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Abstract

As one of the most recently domesticated fruit crops, tremendous genetic resources exist in genetic pools of germplasm repositories and in breeding projects as well as in the wild. This chapter focuses on a wide spectrum of genetic resources that are more important to genetic enhancement for germplasm innovation, breeding practice, and new cultivar development, including species diversity, gender diversity, and genetic variation of important fruit characteristics. Ploidy variation is discussed in Chap. 5.

2.1 Species Diversity of *Actinidia*

The genus *Actinidia* has 54 species and 21 varieties, a total of 75 taxa (Li et al. 2007). Current commercial cultivation is almost entirely based on the *Actinidia chinensis* complex including *Actinidia chinensis* Planchon var. *chinensis* and *Actinidia chinensis* var. *deliciosa* (A. Chevalier) A. Chevalier. The genus has a very wide geographic distribution in Eastern Asia, ranging from the Asian tropics to cold temperate regions as far north as latitude 50° (Liang 1983; Ferguson 1990a). This distribution

pattern is generally of many Chinese endemic plant genera, centering in mainland China but extending to the neighboring countries. The vast majority of *Actinidia* taxa are endemic to China.

There, they occur mostly in the mountains and hills of south-central and southeast China with the QinLing Mountains forming a northern boundary and the HengDuan Mountains forming a western boundary. This distribution pattern is biogeographically structured into six regions from southwest to northeast China: southwest China, southern China, central China, eastern and southeastern China, northern China, and northeastern China (Huang 2014). Small numbers of *Actinidia* taxa extend to other countries, but only two species are found in adjacent countries but not in China itself: *Actinidia stri-gosa* Hook. F. et Thoms., endemic to Nepal, and *Actinidia hypoleuca* Nakai, endemic to Japan.

Most species produce edible fruit and have varying commercial potential as fresh fruit,

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traditional medicines, and other raw materials such as fibers for the paper industry.

The Chinese National Germplasm Repository was initially established at Wuhan Botanical Garden in 1979 soon after the launch of a national survey of *Actinidia* germplasm resources in 1978. So far, as many as 61 taxa (including species, varieties, and forms) and 1467 accessions collected from 27 provinces (or autonomous regions) are managed as the world's most extensive *Actinidia* germplasm collection. In addition, more than 800 genotypes selected from the wild or elite breeding selections as well as 82 cultivars from around the world are maintained for an active breeding program, in which more than 30,000 progenies are under evaluation for new cultivar development. The repository is the largest collection harboring the richest genetic resources of the *Actinidia* in the world.

2.2 Ploidy Variation

Actinidia has the basic chromosome number ($x = 29$) but very wide variation in ploidy ranging from diploid to octoploid with even occasional decaploids and dodecaploids (Huang and Ferguson 2007). In general, there is a structured reticulate pattern of diploids, tetraploids, hexaploids, and octoploids in diminishing frequency within the genus. Ploidy variation is discussed further in Chap. 5.

2.3 Gender Variation

All *Actinidia* taxa appear to be functionally dioecious, although this has been unequivocally established in only a few taxa such as *A. chinensis* and *Actinidia polygama* (Brundell 1975; McKay 1976; Schmid 1978; Ferguson 1984; McNeilage 1988, 1991a, b; Kawagoe and Suzuki 2004; Goodwin et al. 2013).

It is likely that all species have a common genetic mechanism of dioecy. The sex determination mechanism appears to be of the active-Y type (Testolin et al. 1995, 1999, 2004; Harvey et al. 1997; McNeilage 1997; Fraser et al. 2009)

and probably involves at least two tightly linked genes, a dominant allele for pistil suppression closely linked to a dominant gene for pollen development on the Y chromosome and on the equivalent part of the X chromosome, two recessive alleles that allow pistil development and pollen death, respectively (McNeilage 1991a; Fraser et al. 2009). For dioecy to be maintained, recombination in this part of the chromosome would need to be suppressed, even if not completely. In this model, the male would be heterogametic, i.e., X_nX/X_nY (Testolin et al. 1995). This would be consistent with the disomic inheritance and the 1:1 male-to-female sex ratios observed in *Actinidia* in most controlled crosses and in plants raised from seed collected in the wild and at different ploidy levels (McNeilage 1991a, 1997; Testolin et al. 1995, 1999; Harvey et al. 1997). In diploids, females would be XX and males XY, in tetraploids the females XXXX and the males XXXY, in hexaploids the females XXXXXX and the males XXXXXY, etc. Maintenance of dioecy and the 1:1 sex ratios observed at different ploidy levels (with both parents at the same ploidy level) is readily explained by assuming that in *Actinidia*, as in most other plants, sexual polyploidization through the production of numerically unreduced gametes has played an important role in the evolution of the genus (Testolin et al. 1995; McNeilage 1997).

Dioecism is not absolute, and flowers can vary in sex expression (Harvey and Fraser 1988). Gender inconstancy was first observed in New Zealand orchards of *A. chinensis* var. *deliciosa* (Ferguson 1984; Ferguson and Davison 1986). Fruiting ('inconstant' or andromonoecious) male plants carried small fruit, usually on a single shoot or at most only a few shoots (McNeilage 1988). Grafting of scion wood of such shoots resulted in whole plants that can also carry fruit (McNeilage 1988). It is, of course, easier to detect male plants that carry small fruit than apparently female plants that produce viable pollen. Fruiting male plants usually produce both staminate flowers and flowers which are, to varying extents, bisexual (McNeilage 1991a, b). At least six genotypes of gender variants are

found: male, fruiting male, neuter, female, inconstant female, and hermaphrodite (Huang et al. 2000). When fruiting males are selfed, males and females are produced in a 3:1 ratio, confirming that the males are heterozygous and the females homozygous at the sex-determining loci (Testolin et al. 1995; Harvey et al. 1997).

Gender inconstancy is not restricted to *A. chinensis* var. *deliciosa* but has also been observed in *Actinidia arguta* (Hirsch et al. 1990), *Actinidia chinensis* var. *chinensis* (Tang and Jiang 1995), and *Actinidia eriantha* (Cui et al. 2002) and would probably be found in other *Actinidia* species if enough plants were studied. Several seedlings produced by crossing *A. chinensis* var. *chinensis* with *A. eriantha* were probably fruiting males in that they had both staminate flowers (producing viable pollen) and pistillate flowers.

Self-fertile, completely hermaphroditic plants of *A. chinensis* var. *deliciosa*, carrying only bisexual flowers, have been obtained from crosses involving inconstant (fruiting) males (McNeilage 1997; McNeilage and Steinhagen 1998; McNeilage et al. 2007). Hermaphrodites are morphologically indistinguishable from females except in that pollen fertility has been restored and are therefore considered to be phenotypically altered females. Hermaphroditism has proved to be stable and inheritable.

