. 2007). Hermaphroditism in *A. deliciosa* is stable and heritable. It is, therefore, likely that hermaphrodite breeding lines could be developed in different *Actinidia* species by identifying and crossing inconstant males. Variants in sex expression, either collected from the wild (e.g., Tang and Jiang 1995; Mizugami et al. 2007) or from commercial orchards (e.g., Hirsch et al. 1990), could be an important resource for kiwifruit improvement programs.

1.2.5 Fruit Characteristics

Interspecific and intraspecific variation in fruit attributes has understandably received most attention and is well described (Li 1952; Huang et al. 1983, 2000a, b, 2004; Liang 1984; Li et al. 1985; Ferguson 1990a; Cui et al. 2002; Han et al. 2003; Ferguson and Huang 2007; Nishiyama 2007). Infructescence size, fruit size, fruit shape, fruit hairs and skin characteristics, external color, flesh color, ripening indicators, flesh texture, flesh flavor, time of maturity and ripening, handling and storage responses, and yield potential all need to be considered in the development of a commercial cultivar (Fig. 1.3). Wild *Actinidia* species have many fruit characteristics that could, with advantage, be introgressed into cultivated kiwifruit. Achieving this requires a good knowledge of the variability that exists in the wild, the collection and preservation of useful diversity, and a good understanding of the reproductive biology of the genus.

The potential health benefits of kiwifruit deserve special attention. Kiwifruit are often promoted for their high vitamin C (ascorbic acid) content, which probably contributes to the health benefits observed. *A. deliciosa* 'Hayward' and *A. chinensis* 'Hort16A' typically contain 85 and 100 mg/100 g (fresh weight), respectively, and a single fruit can provide the recommended daily intake (Ferguson and Ferguson 2002; Kassardjian et al. 2006). Vitamin C levels vary greatly among and within *Actinidia* species from less than 30 mg/100 g fresh weight to more than 1,000 mg/100 g fresh weight (Nishiyama et al. 2004b; Ferguson and Huang 2007; Nishiyama 2007). The health benefits attributed to vitamin C include antioxidant, antiatherogenic, and anticarcinogenic activity, as well as immunomodulation. Human intervention trials validate some of these health benefits for green kiwifruit (*A. deliciosa* 'Hayward') in the areas of "natural protection" (protection from oxidative stress and DNA damage associated with mutation and cancer), gut health (laxation and healthy bowel habits), and cardiovascular health (reduction in platelet aggregation) (Hunter et al. 2009). A diet rich in fruit and vegetables offers health and wellness benefits, and preliminary evidence suggests that other cultivars such as *A. chinensis* 'Hort16A' or other *Actinidia* species may also have health benefits.

New kiwifruit cultivars could also benefit from the absence of compounds present in 'Hayward'. Oxalate raphides in 'Hayward' are probably not a health issue but can affect palatability especially of processed products. Studies of the concentrations in fruit of *Actinidia* germplasm of ascorbate and oxalate (a product of ascorbate catabolism) indicate that it should be possible to select cultivars that are high in ascorbate but low in oxalate (Rassam and Laing 2005). Allergic