In *Actinidia* species, as in many other higher plants (Ming et al. 2007), there are not obvious differences between putative sex chromosomes. Karyotyping of *Actinidia* is difficult because even diploid species have many chromosomes ($x = 29$) and these are all small ($<1 \mu\text{m}$) (He et al. 2003, 2005). Nevertheless, He et al. (2003) concluded that two nucleolar chromosomes in diploid male of *A. chinensis* var. *chinensis* plants (the heterogametic gender) were unable to pair completely and that they therefore differed in their satellite regions. Analysis of sex-linked markers (Fraser et al. 2009) also indicated putative sex chromosomes, probably at an early stage of evolution.

Breeding in dioecious plants has the disadvantage that pollen parents are usually selected 'in the dark' as fruiting characteristics are not expressed in the male. Progeny testing is required,

but this is expensive and time-consuming. Development of experimental procedures that induce female plants to produce even some viable pollen would allow direct crossing of two selected female cultivars. Furthermore, the pollen parent in intra- and intertaxon crosses may affect both fruit size and fruit quality (Harvey et al. 1992; McNeilage et al. 1992; Buxton 2005; Chen et al. 1996; Qi et al. 2007; Seal et al. 2013a, b). A fully hermaphrodite cultivar that was self-fertile and self-setting would have many economic advantages. The fruit of the hermaphrodite kiwifruit plants so far developed preclude their use as commercial cultivars. It should, however, eventually be possible to select hermaphrodite kiwifruit cultivars with fruit of the required quality.

2.4 Genetic Variation in Important Fruit Characteristics

There is tremendous genetic variation at both the interspecific and the infraspecific level within *Actinidia* in vegetative, floral, and fruit characteristics (Li 1952; Li et al. 1996). Fruit characters are the most important for horticulturists and plant breeders and for those involved in germplasm management and cultivar improvement (Li 1952; Huang et al. 1983; Liang 1984; Li et al. 1985; Ferguson 1990b; Cui et al. 2002; Han et al. 2003; Huang et al. 2000, 2004; Huang and Ferguson 2007).

2.4.1 Fruit Size

Fruit size is the most important trait in determining which *Actinidia* species have commercial potential. Most species have fruit that are much smaller than those of commercial kiwifruit cultivars. The smallest fruit in the genus are those of *Actinidia cylindrica* or *Actinidia rubricaulis* weighing each about 0.8–1.0 g; the largest are generally those of *A. chinensis* complex, averaging mostly 60–120 g. Potential fruit size may not be fully expressed in plants in the wild or plants in germplasm collections, and considerably bigger fruit might be achieved on cultivation.

Within *A. chinensis* var. *chinensis* or *A. chinensis* var. *deliciosa*, there can be great variation in fruit size; e.g., Cheng et al. (2004) found a range in mean fruit size from 14.4 to 127.6 g in a population of 289 female *A. chinensis* var. *chinensis* vines arising from a factorial crossing of 3 females by 13 males from different seed accessions. Such variation was normally found in wild populations during the survey of wild germplasm in China (Huang et al. 2004). Fruit size has traditionally been one of the most important criteria in selecting from the wild in China. Most cultivars of *A. chinensis* var. *chinensis* selected from the wild have fruit on average slightly smaller than those of *A. chinensis* var. *deliciosa*, but the maximum potential fruit size is probably much the same. The cultivar ‘Hayward’ (*A. chinensis* var. *deliciosa*) has large fruit, consistently averaging about 110 g, but some selections have even larger fruit, e.g., ‘Jade Moon’ (a natural mutation of ‘Hayward’) with a mean fruit size of c. 115–120 g. Doubling the chromosome number of diploid selections of *A. chinensis* var. *chinensis* by the use of colchicine can result in autotetraploids with larger fruit (Wu et al. 2012) (Fig. 2.1).

The other taxa with relatively large fruit, e.g., *Actinidia chengkouensis*, *Actinidia chinensis* var. *setosa*, *A. eriantha*, and *Actinidia grandiflora*, are generally those closely related to *A. chinensis*. There is mostly little detailed information available, but in these taxa, fruit size can also be very variable. For example, the fruit of *A. eriantha* are usually cited as being 10–40 g, but one selection from the wild, ‘White,’ has particularly large fruit, averaging 96 g (Wu et al. 2009), four times the average

weight of fruit of ‘Bidan,’ the other described *A. eriantha* cultivar (Jo et al. 2007). An average fruit weight of 96 g is very similar to that of many successful commercial cultivars of *A. chinensis* var. *chinensis* and *A. chinensis* var. *deliciosa*.

2.4.2 Fruit Shape

Fruit of most cultivars of *A. chinensis* var. *chinensis* and *A. chinensis* var. *deliciosa* are generally cylindrical. At least 15 different fruit shape descriptors have been used to describe the variation within the genus: short cylindrical, long cylindrical, cylindrical, ovoid, obovoid, long globose, ovoid-cylindrical, obloid, globose, oblong, near globose, ellipsoid, long conoidal, ovoid-conoidal, and ovoid-globose (Huang et al. 2004). To distinguish commercial cultivars, the UPOV (2001) descriptors for kiwifruit has been used, in addition, the fruit shape in cross section, the ‘squareness’ of the shoulders, the taper to the stalk or stylar end and the general shape of the stylar end. A strong protrusion of the stylar end or ‘beak’ (rostrate) is the characteristic of some cultivars such as *A. chinensis* var. *chinensis* ‘Hort16A’ and *A. chinensis* var. *deliciosa* ‘Qinmei’ and of *A. polygama* fruit (for photographs, see Ferguson 1999; Huang 2014).

2.4.3 Fruit Hairs and Skin

Within the genus, there are many hair types in the different species. Fruit of *Actinidia* species

Fig. 2.1 Fruit variation in *A. chinensis* var. *chinensis* (a) and *A. chinensis* var. *deliciosa* (b)



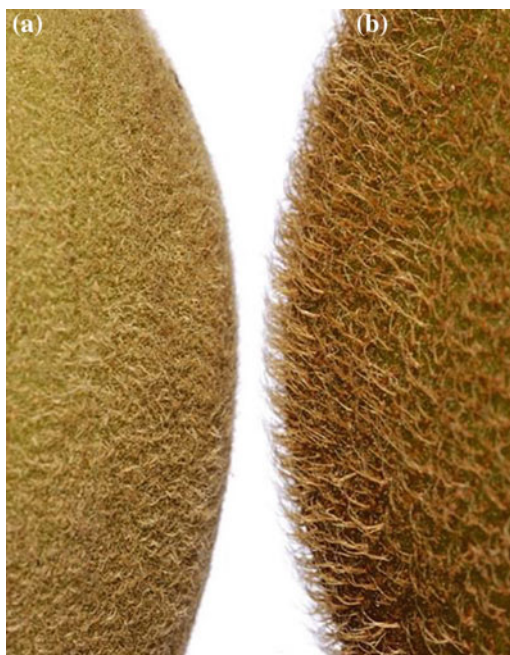


Fig. 2.2 Fruit hairs of (left) *A. chinensis* var. *chinensis* 'Hort16A' and (right) *A. chinensis* var. *deliciosa* 'Hayward' (photograph from Plant & Food Research, New Zealand)

traditionally placed in the *Leiocarpae* (e.g., *A. arguta*, *Actinidia macrosperma*, *Actinidia melanandra*, *A. polygama*, and *Actinidia valvata*) have smooth skins and appear essentially glabrous (Liang 1984; Huang et al. 2004). The isolated hairs found in *A. arguta* early during fruit development are simple, but they have disappeared by the time that the fruit are mature (Hallett and Sutherland 2005). Other species have fruit with varying degrees of pubescence ranging from puberulent or minutely pubescent as in *Actinidia rufa*, to the long, stiff (setose) hairs of *A. chinensis* var. *setosa* to the tomentose to lanate hairs of *A. eriantha* or *Actinidia zhejiangensis* (Huang et al. 2004). *Actinidia* fruit hairs, if present, are generally yellowish brown to gingerish to reddish brown (White 1986b; Cui et al. 2002) with the most notable exception being the pure white hairs of some *A. eriantha* selections.