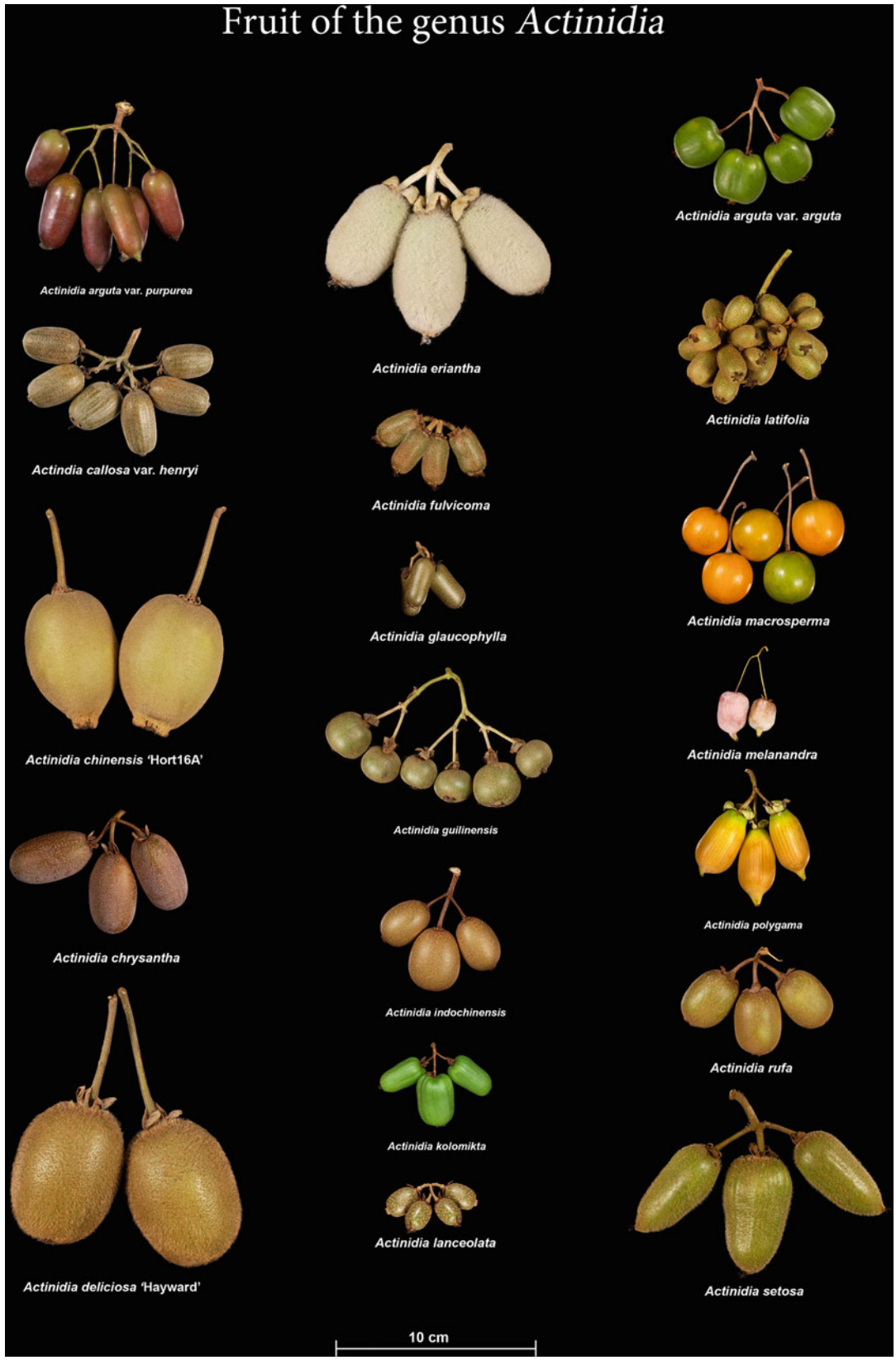

Fig. 1.3 Fruit of 19 taxa of *Actinidia*

responses to kiwifruit have increased with increased kiwifruit production and consumption. Allergenicity has been ascribed to the protease actinidin, which is often present in kiwifruit in large amounts. Actinidin content and protease activity vary in different kiwifruit: fruit of some *A. arguta* cultivars contain more actinidin than *A. deliciosa* 'Hayward', whereas actinidin and protease activity was not detectable or was barely detectable in two *A. rufa* selections (Nishiyama et al. 2004a) and some *A. chinensis* cultivars, including 'Hort16A' (Yamanaka et al. 2004), even though 'Hort16A' fruit still elicit the allergic response (Lucas et al. 2005).

1.2.6 Cytogenetics

The basic chromosome number of *Actinidia* is $x = 29$. Polyploidy in *Actinidia* is common, with diploids, tetraploids, hexaploids, and octoploids occurring in diminishing frequencies (Ferguson and Huang 2007). Although only limited chromosome counts have been made for most taxa, ploidy races have been detected in 15 taxa, suggesting that variation in ploidy may be common. For example, detailed studies have revealed diploid, tetraploid, hexaploid, heptaploid, and octoploid forms of *A. arguta* s.l. in the wild in Japan (Kataoka et al. 2010). The high frequency of polyploids and chromosome races in *Actinidia* is probably due to the production and fusion of numerically unreduced gametes (Yan et al. 1997b). Somatic doubling in bud sports (see Sect. 1.5.1) may also occur in the wild.

Although known ploidy races within taxa are usually separated geographically, they cannot usually be readily distinguished morphologically; e.g., there are no obvious morphological differences between diploid and tetraploid races of *A. chinensis* or between most of the various ploidy races of *A. arguta*. It is likely that within wild populations of *Actinidia* species, there is considerable interspecific hybridization and gene transfer (Liu et al. 2007, 2008), as well as frequent differentiation into ploidy races not yet detected.

The high basic chromosome number of *Actinidia* may be due to chromosome duplication early in the evolution of the genus, followed by rediploidization (McNeilage and Considine 1989; Shi et al. 2010). Comparison of the number and morphology of chromosomes in *Actinidia* with those in the related genera *Clematoclethra* ($x = 12$) and *Saurauia* ($x = 13$) suggests that *Actinidia* ($x = 29$) was derived from a palaeotetraploid ($x = 14$, $2n = 56$) and that an additional chromosome pair was formed through a centromeric chromosome fission (He et al. 2005). An alterative scenario would be the hybridization between $2n = 28$ and $2n = 30$ species followed by a polyploidization event. Frequent duplication of microsatellite loci supports *Actinidia* diploid species being actually polyploid (Huang et al. 1998).

Actinidia chromosomes are relatively small (<1 μm) and it is difficult to observe their morphology. He et al. (2005) characterized the karyotype of diploid *A. chinensis* ($2n = 58$) chromosomes as 38 metacentric + 18 submetacentric (including two satellite chromosomes) + 2 telomeric. The 8th and 9th, and the 11th and 12th pairs of the chromosomes are similar in length and morphology.

1.2.7 Genome Size

Genome size in *Actinidia* has been determined mainly by flow cytometry, with the published 2C-values (holoploid) for hexaploid *A. deliciosa* ranging from 3.8 to 4.5 pg DNA (Hopping 1993, 1994; Ollitrault-Sammarcelli et al. 1994; Ferguson et al. 1997; Start et al. 2007) or 3.7–4.3 $\times$ 10^9 bp (assuming 1 pg DNA = 0.978 $\times$ 10^9 bp), a range that agrees reasonably well with the estimate of Matsunaga et al. (1996) of about 3.5 $\times$ 10^9 bp. *Actinidia* taxa at the one ploidy level vary little in genome size, and polyploidization (increase in ploidy) has not resulted in a loss of nuclear DNA (Ferguson et al. 1997; Zhang et al. 2008). Flow cytometry can, therefore, be used with confidence to determine ploidy in *Actinidia* and the results are consistent with chromosome counts (Ferguson and Huang 2007; A.R. Ferguson unpublished).

1.2.8 *Taxonomic Position of* A. chinensis *and* A. deliciosa

The two commercially important *Actinidia* species, *A. chinensis* and *A. deliciosa*, and a third closely related species restricted to Taiwan, *A. setosa*, have variously been treated either as separate species or as

varieties of the same species. Liang (1975) initially treated *A. chinensis* and *A. deliciosa* as varieties of the same species, but later agreed that there were sufficient morphological differences to differentiate them as separate species (Liang and Ferguson 1984, 1986). *A. setosa*, previously treated as a variety of *A. chinensis*, was also raised to specific status (Liang and Ferguson 1985). The latest taxonomic treatment in the *Flora of China* recombines *A. chinensis, A. deliciosa*, and *A. setosa* into *A. chinensis* (Li et al. 2007a, b, 2009), but we have, for convenience, retained them as separate species. The relationships between *A. chinensis* and *A. deliciosa* and other *Actinidia* species are discussed further in Sect. 1.4.