The fruit hairs of *A. chinensis* var. *deliciosa* are well studied and described: multiserial, tapering hairs with very long apical cells

intermixed with much shorter, uniseriate hairs that may be arrested stages in the development of the longer hairs (White 1986a). Different cultivars of *A. chinensis* var. *deliciosa* show large variation in the relative abundance of the two types of hairs and the dimensions of the larger hairs (White 1986b). This variation in the hair covering ranges from downy (e.g., the selection 'Downy') or bristly or setose (e.g., 'Bruno') or hispid (e.g., 'Hayward'). Some mutations can be hairless, e.g., Top Star® is a bud mutation of *A. chinensis* var. *deliciosa* 'Hayward' in which the fruit are essentially hairless (Bergamini 1991). At flowering, the ovary is normally completely covered with fully developed hairs, and as the fruit develops, the hairs are moved apart. They also start dying, and by 60 days after fruit set, all the cells of the hairs are dead (Montanaro et al. 2012). Electron microscopy shows that the fruit surface of *A. chinensis* var. *deliciosa* has only small, uniseriate hairs (White 1986b). However, in other species such as *A. eriantha*, the fruit have both small, uniseriate, two-celled hairs with a long tapering apical cell and abundant, much longer, slender, multicelled hairs, often branching near the base to form a cluster of 3 hairs, each terminating in a very long thin apical cell (White 1986b).

Whereas all commercial *A. chinensis* var. *deliciosa* cultivars have skins with abundant stiff hairs (e.g., 'Hayward,' Fig. 2.2), most genotypes of *A. chinensis* var. *chinensis* have fine hairs, almost like the bloom on a peach (e.g., 'Hort16A,' Fig. 2.2), often largely lost as the



Fig. 2.3 Hairless fruit of *A. arguta* (photograph from Plant & Food Research, New Zealand)

fruit mature. This is the easiest and most obvious way of distinguishing the two varieties of *A. chinensis* (Li et al. 2010a). A recently released cultivar, ‘Jinyan,’ an interspecific hybrid *A. eriantha* x *A. chinensis* var. *chinensis*, has mostly small, sparse uniseriate hairs and only a few multiseriate longer hairs (Zhong et al. 2012).

The abundant stiff hairs of cultivars such as *A. chinensis* var. *deliciosa* ‘Hayward’ are commonly considered to be a disadvantage to consumers that should be selected against. Such hairs could, however, be an advantage for their effects on the physiology of the developing fruit (Montanaro et al. 2012). They could also protect the developing fruit from mechanical damage or some insect pests. For example, oviposition rates of the Mediterranean fruit fly (*Ceratitis capitata*) were much lower on ‘Hayward,’ the cultivar of *A. chinensis* var. *deliciosa* with markedly hairy fruit skins, than on ‘Soreli,’ a relatively smooth-skinned *A. chinensis* var. *chinensis* cultivar. The hairs of harvested *A. chinensis* var. *deliciosa* fruit are largely removed by brushing or are lost during grading in packhouses. Many *A. chinensis* var. *chinensis* cultivars or selections with fine soft hairs on the fruit can be more attractive to consumers.

The skins of most *Actinidia* species are considered unpalatable, and the fruit are normally eaten with a spoon or after peeling using a knife so that kiwifruit can therefore be considered as inconvenient (Jack et al. 1997; Gamble et al. 2010). A peelable kiwifruit, with a skin that could be removed easily, could have commercial potential (Hallett and Sutherland 2007; Atkinson et al. 2009; Gamble et al. 2010; Harker et al. 2011). Fruit of individual selections of *A. chinensis* var. *chinensis*, *A. chinensis* var. *deliciosa*, and *A. eriantha* vary in the ease with which their skins can be peeled, once fruit have ripened. If a commercial cultivar with an easily removed fruit skin can be achieved, it is probably important that the hairs be either already shed or consistently persistent so that the fruit flesh is not contaminated with hairs.

The underlying fruit skin can be light green or dark green to brown to reddish brown. The structure of *Actinidia* fruit skins explains why only

some skins are palatable (Hallett and Sutherland 2005, 2007). The skins of the 16 *Actinidia* species studied could be separated into three types:

1. soft, hairless skins of species such as *A. arguta* (Fig. 2.3). The skins are edible if somewhat chewy. They consist of an outer surface of epidermal cells usually with a thick cuticle. There are one or two layers of small hypodermal cells and then the fleshy, outer pericarp cells. Such soft skins make fruit more susceptible to mechanical damage and more prone to water loss, and hence shriveling, on ripening and storage (Hassall et al. 1998). *A. arguta* has been crossed with *A. chinensis* var. *deliciosa* in an attempt to develop large kiwifruit with smooth, hairless skins (White and Beatson 1993).
2. hairless but rough and ‘warty’ skins of species such as *Actinidia indochinensis*. The skin consists of several layers of dead, compressed cells with interspersed lenticels (‘spots’).
3. rough, hairy skins as in *A. chinensis* var. *chinensis*, *A. chinensis* var. *deliciosa*, and *A. eriantha*, varying in hairiness. There may also be brachysclereids (stone cells) separating the hypodermis and the cells immediately below from the bulk of the pericarp, either scattered as in *A. chinensis* var. *chinensis* ‘Hort16A’ or more continuous as in *A. indochinensis*. Stone cells also occur in some other genotypes of *A. chinensis* var. *chinensis* (Hallett and Sutherland 2005), but not in *A. chinensis* var. *deliciosa* (Hallett and Sutherland 2005).

2.4.4 Fruit Color

Externally, most *Actinidia* fruit are brownish green to yellowish brown if hairs are removed. Internally, the inner and outer pericarps are almost always green and the fruit core is white, cream, or pale green.