1.2.9 Agricultural Status

Each year, 100,000–150,000 tons of *Actinidia* fruit are collected from the wild in China (Huang and Ferguson 2001; Chen 2003). Most of these fruit would be of *A. chinensis* or *A. deliciosa*, but other *Actinidia* species are also harvested. The total quantity of fruit collected indicates that millions of plants must remain in the wild. Many *Actinidia* species establish readily, especially in cutover or regenerating forests, and they grow so vigorously that they can envelop large trees: *Actinidia* thus have the potential to become serious weeds in those areas in which the climate allows successful kiwifruit cultivation. In New Zealand, in the main growing area of the Bay of Plenty, naturalized kiwifruit have become so abundant that plant pest control programs have been initiated (Sullivan et al. 2007). New Zealand is possibly unusual in that there are often native forests or commercial plantations close to kiwifruit orchards and these provide suitable conditions for the establishment and spread of weed kiwifruit. Occasional wild kiwifruit have been recorded in Germany (Kasperek 2003) and the United Kingdom (Payne 1997) presumably from seed from imported fruit. In other parts of the world in which kiwifruit are grown commercially, they could easily become serious weeds.

In China, *Actinidia* fruit have been collected from the wild for many centuries. Such fruit are generally small and are of poor quality. The success of *A. deliciosa*, first in New Zealand, and then in other countries, stimulated Chinese interest in kiwifruit cultivation. Now fruit from commercial orchards of *A. chinensis* and *A. deliciosa* in China are much more important than fruit collected from the wild, and China has a greater area in kiwifruit orchards than any other country.

Commercial plantings of kiwifruit around the world now amount to about 150,000 ha and total annual production to about 1.8 million tons (Belrose Inc. 2010). Outside China, the *A. deliciosa* cultivar 'Hayward' and its associated males still predominate. 'Hayward' is the traditional "green" kiwifruit well known to consumers for its bright green fruit flesh. 'Hayward' was favored over other *A. deliciosa* cultivars because its fruit have a better flavor, are larger, and store for much longer. Newer cultivars of "green" kiwifruit, usually sports or seedlings of 'Hayward', are now emerging, particularly in Italy (Testolin and Ferguson 2009), although none is yet widely grown. "Gold" kiwifruit, which are yellow-fleshed cultivars of *A. chinensis*, are becoming increasingly important. In New Zealand, gold kiwifruit from the cultivar 'Hort16A' now account for around 30% of the total production of kiwifruit. In Europe and South America, 'Hort16A' and another yellow-fleshed cultivar, 'Jintao', are being planted. 'Jintao' is a selection from the wild; 'Hort16A' is only a couple of generations removed from germplasm introduced from the wild. This demonstrates the importance of germplasm resources for kiwifruit improvement.

In China, kiwifruit plantings are genetically much more diverse, but apart from cultivars of New Zealand origin, they are nearly all essentially selections from the wild (Ferguson and Huang 2007; Li et al. 2010). About one quarter would be of *A. chinensis* and the remainder of *A. deliciosa*.

1.3 Conservation Initiatives

Cultivated kiwifruit are still very similar to plants in the wild. Breeders of crops with little history of improvement tend to make the greatest use of collections of raw germplasm, and horticultural crops in general are noted for having greater intrataxon variation than do agricultural crops (Engels and Thormann 2007). Since nearly all kiwifruit cultivars grown in China are direct selections from the wild, they themselves represent a valuable resource of genetic diversity (Zhen et al. 2004).

Many of the existing kiwifruit cultivars available outside China come from a very narrow genetic base, and although *A. chinensis* and *A. deliciosa* are highly heterozygous (Ferguson and Huang 2007), it is likely that the development of really novel types of kiwifruit will come from the introgression of genes from other *Actinidia* species. Recognition and acquisition from the wild and the maintenance and evaluation of *Actinidia* germplasm are therefore essential for kiwifruit improvement programs.

1.3.1 Genetic Erosion

Although *Actinidia* species are widely dispersed throughout much of China, they are found mainly in relatively inaccessible or mountainous areas. Intensified land use means that most wild *Actinidia* populations are now mainly remnant populations and this could lead to genetic drift. Even these remnant populations are under increasing threat because of land clearance and with vines often being cut down to collect the fruit (Li and Lowe 2007). Nearly 20 *Actinidia* taxa are currently considered endangered (Zhang 2000; Zhang et al. 2000). Many of the wild *Actinidia* resources recorded only 25 years ago in Sichuan have now dwindled considerably and some taxa have disappeared completely (Li and Lowe 2007). Such losses are probably common throughout the rest of China and both in situ and ex situ conservation are required to protect genetic resources.

1.3.2 Sampling Genetic Diversity

Even large germplasm collections can conserve only a very small part of the wild diversity, especially as *Actinidia* appears to be such a variable genus. It is most unlikely that just a few genotypes will give an adequate representation of the variation within any given taxon. Yet, apart from *A. chinensis*, *A. deliciosa*, and, possibly, *A. arguta*, most *Actinidia* germplasm collections contain only a small number of representatives of any taxon. Furthermore, many of the genotypes held in different germplasm collections have been obtained by exchange with other collections and the sampling of the wild diversity is even more limited than might be first thought. Huang (2003) proposed that the sampling and conservation of *Actinidia* germplasm be made more systematic by considering geographic distribution (since isolated populations may be undergoing genetic drift), gender variation, ploidy races, and chloroplastic and mitochondrial DNA variation, as well as nuclear genome diversity. This is ambitious: in the meantime he recommended that at least five female and four male plants be conserved for each taxon. Patterns of genetic variation within wild populations of *A. chinensis* and *A. deliciosa* suggest that when making ex situ collections from a particular area, plants more than 100 m apart should be sampled first (Liu et al. 2007, 2008). Molecular markers are proving useful data for determining genetic diversity between and within species and within accessions of a particular species (Zhang et al. 2007; LG Fraser personal communication). Considerable diversity can be expected within seed accessions because *Actinidia* are obligatorily outcrossing.

Molecular markers could then be used when choosing genotypes for retention in germplasm collections to maintain maximum diversity.

Viruses have recently been detected in some *Actinidia* genotypes (Nitta and Ogasawara 1997; Clover et al. 2003; Pearson et al. 2007). The implications for commercial production are not clear, but as a precaution, new accessions of *Actinidia* material (both seed and budwood) should be checked for possible infection.

1.3.3 Ex Situ Germplasm Resources

1.3.3.1 China

The repositories in China have the greatest representation in terms of numbers of taxa. The national germplasm repository for *Actinidia* at the Wuhan Institute of Botany, Chinese Academy of Sciences, has as its goal the conservation of natural resources of *Actinidia* in China and the development of superior cultivars (Huang 2003). Nearly 60 taxa of more than 40 species, comprising more than 200 accessions from the wild or from exchange, are conserved as a living collection in the Wuhan Botanic Garden, Moshan, Wuhan, Hubei (Wang et al. 2003). The fruit characteristics have been summarized in Huang et al. (2003, 2004). Most of the

plants come from Hubei, Guangxi, Hunan, Jiangxi, and Fujian and there are 63 named cultivars or selections. To cover the range of growing conditions required by *Actinidia*, complementary collections are held under cooler conditions at Lushan, Jiangxi, or the moister, more subtropical conditions of the Guilin Botanic Garden, Guangxi. The collection at the Guangxi Institute of Botany, Guilin, occupies 0.3 ha and contains representatives of 74 taxa and 69 clones or cultivars (Li et al. 2000b). Phenological and fruit characteristics of plants in the collection have been described in a series of papers (e.g., Huang et al. 1983; Li et al. 1985, 1996). Another important collection is that of the Sichuan Provincial Natural Resources Research Institute, Chengdu, which has a collection of vines of eight species from the Three Gorges region of the Yangzi River and surrounding areas of Sichuan and Chongqing (Li and Lowe 2007).

1.3.3.2 New Zealand

The Plant & Food Research (formerly HortResearch) *Actinidia* germplasm collection occupies 6.2 ha at three research orchards at Kerikeri, Te Puke, and Riwaka. It currently contains about 3,500 genotypes from 310 accessions of 24 taxa (Ferguson 2007), mostly of *A. chinensis* and *A. deliciosa*, but in addition to these two species there are 372 genotypes from 92 accessions of other species. There is a collection of 80 cultivars or named selections, many of them originating outside New Zealand. A few taxa are represented by only a single genotype or genotypes of one gender so, in total, 18 species are fruiting.

1.3.3.3 Europe

The most important collection in Europe is that of the Dipartimento di Scienze Agrarie e Ambientali, University of Udine, Italy. This occupies 0.5 ha and has about 138 accessions of 23 *Actinidia* taxa (mainly separate species) from introductions of budwood or seed and named cultivars or selections (R. Testolin personal communication). The collection is particularly strong in *A. chinensis* cultivars (directly or indirectly from China), and *A. deliciosa* cultivars and selections mainly of Italian or New Zealand origin. This collection includes 48 accessions of taxa other than *A. chinensis*, *A. deliciosa*, or *A. arguta*, including some interesting species seldom found in other repositories.

1.3.3.4 United States of America

The United States Department of Agriculture National Clonal Germplasm Repository for *Actinidia* is mainly at Corvallis, Oregon, with some additional material held at Davis, California. The repository has a particularly good collection of cold-hardy *Actinidia* including 103 genotypes of *A. arguta* and *A. arguta* var. *purpurea* and 48 of *A. kolomikta*; these are mainly named selections. Most other taxa are represented by only a few genotypes, although there are 32 of *A. chinensis* and 15 of *A. deliciosa*, again mostly cultivars or selections. There is also a good collection of cold-hardy *Actinidia* at the University of Minnesota (Start et al. 2007).

1.3.3.5 Korea

Sung Kyun Kwan University in Suwon has collected 20 *Actinidia* species and 18 cultivars (Shim and Ha 1999) and the Subtropical Fruits Experimental Station in Haenam and the Forest Genetics Research Institute in Suwon have collected wild germplasm of *A. arguta* as well as representatives of other taxa.

1.3.3.6 Japan

The Kagawa Prefectural Experiment Station has a collection of cultivars of *A. chinensis*, *A. deliciosa*, *A. rufa*, *A. arguta*, and interspecific hybrids (Kokudo et al. 2003; Mizugami et al. 2007). Kagawa University also has a collection particularly rich in species native to Japan, such as *A. arguta*, *A. hypoleuca*, and *A. rufa*, and selections of these (Phivnil et al. 2005; I. Kataoka personal communication).

1.3.4 Maintenance of Germplasm

Actinidia germplasm vines are usually grown on the support structures and following the procedures of commercial orchards. Vines should preferably be on their own roots as some species are graft-incompatible

(Chartier and Blanchet 1997). Climatic requirements mean that not all *Actinidia* can be grown well at any one site. Thus, more subtropical species, such as *A. indochinensis*, do not survive the winters of Udine, Italy, whereas the warmer conditions of Wuhan, China, or Te Puke, New Zealand, do not suit cold-hardy species such as *A. kolomikta*. Plants of some taxa, e.g., *A. arguta* var. *purpurea*, will grow well at Te Puke but do not flower or fruit adequately: any such requirement for winter chilling will probably vary according to the genotype and possibly the provenance. Vine vigor may also vary in different repositories. *Actinidia* vines are usually long-lived under cultivation – one notable cultivated vine of *A. arguta* in Korea is at least 600 years old (Shim and Ha 1999). Some species, however, are less vigorous and mature plants of *A. polygama* will occasionally suddenly die back to their roots (New Zealand) as can plants of *A. arguta*, *A. hemsleyana*, *A. kolomikta*, and *A. polygama* in Udine, Italy (R. Testolin personal communication).