The fruit pericarp color in *Actinidia* is determined by pigments that are chlorophylls, carotenoids, and anthocyanins. The pericarp of the best-known kiwifruit, *A. chinensis* var. *deliciosa* ‘Hayward,’ is a brilliant, translucent, jade green which contrasts with the white core and the black

seed. The fruit flesh is green because the chloroplasts and chlorophyll in fruit are retained even when the fruit mature and ripen (Possingham et al. 1980; Hallett et al. 1995; Montefiori et al. 2007; 2009). In fact, the pericarp of most *Actinidia* species remains green once fruits ripen (Huang et al. 2004) and kiwifruit can therefore be classified as ‘stay-green’ fruit. Kiwifruit are unusual in comparison with most other cultivated fruit crops because chlorophyll is not lost on ripening and the chloroplasts are not transformed into chromoplasts. They may, however, lose some of their chlorophyll during prolonged storage (Burdon and Lallu 2011). The chlorophyll and carotenoid composition of the green fruit pericarp of *A. chinensis* var. *deliciosa* is similar to that of normal photosynthetically active chloroplasts (Possingham et al. 1980; Ben-Arie et al. 1982; Fuke et al. 1985; Watanabe et al. 1986; Cano 1991; McGhie and Ainge 2002; Nishiyama et al. 2005). Chlorophylls and associated carotenoids have also been found at higher concentrations in the green-fleshed fruit of *A. arguta* and *A. rufa* (Nishiyama et al. 2005) although these concentrations are still much lower than in leaves. Fruit that appear deeper green to the eye have higher concentrations of chlorophyll (Nishiyama et al. 2005, 2007); e.g., the very dark green fruit of *A. eriantha* have at least twice the chlorophyll content of *A.*

chinensis var. *deliciosa* ‘Hayward’ fruit (Montefiori et al. 2007) (Fig. 2.4).

Among cultivars and selections of the *A. chinensis* complex, there can be great variation in fruit colors. In general, *A. chinensis* var. *deliciosa* fruit are almost always green. In most cultivars of *A. chinensis* var. *chinensis*, however, the pericarp color ranges from lime green to a bright golden yellow. The fruit flesh of such yellow-fleshed cultivars, e.g., ‘Jintao,’ is initially green during fruit growth and development, and the change in color from green to varying shades of yellow has been ascribed to a gradual loss of chlorophyll during maturation, so that the yellow due to carotenoids is unmasked, without concomitant increase in carotenoids (McGhie and Ainge 2002; Montefiori et al. 2007, 2009). The concentrations of carotenoids in ripe fruit of *A. chinensis* var. *chinensis* ‘Hort16A’ (golden yellow flesh) and *A. chinensis* var. *deliciosa* ‘Hayward’ (green flesh) are very similar (McGhie and Ainge 2002). The hue of the flesh when ripe therefore depends largely on the amount of chlorophyll retained: There is variation in the timing and the extent to which chlorophyll is degraded during ripening and storage, the resultant extremes being yellow or green flesh at eating ripeness. The change in flesh color on maturation of yellow-fleshed cultivars such as ‘Jintao’ can be important commercially. Harvesting indices based on flesh color have been

Fig. 2.4 Diversity of fruit flesh colors in *Actinidia* (photograph from Plant & Food Research, New Zealand)



developed, and in general, the hue of the flesh 102–104 °h is used as harvest index for yellow-fleshed cultivars. Customers expect fruit that are sold as ‘golden yellow’ not to be lime green or greenish yellow. ‘Hort16A’ fruit become yellow late in development. ‘Degreening’ may be achieved by holding the fruit postharvest at 5–10 °C, but conditions need to be modified (e.g., by the use of controlled atmosphere) to reach a compromise between adequate degreening and preventing rapid fruit softening and the development of fungal rots (Burdon and Lallu 2011). In contrast, at eating ripeness, the fruit flesh of some cultivars of *A. chinensis* var. *chinensis* is still bright green, e.g., ‘Wuzhi No. 3.’

Some genotypes of *A. chinensis* var. *chinensis* and *A. chinensis* var. *deliciosa* also have red pigmentation, mainly in the inner pericarp around the core. The term ‘red-fleshed kiwifruit’ is generally used to refer to genotypes of *A. chinensis* var. *chinensis* and *A. chinensis* var. *deliciosa* (Montefiori et al. 2005, 2011). Red pigmentation was first found in fruit of wild plants of *A. chinensis* var. *chinensis* from Hubei and subsequently from Henan and other parts of China. These variants have, at times, been classified as *A. chinensis* f. *rufopulpa* C.F. Liang and R.H. Huang or *Actinidia chinensis* var. *rufopulpa* (C.F. Liang and R.H. Huang) C.F. Liang and A. R. Ferguson. Similar variants of *A. chinensis* var. *deliciosa* have sometimes been classified as *Actinidia deliciosa* var. *coloris* T.H. Lin and X. Y. Xiong. Red-fleshed *A. chinensis* var. *chinensis* occur mainly in Henan, Jiangxi, and Hunan and red-fleshed *A. chinensis* var. *deliciosa* at higher altitudes in Hunan, Hubei, and Sichuan (Lin and Xiong 1991; Sui et al. 2013). The red pigments are often restricted to a bright central ring around the core (Montefiori et al. 2005; Sui et al. 2013), but they can extend right to the skin. The intensity and distribution of the red pigments vary with genotype and with environmental conditions. In regions with warmer climates, the red flesh color is present during the early stages of fruit growth but fades by midsummer when there is little difference between day and night temperatures (Huang et al. 2004; Zhong et al. 2007). However, the red color is more consistently

expressed in regions with large diurnal changes in temperature, especially in the mountains at higher elevations. In *A. chinensis* var. *chinensis*, the main red pigments, anthocyanins, appear to be cyanidin 3-*O*-xylo(1-2)-galactoside followed by cyanidin galactoside and in *A. chinensis* var. *deliciosa*, cyanidin glucoside followed by cyanidin galactoside (Montefiori et al. 2003, 2005, 2009; Comeskey et al. 2009).

Anthocyanins are also found in some other *Actinidia* species. They may occur throughout the fruit or may be limited to certain tissues, the core, the inner pericarp, the outer pericarp, or as a blush on the skin (Cui et al. 2002; Montefiori et al. 2011). Fruit that are fully red (or purple) when ripe are found in *A. melanandra* and *A. arguta*; the purple-fleshed genotypes of *A. arguta* have sometimes been segregated into *Actinidia arguta* var. *purpurea* (Rehder) C.F. Liang or even as a distinct species *Actinidia purpurea* Rehder. ‘Rubystar’ is a selection from the wild of what was described as *Actinidia henanensis* C.F. Liang (Qi et al. 2011), but now included in *A. melanandra*. Anthocyanins are probably responsible for the rather murky purple of ripe fruit of some variants of *A. arguta* and the pink or red coloration in the fruit of some genotypes of other varieties of *A. arguta*, *A. melanandra*, and *A. arguta* × *A. melanandra* hybrids. Some of these fruit also change color as they ripen (Seager 1997). *Actinidia* fruit contain much lower concentrations of anthocyanins than many common berry fruit (Boyes et al. 1997; Montefiori et al. 2005).