1.3.5 In Vitro Preservation

Both slow-growth systems, in which conditions are modified so that cultures can be held for extended periods, and cryopreservation have been successful with kiwifruit (Monette 1995). Tips of micropropagated shoots have been held at low temperatures (8°C) for a year (Monette 1995), and stem segments (Jian and Sun 1989), calli derived from hypocotyls (Hakozaki et al. 1996), seedling shoot tips (Suzuki et al. 1995), and encapsulated shoots (Bachiri et al. 2001) have been stored in liquid nitrogen and successfully regenerated. Such systems avoid the considerable maintenance requirements of extensive germplasm repositories of living plants. Nevertheless, these procedures have not been adopted for long-term storage of germplasm by any of the major *Actinidia* collections. Seed is routinely stored at −18 to −25°C, sometimes under vacuum, but it is not known for how long it remains viable.

1.4 Origin and Evolution of Kiwifruit

Actinidia are often so variable vegetatively that using morphological characters to delimit taxa is not always satisfactory (Dunn 1911; Huang et al. 1999; Li et al. 2009). Application of biochemical and molecular markers has added greatly to our understanding of phylogenetic relationships within the genus and of the relationships of wild taxa to cultivated kiwifruit.

1.4.1 Phylogenetic Relationships Within Actinidia

Molecular studies using genotypes of known provenance from the wild strongly suggest that the current infrageneric subdivision of *Actinidia* based on morphological characters is not natural (Li et al. 2000a, 2002). The *Leiocarpae*, which have glabrous ovaries and fruit, are probably monophyletic (see Ferguson and Huang 2007), perhaps excluding *A. kolomitka* (Testolin et al. 1997; Cipriani et al. 1998), but the remaining three traditional sections seem artificial. *Actinidia* taxa within China are more easily grouped if their geographic distributions are also considered: north China, the Yangzi River Valley, south-eastern China, southern China, and south-western China (Huang et al. 1999; Li et al. 2000a, 2002, 2003; Huang et al. 2002). *Actinidia* should perhaps be divided into two sections, *Leiocarpae* and *Maculatae*, the latter being further divided into four series containing taxa from the Yangzi Valley and from the three southern parts of China (Ferguson and Huang 2007). This may help to resolve the delimitation of many species within *Actinidia*.

Evidence from morphological, biochemical, and molecular approaches should be considered together. It is likely that there has been frequent polyploidization, hybridization, and reticulate evolution, particularly as there often seems incongruence between nuclear, mitochondrial, and chloroplastic markers (Chat et al. 2004). Many species appear to be polyphyletic in their mitochondrial DNA, in chloroplastic DNA, or in both (Chat et al. 2004), demonstrating the dangers of studying only a limited number of genotypes in each taxon. Molecular studies are like morphological studies in that any conclusions drawn will be more reliable the more extensive the germplasm resources examined (Li et al. 2009).

1.4.2 *Origin of Tetraploid* A. chinensis *and* A. deliciosa

A. chinensis and *A. deliciosa* are by far the most important *Actinidia* in cultivation. Understanding better the relationships between these closely related taxa should facilitate kiwifruit improvement programs. *A. chinensis* has both diploid and tetraploid chromosome races (Xiong 1992; Yan et al. 1994), whereas *A. deliciosa* is hexaploid (Zhang 1983; McNeilage and Considine 1989). A basic question, as yet unresolved, is whether tetraploid *A. chinensis* and *A. deliciosa* are allopolyploid or autopolyploid in origin. Morphologically similar taxa warrant further study: an example is *A. setosa* from Taiwan which was originally included as a variety of *A. chinensis* s.l. (Li 1952), was subsequently elevated as a distinct species (Liang and Ferguson 1986), and then again reduced to a variety of *A. chinensis* (Li et al. 2007b).

Tetraploid forms of *A. chinensis* are apparently restricted to a limited geographic area in eastern China (Xiong 1992; Yan et al. 1994). Many of the most important Chinese cultivars of *A. chinensis* are tetraploid and were originally selected from this area (Fujian and Jiangxi provinces) (Li et al. 2010). Tetraploid cultivars identified as *A. chinensis* have been selected from other provinces, but at least some may be hybrids between *A. chinensis* and *A. deliciosa* (Li et al. 2010). Tetraploid wild resources of *A. chinensis* appear therefore to be a particularly valuable genetic resource.

Morphologically, tetraploid forms of *A. chinensis* are very similar to diploid forms and the small differences in phenology may simply indicate adaptation to the climate of where they were collected. Molecular evidence suggests that at least some genotypes of tetraploid *A. chinensis* are allopolyploid in origin (Atkinson et al. 1997), whereas allelic segregation at ten isozyme loci in hybrids of *A. chinensis* ($4x$) × *A. eriantha* ($2x$) indicated that those particular tetraploid genotypes of *A. chinensis* used were autoploid (Huang et al. 1997). Such differing conclusions as to the nature of tetraploid *A. chinensis* may simply be a result of different genotypes having been studied. It is possible that tetraploid *A. chinensis* has evolved several times, despite being apparently limited to a restricted part of the species distribution.

The presence of a DNA repeat in *A. deliciosa* and in some tetraploid *A. chinensis* accessions but not in any diploid accessions of *A. chinensis* tested or other tetraploid accessions (Crowhurst and Gardner 1991; Yan et al. 1997a) has likewise been taken as indicating that there may be tetraploid *A. chinensis* groups with differing evolutionary histories (Murray 2002). However, the DNA repeat was also detected in *A. chrysantha*, not thought to be closely related to *A. deliciosa* or *A. chinensis* (Liang 1984), suggesting that the repeat may have been horizontally transferred within the genus or may have been lost from some lineages. It is, therefore, difficult to make firm conclusions about evolutionary history from the presence or absence of the repeat. Further studies with a wider range of genotypes are required.

There is likewise no clear consensus whether *A. deliciosa* is an autopolyploid derived solely from *A. chinensis* or whether any other *Actinidia* species might have contributed. The holoploid genomes of *A. chinensis* and *A. deliciosa* are undoubtedly similar (Testolin and Ferguson 1997; Li et al. 2002; Zhen et al. 2004) and it is likely that *A. chinensis* is the paternal progenitor of *A. deliciosa* (Cipriani et al. 1998; Li et al. 2002). Some molecular evidence suggests that *A. deliciosa* is allopolyploid (Crowhurst et al. 1990; Atkinson et al. 1997; Huang et al. 1997), whereas sequencing of nuclear ribosomal DNA internal transcribed spacers in *A. deliciosa* showed no evidence of *A. deliciosa* being allohexaploid (Li et al. 2002). This is not necessarily conclusive, however, as homogenization of such tandem repeats can obscure evidence of hybridism (Fuertes Aguilar et al. 1999).

If genomes were contributed from another species, then *A. deliciosa* and *A. chinensis* would be better treated as separate species. After the initial polyploidization event or hybridization, the newly formed *A. deliciosa* would have evolved independently from its progenitor species. The presence in *A. deliciosa* of isoyzme or microsatellite alleles absent from *A. chinensis* could thus be interpreted either as indicating subsequent independent evolution or as evidence that another progenitor species was involved. However, this second progenitor species might have been closely related to *A. chinensis* and would therefore share genomic markers with it through coancestry. Recurrent polyploidization or hybridization could add further complications.

Patterns of chromosome association during meiosis are sometimes used to deduce whether a plant is alloploid or autoploid in origin, bivalent pairing being

taken as evidence of alloploidy. The chromosomes of *A. deliciosa* predominantly form bivalents during pollen mother cell meiosis (McNeilage and Considine 1989), but this could be due to "diploidization" after allopolyploid formation or to the existence of a meiotic pairing control system. It is not known whether chromosomes that form bivalents show preferential pairing for a particular partner, or randomly pair with any of their five potential partners.

The morphological differences between *A. chinensis* and *A. deliciosa* are considerably greater than those between diploid and tetraploid races of *A. chinensis*, suggesting that another species morphologically similar to *A. deliciosa* might have contributed a genome to *A. deliciosa*. Possible candidate species, considered to be morphologically close to *A. chinensis* or *A. deliciosa*, include *A. chengkouensis*, *A. hubeiensis*, *A. obovata*, *A. setosa*, *A. sorbifolia*, and *A. stellatopilosa*. Both *A. hubeiensis* (He et al. 1998) and *A. setosa* (Yan et al. 1997c) are diploid, but the ploidy of the other species is not known. Most of these species have not been used in molecular studies of *Actinidia* except that chloroplastic and mitochondrial DNA studies make it unlikely that *A. setosa* is a progenitor of *A. deliciosa* (Chat et al. 2004).

Further studies using a greater range of genotypes from such species should help to determine possible origins of *A. deliciosa*. Detailed studies of sympatric populations of diploid and tetraploid *A. chinensis* and that of *A. chinensis* and *A. deliciosa* would also be useful (Li et al. 2010).

1.5 Cytogenetic Stocks

Variation in ploidy between taxa and within taxa can create obvious difficulties when trying to introgress characters from the different *Actinidia* species into the current commercially important species. The ploidy of parents to be used in crosses can be manipulated or progeny from crosses can be screened by flow cytometry to select for progeny at the desired ploidy. By choosing parents of different ploidies, offspring at a whole range of ploidies can be produced. However, the plants produced by interploidy crosses are often not at the expected ploidy (Ferguson 2009). Tissue culture can be used to regenerate plants from a variety of tissues, but the procedures used may result in somaclonal variation (Marino et al. 1998).

1.5.1 Ploidy Variants

Pollination of *A. deliciosa* (6*x*) female flowers with lethally irradiated pollen stimulated parthenogenetic development of unfertilized egg cells (Pandey et al. 1990; Chalak and Legave 1997). The resulting trihaploid plants, which had 87 chromosomes (Yan et al. 1997c), were unthrifty, grew poorly, and carried very few fruit. It seems that parthenogenesis can also be stimulated by interploidy pollination, as shown by the production of diploid plants from *A. arguta* (4*x*) × *A. deliciosa* (6*x*) (Chat and Dumoulin 1997) and that of triploid plants from *A. deliciosa* (6*x*) × *A. chinensis* (2*x*) (A.G. Seal and A.R. Ferguson, unpubl.). Development of individuals, which display parthenogenesis in interspecific hybrid populations, could enable greater fruit production from hybrids that normally have poor fruit set owing to low fertility; parthenogenetic individuals would also eliminate the requirement of males for pollination.

Crossing 4*x* × 2*x* *A. chinensis* (or in the reverse direction) produces large numbers of triploid plants, which grow vigorously but usually produce no fruit. Some triploid plants ($3x = 87$) have also been regenerated from endosperm of *A. chinensis* ($2x = 58$) (Huang and Tan 1988; Gui et al. 1993), but many of the plants produced were aneuploid. Endosperm cultures from seed produced by interspecific crosses can give rise to plants with a range of ploidies (Mu et al. 1990; Fraser et al. 1991), as can interploidy crosses.

Antimitotic agents have been successfully used in *Actinidia* to double chromosome numbers. Trihaploids have been efficiently doubled using oryzalin (Chalak and Legave 1996). Calli of triploid embryos arising from an interspecific cross between a diploid and a tetraploid (*A. chinensis* × *A. melanandra*) were treated with colchicine and at least some hexaploids regenerated, as well as plants at other ploidy levels (Harvey et al. 1995). Autotetraploid plants of *A. chinensis* 'Hort16A' have also been produced by treatment with colchicine and some of these plants produced carry fruit that are on average much larger (Wu et al. 2009).