Different combinations of chlorophylls, carotenoids, and anthocyanins can result in a wide range of fruit colors. The pericarp of ripe fruit of some genotypes of *A. arguta* and *A. melanandra* can be brick red to purplish red, of *Actinidia kolomikta*, pale yellow to pale orange, of *A. polygama* apricot yellow, and of *A. macrosperma*, *Actinidia tetramera* and *A. valvata*, bright, intense orange. Offspring produced by crossing *A. macrosperma* (fruit orange when ripe) with *A. melanandra* (fruit brick red when ripe) have fruit with a spectacular range of colors when ripe from deep red, to orange, yellow, yellow-green to green.

The fruit of *A. macrosperma*, *A. polygama*, *A. tetramera*, and *A. valvata* change rapidly during

maturation and ripening from bright green to a yellowish orange or bright orange (Montefiori et al. 2003). This change in color has likewise been ascribed to a loss of chlorophyll and extensive conversion of the chloroplasts to chromoplasts (McGhie and Ainge 2002). However, unlike in *A. chinensis* var. *chinensis*, the change in color is more than just a demasking of the yellow color of the carotenoids as the chlorophyll is lost. For example, in *A. macrosperma*, maturation is accompanied by a large increase in carotenoids (Montefiori et al. 2004). The final color achieved depends on the particular carotenoids present, indicating that it might be possible to select new cultivars whose flesh color varied from yellow through bright orange (McGhie and Ainge 2002).

2.4.5 Fruit Texture

Actinidia fruit can be divided into four main zones: the skin, the outer pericarp, the inner pericarp surrounding the locules containing the seed, and the central core or columella (Ferguson 1984; Jackson and Harker 1997; Richardson et al. 2011). The relative proportions of these tissues can vary with genotypes and with species, especially in the ratio of the core to the pericarp diameter (Cotter et al. 1991; Huang et al. 2004). In a comprehensive study of 25 genotypes from 14 different *Actinidia* species, White et al. (2005) found that the softening of the three edible tissue zones during ripening followed much the same pattern as for the whole fruit. However, in some genotypes (*Actinidia fortunei* classified as *Actinidia glaucophylla* in the original paper and one genotype of *A. rufa*), the core did not soften even though it had the inner and outer pericarp, and in two other genotypes (*A. chinensis* var. *chinensis* ‘Wuzhi No 2’ and a second genotype of *A. rufa*), the core did soften but remained significantly firmer than the pericarp, even when the fruit were very ripe. Among *A. chinensis* var. *deliciosa* cultivars, the cores of ‘eating-ripe’ ‘Gracie’ fruit tend to be larger and remain harder (Cotter et al. 1991). A hard core can affect consumer acceptability.

In the recently released interspecific hybrid cultivar ‘Jinyan,’ the softening progress is different from that of most other commercial cultivars, and softening is from the core to the outer pericarp with a melting core when fully ripe: This improves storage quality and prolongs fruit shelf-life. In commercial ‘Hayward’ kiwifruit, a hardcore can be due to unsuitable storage and handling.

Ripe kiwifruit can range in texture from juicy (e.g., *A. chinensis* var. *chinensis*) to almost gelatinous (e.g., *A. arguta*), although individual genotypes within a species vary in texture, particularly flesh smoothness and flesh stringiness (Stec et al. 1989; Cotter et al. 1991; Jaeger et al. 2003). Larger fruit (*A. chinensis* var. *chinensis*, *A. chinensis* var. *deliciosa*, and *A. eriantha*) tend to be consistently softer when fully ripe than fruit from small-fruited species (White et al. 2005). However, the woody spike sometimes found at the stalk end is usually found only in larger fruit, especially those of *A. chinensis* var. *chinensis* and *A. chinensis* var. *deliciosa*, and is particularly noticeable in cultivars such as *A. chinensis* var. *chinensis* ‘Ganmi No 2’ (‘Kuimi’). Hard cores could rule out some selections as commercial cultivars.

2.4.6 Fruit Flavor

Most *Actinidia* fruit are edible even if only a few are really palatable (Ferguson 1990b). Individual genotypes of species such as *A. chinensis*, *A. arguta*, and *A. kolomikta* are variously described as having fruit with an excellent flavor; other genotypes of the same species have fruit bland and boring or even mildly unpleasant. The unripe fruit of *A. polygama* are mouthnumbing, shocking, and peppery (chili). This pungency has been ascribed to a monoterpene dehydroiridodial (Yoshihara et al. 1978). The pungency of *A. macrosperma* and *A. valvata* decreases as the fruit ripen.

Flavor is the combination of taste and odor (aroma). Flavors can change dramatically as fruit mature from underripe to overripe, and the window of flavor acceptability varies according to genotype, with overripe fruit of some kiwifruit genotypes developing off-flavors, especially the

so-called vomit flavors. Factors such as dry matter content, maturity at harvest, storage, firmness, length of storage, and even the temperature of storage can all affect flavor perceptions and preferences in fruit of one particular genotype, such as *A. chinensis* var. *deliciosa* ‘Hayward’ (e.g., Young and Paterson 1985; Stec et al. 1989; MacRae et al. 1990; Jaeger et al. 2003; Burdon et al. 2004; Marsh et al. 2004; Harker et al. 2009; Garcia et al. 2012). Similar results have been obtained for *A. arguta* ‘Ananasnaya’ (Fisk et al. 2006). This shows the difficulty of making meaningful comparisons of the flavors of fruit from different genotypes of a single *Actinidia* species or from genotypes of different species.

Consumers normally segregate according to their preference for different types of kiwifruit: Some prefer the acid/green/grassy flavors of *A. deliciosa* ‘Hayward’ and others the sweet/blackcurrant/tropical flavors of *A. chinensis* ‘Hort16A’ (Jaeger et al. 2003; Wismer et al. 2005). The diversity within *Actinidia* thus allows for many new breeding targets and new and distinct flavor profiles that create new product niches (Wismer et al. 2005).

The characteristic ‘kiwifruit’ flavor seems to be associated mainly with ethyl butanoate, (*E*)-2-hexenal, and some C6 alcohols (Gilbert et al. 1996; Jordán et al. 2002). The volatile components of ‘Hayward’ and ‘Hort16A’ differ in only a few compounds, and it is probably the proportions of each compound that are important in determining the overall flavors (Garcia et al. 2012). For example, aldehydes such as (*E*)-2-hexenal and hexenal are much higher in ‘Hayward,’ whereas ‘Hort16A’ has more of the esters such as ethyl butanoate responsible for ‘fruitiness.’ The fruit of *A. arguta*, with their very distinct aromas, likewise have complex mixtures of volatiles, particularly esters that have sweet ‘fruity’ odors (Matich et al. 2003) (Table 2.1).

Taste is largely determined by the balance between organic acids and the soluble sugars as well as the particular sugars and organic acids present (Nishiyama et al. 2008). Fruit of the different *Actinidia* species can contain different amounts of total sugars and total acids as well as the individual compounds (Huang et al. 1983; Li

et al. 1985; Chen et al. 1987; Huang et al. 2000, 2004; Nishiyama et al. 2008; Table 2.2). Even within seedling populations of the one species (*A. chinensis* var. *chinensis*), there can be considerable variation in dry matter, soluble solids concentration, fruit flesh pH, and the concentrations of total acids, individual acids, and sugars. Many of these characters are highly heritable, indicating that they are amenable to selection (Cheng et al. 2004). In *A. chinensis* var. *deliciosa*, differences between genotypes in fruit size and dry matter content are reflected in perceptions of flavor and texture (Nardozza et al. 2011).

2.4.7 Health Benefits of Kiwifruit

The potential benefits of kiwifruit consumption have long played an important role in the commercial promotion of kiwifruit in the fresh fruit market (Ferguson and Ferguson 2003; Ferguson and Stanley 2003; Kassardjian et al. 2006; Drummond 2013; Ward and Courtney 2013). And in some cases, there is increasing scientific evidence that kiwifruit could improve human health (Singletary 2012; Collins 2013; Drummond and Geary 2013; Duttaroy 2013; Skinner et al. 2013a, b; Stonehouse et al. 2012). The most convincing evidence is probably that kiwifruit consumption can improve gastrointestinal function, especially in those with constipation (Singletary 2012). Most of these studies have used *A. chinensis* var. *deliciosa* and some *A. chinensis* var. *chinensis*. There is almost no such work dealing with other *Actinidia* species although there are anecdotal reports of fruit of *A. arguta* being laxative and of fruit and stem or root saps of some species being anticancer.

2.4.8 Nutrient Composition

Information is given in Table 2.2 although results for a single or only a few genotypes of any particular species should be interpreted cautiously as there can be great intraspecific variation.

Detailed and comprehensive nutritional data are available for the fruit of *A. chinensis* var.

Table 2.1 Accepted *Actinidia* taxa and some important synonyms

Distribution	Species and varieties	Chinese name	Important synonyms	Chinese name
China				
1	<i>A. arguta</i> (Siebold and Zuccarini) Planchon ex Miquel	软枣猕猴桃		
1a	<i>A. arguta</i> var. <i>arguta</i>	软枣猕猴桃 (原变种)	<i>A. arguta</i> var. <i>purpurea</i> (Rehder) C.F. Liang <i>A. cordifolia</i> Miquel	紫果猕猴桃 心叶猕猴桃
1b	<i>A. arguta</i> var. <i>giraldii</i> (Diels) Voroshilov	陕西猕猴桃	<i>A. arguta</i> var. <i>nervosa</i> C.F. Liang; <i>A. kwangsiensis</i> H.L. Li	凸脉猕猴桃 广西猕猴桃
2	<i>A. callosa</i> Lindley	硬齿猕猴桃		
2a	<i>A. callosa</i> var. <i>callosa</i>	硬齿猕猴桃 (原变种)	<i>A. callosa</i> var. <i>formosana</i> Finet and Gagnepain <i>A. callosa</i> var. <i>pubiramula</i> C.Y. Wu	台湾猕猴桃 毛枝秤杆藤
2b	<i>A. callosa</i> var. <i>acuminata</i> C.F. Liang	尖叶猕猴桃		
2c	<i>A. callosa</i> var. <i>discolor</i> C.F. Liang	异色猕猴桃	<i>A. fanjingshanensis</i> S.D. Shi and Q.B. Wang	梵净山猕猴桃
2d	<i>A. callosa</i> var. <i>henryi</i> Maximowicz	京梨猕猴桃	<i>A. callosa</i> var. <i>ephippioidea</i> C.F. Liang	驼齿猕猴桃
2e	<i>A. callosa</i> var. <i>strigillosa</i> C.F. Liang	毛叶硬齿猕猴桃		
3	<i>A. chengkouensis</i> C.Y. Chang	城口猕猴桃		
4	<i>A. chinensis</i> Planchon	中华猕猴桃		
4a	<i>A. chinensis</i> var. <i>chinensis</i>	中华猕猴桃 (原变种)	<i>A. chinensis</i> f. <i>jinggangshanensis</i> C.F. Liang <i>A. chinensis</i> f. <i>rufopulpa</i> C.F. Liang and R.H. Huang <i>A. multipetaloides</i> H.Z. Jiang	井岗山猕猴桃 红肉猕猴桃 重瓣猕猴桃
4b	<i>A. chinensis</i> var. <i>deliciosa</i> (A. Chevalier) A. Chevalier	美味猕猴桃	<i>A. deliciosa</i> var. <i>coloris</i> T.H. Lin and X.Y. Xiong <i>A. chinensis</i> f. <i>chlorocarpa</i> C.F. Liang <i>A. chinensis</i> f. <i>longipila</i> C.F. Liang and R.Z. Wang <i>A. chinensis</i> var. <i>hispida</i> C.F. Liang	彩色猕猴桃 绿果猕猴桃 长毛猕猴桃 硬毛猕猴桃
4c	<i>A. chinensis</i> var. <i>setosa</i> H.L. Li	刺毛猕猴桃	<i>A. setosa</i> (H.L. Li) C.F. Liang and A.R. Ferguson	刺毛猕猴桃
5	<i>A. chrysantha</i> C.F. Liang	金花猕猴桃		
6	<i>A. cylindrica</i> C.F. Liang	柱果猕猴桃		
6a	<i>A. cylindrica</i> var. <i>cylindrica</i>	柱果猕猴桃 (原变种)	<i>A. cylindrica</i> f. <i>obtusifolia</i> C.F. Liang	钝叶猕猴桃

(continued)

Table 2.1 (continued)