Spontaneous doubling can occur. Some of the trihaploid plants of Chalak and Legave (1996) spontaneously doubled in chromosome number. Bud mutations of diploid *A. chinensis* 'Hort16A' in commercial orchards have been recognized because shoots carry fruit that are much larger than normal (Martin 2005). When such shoots are propagated by grafting, some of the plants seem cytologically unstable. Others appear to be stable and can be vegetatively propagated. At least some of these large-fruited mutants are mixoploid (2*x*, 4*x*) or tetraploid (Ferguson 2009). 'Hort16A' has proved to be a good parent in breeding programs (A.G. Seal personal communication) and these mutants allow it to be used at the tetraploid level giving new breeding opportunities.

1.5.2 Unreduced Gametes

Production of numerically unreduced (2*n*) gametes has probably played an important role in the evolution of polyploidy in *Actinidia* (Yan et al. 1997b). It appears that diploid *A. chinensis* plants introduced from the wild in different parts of China produce unreduced gametes to varying extents (A.G. Seal and A.R. Ferguson, unpubl. Unreduced gametes can be very useful in kiwifruit breeding as they could facilitate the transfer of the genomes of selected female genotypes to higher ploidy levels. Even if only a small proportion of the gametes were unreduced, flow cytometric screening of the offspring would allow selection of plants of the desired ploidy. It is likely that other *Actinidia* species also produce unreduced gametes.

1.6 Classical and Molecular Genetic Studies

Wild *Actinidia* have been used in a limited number of genetic studies. Offspring from the cross between *A. chinensis* and *A. callosa* were used to construct the first genetic map of kiwifruit using a combination of microsatellites and amplified fragment length polymorphism (AFLP) markers (Testolin et al. 2001). Recently, a second, more comprehensive genetic map of *A. chinensis* has been produced from a F_1 family resulting from an intraspecific cross between two distantly related *A. chinensis* genotypes, which came from the wild in different parts of China and were expected to differ in important characters (Fraser et al. 2009).

Genetic markers that can be amplified across many *Actinidia* species are potentially much more useful, especially when interspecific hybrid populations are being studied. Testolin et al. (2001), using microsatellites derived from genomic libraries, found insufficient cross-species amplification between two taxonomically distant *Actinidia* species. Expressed sequence tag (EST)-derived microsatellites should be more conserved because of the selection pressure operating on functional and regulatory genes: such markers that were developed in an *A. chinensis* mapping family showed at least some level of cross amplification over 26 different *Actinidia* taxa (Fraser et al. 2005; Tsang et al. 2007). This should enable the development of genetic maps in other *Actinidia* species using a standard set of microsatellite markers.

A selection of microsatellite markers representing genes in the anthocyanin pathway and some of their controlling elements have been tested in an interspecific *Actinidia* population, the result of a cross between an orange-fruited species, *A. macrosperma*, and a red-fruited species, *A. melanandra*. A single marker was found to segregate with the red fruit color phenotype (Fraser et al. 2006).

1.7 Crop Improvement

Although existing kiwifruit cultivars are highly heterozygous, they still have a fairly narrow genetic base, especially cultivars that have been developed outside China. Within China, most of the more important *A. chinensis* cultivars are tetraploid and most of these come from a limited part of the total geographic range of the species (Li et al. 2010). There is thus potential to improve cultivars further through crossing with wild material. There are also many traits within non-cultivated *Actinidia* species that could have commercial potential if transferred into cultivated kiwifruit. By incorporating fruit traits such as different colors, ripening indicators, edible or peelable skins, different flavors, and nutrient compositions (Ferguson 1990b; Testolin and Costa 1994; Huang et al. 2004; Ferguson and Huang 2007) into the currently cultivated species,

there is potential to develop many new kiwifruit cultivars (Ferguson 2007, 2009; Ferguson and Seal 2008). It should also be possible to introduce new vine growth characteristics, such as a reduced requirement for winter chilling, greater cold hardiness, or disease resistance.

1.7.1 Interspecific Crosses

Many successful interspecific *Actinidia* crosses have been described (e.g., Fairchild 1927; Pringle 1986; Wang et al. 1989, 1994, 2000; Ke et al. 1992; Testolin and Costa 1994; An et al. 1995). Some crosses are very successful allowing thousands of hybrid plants to be raised, e.g., *A. chinensis* × *A. eriantha* (Wang et al. 2000); others, especially interploidy crosses, may set only a few fruits containing a very small number of viable seed. Embryo-rescue enables certain cross combinations that would otherwise fail (Harvey et al. 1995; Hirsch et al. 2001). Most F_1 hybrids are unlikely to have immediate commercial potential and further crossing or backcrossing of the hybrids is therefore necessary. Hybrid fertility requires good pairing of the chromosomes and the production of balanced gametes. In polyploid hybrids, chromosome pairing can be allosyndetic or autosyndetic. The type of pairing that does occur can be determined by genomic in situ hybridization (GISH) on the hybrid meiocytes (Datson et al. 2006). Good chromosome pairing between parental genomes is also required for the introgression of characters. In *Actinidia* hybrids, chromosome pairing is usually better the more closely are the parents related. Knowing the type of chromosome pairing in hybrids helps in making decisions as to whether the production of F_2 hybrids is a better breeding strategy than backcrossing to one or other of the parents. The ability of many *Actinidia* species to hybridize should enable transfer of many traits into cultivated species.

1.7.2 Somatic Hybridization

Although somatic hybridization has great potential, it has so far proved difficult in *Actinidia*. Protoplasts have been successfully isolated and cultured in *A. arguta* var. *arguta*, *A. arguta* var. *purpurea*, *A. chinensis*, *A. deliciosa*, *A. eriantha, A. kolomikta*, and *A. polygama* and many plants were obtained (Oliveira and Pais 1991, 1992; Derambure and Hirsch 1995; Zhang et al. 1995; Xiao and Hirsch 1996, 1997). There are reports of successful somatic fusion and regeneration of protoplasts from *A. chinensis* and *A. deliciosa* and of *A. chinensis* and *A. kolomikta* (Xiao and Han 1997; Xiao et al. 2004). Chromosome counts, ploidy measurements, and DNA analyses confirmed that at least one of the plants raised was a somatic hybrid between *A. chinensis* and *A. kolomikta*, apparently with chilling tolerance similar to that of *A. kolomikta* (Xiao et al. 2004).