Distribution	Species and varieties	Chinese name	Important synonyms	Chinese name
6b	<i>A. cylindrica</i> var. <i>reticulata</i> C.F. Liang	网脉猕猴桃		
7	<i>A. eriantha</i> Benth	毛花猕猴桃	<i>A. eriantha</i> f. <i>alba</i> C.F. Gan <i>A. eriantha</i> var. <i>brunnea</i> C.F. Liang <i>A. eriantha</i> var. <i>calvescens</i> C.F. Liang <i>A. fulvicoma</i> Hance var. <i>lanata</i> (Hemsley) C.F. Liang	白色毛花猕猴桃 棕毛毛花猕猴桃 秃果毛花猕猴桃 绵毛猕猴桃
8	<i>A. farinosa</i> C.F. Liang	粉毛猕猴桃		
9	<i>A. fasciculoides</i> C.F. Liang	簇花猕猴桃		
9a	<i>A. fasciculoides</i> var. <i>fasciculoides</i>	簇花猕猴桃 (原变种)		
9b	<i>A. fasciculoides</i> var. <i>cuneata</i> C.F. Liang	楔叶猕猴桃		
9c	<i>A. fasciculoides</i> var. <i>orbiculata</i> C.F. Liang	圆叶猕猴桃		
10	<i>A. fortunatii</i> Finet and Gagnepain	条叶猕猴桃	<i>A. glaucophylla</i> F. Chun <i>A. glaucophylla</i> var. <i>asymmetrica</i> (F. Chun) C.F. Liang <i>A. glaucophylla</i> var. <i>rotunda</i> C.F. Liang <i>A. glaucophylla</i> var. <i>robusta</i> C.F. Liang <i>A. gracilis</i> C.F. Liang	华南猕猴桃 耳叶猕猴桃 团叶猕猴桃 粗叶猕猴桃 纤小猕猴桃
11	<i>A. fulvicoma</i> Hance	黄毛猕猴桃		
11a	<i>A. fulvicoma</i> var. <i>fulvicoma</i>	黄毛猕猴桃 (原变种)	<i>A. fulvicoma</i> f. <i>arachnoidea</i> C.F. Liang	丝毛猕猴桃
11b	<i>A. fulvicoma</i> var. <i>cinerascens</i> (C.F. Liang) J.Q. Li and D.D. Soejarto	灰毛猕猴桃	<i>A. cinerascens</i> C.F. Liang <i>A. cinerascens</i> var. <i>longipetiolata</i> C.F. Liang <i>A. cinerascens</i> var. <i>tenuifolia</i> C.F. Liang	灰毛猕猴桃 长叶柄猕猴桃 菲叶猕猴桃
11c	<i>A. fulvicoma</i> var. <i>hirsuta</i> Finet and Gagnepain	糙毛猕猴桃		
11d	<i>A. fulvicoma</i> var. <i>pachyphylla</i> (Dunn) H.L. Li	厚叶猕猴桃		
12	<i>A. glaucocallosa</i> C.Y. Wu	粉叶猕猴桃		
13	<i>A. grandiflora</i> C.F. Liang	大花猕猴桃		
14	<i>A. hemsleyana</i> Dunn	长叶猕猴桃	<i>A. kengiana</i> F.P. Metcalf	粗齿猕猴桃
15	<i>A. henryi</i> Dunn	蒙自猕猴桃	<i>A. carnosifolia</i> C.Y. Wu <i>A. carnosifolia</i> var. <i>glaucescens</i> C.F. Liang <i>A. henryi</i> var. <i>polyodonta</i> Handel-Mazzetti	肉叶猕猴桃 奶果猕猴桃 多齿猕猴桃

(continued)

Table 2.1 (continued)

Distribution	Species and varieties	Chinese name	Important synonyms	Chinese name
16	<i>A. holotricha</i> Finet and Gagnepain	全毛猕猴桃		
17	<i>A. hubeiensis</i> H.M. Sun and R.H. Huang	湖北猕猴桃		
18	<i>A. indochinensis</i> Merrill	中越猕猴桃		
18a	<i>A. indochinensis</i> var. <i>indochinensis</i>	中越猕猴桃 (原变种)	<i>A. flavofloris</i> H.Z. Jiang	黄花猕猴桃
18b	<i>A. indochinensis</i> var. <i>ovatifolia</i> R.G. Li and L. Mo	卵圆叶猕猴桃		
19	<i>A. kolomikta</i> (Ruprecht and Maximowicz) Maximowicz	狗枣猕猴桃	<i>A. leptophylla</i> C.Y. Wu <i>A. maloides</i> H.L. Li <i>A. maloides</i> f. <i>cordata</i> C.F. Liang	薄叶猕猴桃 海棠猕猴桃 心叶海棠猕猴桃
20	<i>A. laevisissima</i> C.F. Liang	滑叶猕猴桃	<i>A. jiangkouensis</i> S.D. Shi and Z.S. Zhang <i>A. laevisissima</i> var. <i>floscula</i> S.D. Shi)	江口猕猴桃 小花猕猴桃
21	<i>A. lanceolata</i> Dunn	小叶猕猴桃		
22	<i>A. latifolia</i> (Gardner and Champion) Merrill	阔叶猕猴桃		
22a	<i>A. latifolia</i> var. <i>latifolia</i>	阔叶猕猴桃 (原变种)	<i>A. guilinensis</i> C.F. Liang	桂林猕猴桃
22b	<i>A. latifolia</i> var. <i>mollis</i> (Dunn) Handel-Mazzetti	长绒猕猴桃		
23	<i>A. liangguangensis</i> C.F. Liang	两广猕猴桃		
24	<i>A. lijiangensis</i> C.F. Liang and Y.X. Lu	漓江猕猴桃		
25	<i>A. linguensis</i> R.G. Li and X.G. Wang	临桂猕猴桃	<i>A. wantianensis</i> R.G. Li and L. Mo	宛田猕猴桃
26	<i>A. longicarpa</i> R.G. Li and M.Y. Liang	长果猕猴桃	<i>A. rubrafilmenta</i> R.G. Li and J.W. Li	红丝猕猴桃
27	<i>A. macrosperma</i> C.F. Liang	大籽猕猴桃		
27a	<i>A. macrosperma</i> var. <i>macrosperma</i>	大籽猕猴桃 (原变种)		
27b	<i>A. macrosperma</i> var. <i>mumoides</i> C.F. Liang	梅叶猕猴桃		
28	<i>A. melanandra</i> Franchet	黑蕊猕猴桃		
28a	<i>A. melanandra</i> var. <i>melanandra</i>	黑蕊猕猴桃 (原变种)	<i>A. globosa</i> C.F. Liang <i>A. henanensis</i> C.F. Liang <i>A. melanandra</i> var. <i>cretacea</i> C.F. Liang <i>A. melanandra</i> var. <i>subconcolor</i> C.F. Liang	圆果猕猴桃 河南猕猴桃 歪叶猕猴桃 褪粉猕猴桃
28b	<i>A. melanandra</i> var. <i>glabrescens</i> C.F. Liang	无髯猕猴桃		
29	<i>A. melliana</i> Handel-Mazzetti	美丽猕猴桃		

(continued)

Table 2.1 (continued)