1.7.3 Genetic Transformation

Research on transgenics in *Actinidia* started when Rugini et al. (1989) reported genetic transformation and plant regeneration from leaf disks of *A. deliciosa* with the *rol* genes of *A. rhizogenes*, and subsequently the field evaluation of transgenic *rolABC* plants (Rugini et al. 1991, 1997). Furthermore, resistant fruits to *Botrytis cinerea* have been evaluated from 10-year-old transgenic plants overexpressing the *osmotin* gene (Gutiérrez-Pesce and Rugini 2008). Subsequently, *Agrobacterium*-mediated transformation has been reported in *A. arguta*, *A. chinensis*, *A. deliciosa*, *A. eriantha*, and *A. kolomikta* and transgenic plants of *A. chinensis*, *A. deliciosa*, and *A. eriantha* have been grown to flowering and fruiting maturity to demonstrate transmission of transgenes to progeny (Firsov and Dolgov 1997; Fung et al. 1998; Wang et al. 2006). *A. eriantha* has advantages over the commercial species for transformation studies because flowering and fruiting can be achieved under containment conditions less than 2 years after inoculation with *Agrobacterium*. *Actinidia* have also been transformed using PEG-mediated transfection and electroporation (Oliveira et al. 1991; Raquel and Oliveira 1996). Electroporation involves the formation of transient pores in biological membranes by the discharge of altering electrical current. The use of protoplasts in these systems is necessary, since they have an exposed plasmalemma. Hence, highly efficient plant regeneration protocols are necessary.

At present, transformation is being used experimentally and there are no genetically modified commercial kiwifruit. However, transformation of

kiwifruit is relatively easy and there are good prospects for developing kiwifruit with improved agronomic traits by using biotechnological techniques. Current genetic transformation programs are focused on improving kiwifruit by transferring one or more foreign genes, or by limiting the expression of endogenous genes.

1.8 Genomic Resources

Plant & Food Research, New Zealand, has available a large database of more than 130,000 expressed sequence tags (ESTs) from kiwifruit (Crowhurst et al. 2008). Most ESTs (>80%) have been developed from cDNA libraries from *A. chinensis* and *A. deliciosa*, but there are also ESTs from *A. arguta*, *A. eriantha*, *A. hemsleyana*, *A. polygama*, and *A. setosa* (Atkinson and MacRae 2007). The ESTs have been used in the preparation of a genetic map (Fraser et al. 2009), in the cloning, ordering, and sequencing of genomic DNA libraries (Hilario et al. 2007), and in studies on genome duplication in the evolution of *Actinidia* (Shi et al. 2010). A microarray of >17,000 kiwifruit genes has also been developed to monitor patterns of gene expression (Walton et al. 2007).

More than 240 compounds have been detected in the volatile components of flowers and fruit from nine *A. arguta* genotypes. Around 60–70 different compounds were extracted from individual tissues of each genotype (Matich et al. 2003).

1.9 Future Prospects

The process of domestication of the green kiwifruit, *A. deliciosa*, started about 100 years ago and the first kiwifruit orchards were planted about 70 years ago. After another quarter of a century came the hesitant beginnings of international trade in kiwifruit. Now green kiwifruit are familiar to most western consumers. Only in the last few years have such consumers begun to realize that not all kiwifruit are green or have a sharp acid flavor, but that some kiwifruit are sweet and aromatic and have golden-yellow flesh. Plants of *A. chinensis* were first successfully established outside China about 30 years ago and commercial trade in yellow kiwifruit began only during the last years of the twentieth century. The arrival of yellow-fleshed kiwifruit was the biggest change to the industry since kiwifruit were first introduced to consumers (Ferguson 2009). The establishment of orchards outside China and the successful development of trade in fruit of *A. chinensis* and *A. deliciosa* were based on tentative explorations of the wild germplasm and a few remarkably limited accessions of seed. The kiwifruit orchards of China are genetically more diverse, but even so are based almost entirely on good selections from the wild. Exploitation of the diversity in the wild germplasm has only just begun.

The world kiwifruit industries were developed primarily to supply fresh fruit to consumers. Kiwifruit are enjoyable to eat. However, expansion of production and increased consumer demand will depend on new cultivars meeting some of the important requirements of new food product development: enhanced pleasure, convenience, and health. Kiwifruit that lack hair, have edible or peelable skins, have different flavors or different flesh colors, store better and ripen more consistently or change color as they ripen, and are different and novel should appeal to consumers. From the diversity that exists in the wild germplasm, we know these are realistic possibilities.

Most consumers recognize that kiwifruit are high in vitamin C and that kiwifruit are, therefore, good for their heath. The fruits of some wild *Actinidia* contain much higher concentrations of vitamin C, and therefore breeding of commercial kiwifruit cultivars that are much richer in vitamin C is possible. However, in addition to vitamin C, kiwifruit contain many compounds that may provide health benefits beyond contributing to basic nutrition (Hunter et al. 2009). There is increasing evidence that eating green kiwifruit (*A. deliciosa* 'Hayward') has positive effects on cardiovascular and gut health. The immune system may also benefit. As we understand better the contribution that kiwifruit consumption makes to health, we will probably find that the wild germplasm can add to the health benefits provided by new cultivars.

Kiwifruit were domesticated and much of the initial development of kiwifruit as a crop occurred long before much was known of kiwifruit in the wild or of the diversity that exists within *Actinidia*. We now know much more, but there remains much we do not know about the genus and about how to exploit its diversity. There is still a need for greater effort on

conserving wild germplasm. We need to know more of the genetics of the commercial cultivars and of the wild species. Genomics and biotechnology may help us to identify the genes controlling traits currently absent from cultivars. We need to know how to transfer these desirable qualities into the kiwifruit of the future.

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