Distribution	Species and varieties	Chinese name	Important synonyms	Chinese name
30	<i>A. obovata</i> Chun ex C.F. Liang	倒卵叶猕猴桃		
31	<i>A. persicina</i> R.G. Li and L. Mo	桃花猕猴桃		
32	<i>A. pilosula</i> (Finet and Gagnepain) Stapf ex Handel-Mazzetti	贡山猕猴桃		
33	<i>A. polygama</i> (Siebold and Zuccarini) Maximowicz	葛枣猕猴桃		
34	<i>A. rongshuiensis</i> R.G. Li and X.G. Wang	融水猕猴桃		
35	<i>A. rubricaulis</i> Dunn	红茎猕猴桃		
35a	<i>A. rubricaulis</i> var. <i>rubricaulis</i>	红茎猕猴桃 (原变种)		
35b	<i>A. rubricaulis</i> var. <i>coriacea</i> (Finet and Gagnepain) C.F. Liang	革叶猕猴桃		
36	<i>A. rubus</i> H. Léveillé	昭通猕猴桃		
37	<i>A. rudis</i> Dunn	糙叶猕猴桃		
37a	<i>A. rudis</i> var. <i>rudis</i>	糙叶猕猴桃 (原变种)	<i>A. petelotii</i> Diels	沙巴猕猴桃
37b	<i>A. rudis</i> var. <i>glabricaulis</i> C.Y. Wu	光茎猕猴桃		
38	<i>A. rufa</i> (Siebold and Zuccarini) Planchon ex Miquel	山梨猕猴桃		
39	<i>A. rufotricha</i> C.Y. Wu	红毛猕猴桃		
39a	<i>A. rufotricha</i> var. <i>rufotricha</i>	红毛猕猴桃 (原变种)		
39b	<i>A. rufotricha</i> var. <i>glomerata</i> C.F. Liang	密花猕猴桃		
40	<i>A. sabiifolia</i> Dunn	清风藤猕猴桃		
41	<i>A. sorbifolia</i> C.F. Liang	花楸猕猴桃	<i>A. truncatifolia</i> C.Y. Chang and P.S. Liu	截叶猕猴桃
42	<i>A. stellato-pilosa</i> C.Y. Chang	星毛猕猴桃		
43	<i>A. styracifolia</i> C.F. Liang	安息香猕猴桃		
44	<i>A. suberifolia</i> C.Y. Wu	栓叶猕猴桃		
45	<i>A. tetramera</i> Maximowicz	四萼猕猴桃	<i>A. tetramera</i> var. <i>badongensis</i> C.F. Liang	巴东猕猴桃
46	<i>A. trichogyna</i> Franchet	毛蕊猕猴桃		
47	<i>A. ulmifolia</i> C.F. Liang	榆叶猕猴桃		
48	<i>A. umbelloides</i> C.F. Liang	伞花猕猴桃		
48a	<i>A. umbelloides</i> var. <i>umbelloides</i>	伞花猕猴桃 (原变种)		
48b	<i>A. umbelloides</i> var. <i>flabellifolia</i> C.F. Liang	扇叶猕猴桃		

(continued)

Table 2.1 (continued)

Distribution	Species and varieties	Chinese name	Important synonyms	Chinese name
49	<i>A. valvata</i> Dunn	对萼猕猴桃	<i>A. valvata</i> var. <i>boehmeriifolia</i> C.F. Liang <i>A. valvata</i> var. <i>longipedicellata</i> L.L. Yu	麻叶猕猴桃 长柄对萼猕猴桃
50	<i>A. venosa</i> Rehder	显脉猕猴桃	<i>A. venosa</i> f. <i>pubescens</i> H.L. Li	柔毛猕猴桃
51	<i>A. vitifolia</i> C.Y. Wu	葡萄叶猕猴桃		
52	<i>A. zhejiangensis</i> C.F. Liang	浙江猕猴桃	<i>A. persicina</i> R.H. Huang and S.M. Wang	繁花猕猴桃
53 Japan	<i>A. hypoleuca</i> Nakai	白背叶猕猴桃		
54 Nepal	<i>A. strigosa</i> Hooker F. and Thomson	尼泊尔猕猴桃		

chinensis and *A. chinensis* var. *deliciosa* (Ferguson and Ferguson 2003; Stonehouse et al. 2012; Drummond 2013). Kiwifruit are a good source of minerals and of dietary fiber and contain a most effective laxative. Their outstanding nutritional quality is their very high content of vitamin C (ascorbate). In China, the kiwifruit was formerly called king of the fruits because of its remarkably high vitamin C content.

Although kiwifruit are a good source of minerals, especially potassium, any differences in mineral content are usually small and not likely to be important nutritionally (Samadi-Maybodi and Shariat 2003). Likewise, although there are considerable differences among species in the concentrations of total soluble solids, total acids, and total sugars in the fruit and of individual sugars and acids (Huang et al. 2004; Nishiyama et al. 2008), these differences are likely to be important in terms of flavor, not nutrition. As far as human health and nutrition are concerned, the important differences among genotypes are mostly in vitamin C content.

Other constituents may also have health benefits, e.g., folate, vitamin E, and the dietary fiber, but the information available is almost entirely for ‘Hayward’ (Drummond 2013).

2.4.8.1 Vitamin C

A typical *A. chinensis* var. *deliciosa* ‘Hayward’ kiwifruit contains about 85 mg ascorbate/100 g

FW, a fruit of *A. chinensis* var. *chinensis* ‘Hort16A’ up to 30 % more, about 105–110 mg ascorbate/100 g FW (Ferguson and MacRae 1992; Ferguson and Ferguson 2003). On average of a fresh weight basis, kiwifruit contain about 1–2 times more vitamin C than orange, 10 times as much as a banana, or up to 15 times as much as an apple (Visser et al. 2013). The USRDI (recommended daily intake) for vitamin C is currently 90 mg for an adult man and 75 mg for an adult woman with higher levels recommended for smokers or lactating mothers (Visser et al. 2013). One average-sized kiwifruit could by itself, therefore, provide the daily intake recommended for the general population. In terms of vitamin C, there is probably little advantage in consuming more than two or three kiwifruit in a day.

The vitamin C contents in Huang et al. (2004) indicate that there can be considerable variation from different genotypes. For *A. chinensis* var. *chinensis*, Huang et al. (2004) cited a range 50–420 mg ascorbate/100 g FW; ascorbate concentrations in fruit of 200 wild vines of from Henan varied from 56.6 to 400 mg/100 g FW (Yin and Li 1982); in vines from Guangxi 60–180 mg/100 g FW (Li et al. 1985); in a population of 289 female vines arising from a factorial crossing of 3 females by 13 males, the family means for ascorbate content ranged from 21.4–238.1 mg/100 g FW

Table 2.2 Main composition in *Actinidia* fruit^a

Species	Vitamin C (mg/100 g)	Soluble solids concentration (%)	Titrateable acidity (%)	Total sugars (%)	Amino acids (% W/W)
<i>A. arguta</i>	81–430	14–15	0.88–1.26	8.8–11	5.18
<i>A. callosa</i> var. <i>callosa</i>	50	14	2.3	4.91	
<i>A. callosa</i> var. <i>discolor</i>	162	13	3.6	5.2	
<i>A. callosa</i> var. <i>henryi</i>	15.5	11	1.0	7.4	
<i>A. chengkouensis</i>	44.0		2.4	3.30	
<i>A. chinensis</i> var. <i>chinensis</i>	50–420	7–19.2	0.9–2.2	4.5–11.5	3.2–5.8
<i>A. chinensis</i> var. <i>deliciosa</i>	50–250	8–25	1.1–1.6	6.9–13.2	4.1–6.0
<i>A. chinensis</i> var. <i>setosa</i>	79	10.5	1.3	7.1	
<i>A. chrysantha</i>	57–71.7	11	1.3	4.5–8.3	
<i>A. cylindrica</i>	30–100	7–13.2	1.1–1.3	4.5–6.1	6.6
<i>A. eriantha</i>	137–500	5–16	1.3–2.9	9.7	7.93
<i>A. farinosa</i>	10–20		1.8		
<i>A. fasciculoides</i>	7–8		0.3		
<i>A. fulvicoma</i> var. <i>fulvicoma</i>	30–117.8	9.5	1.0–1.4	2.6–5.3	
<i>A. fulvicoma</i> var. <i>cinerascens</i>	50–420	7.0–19	0.9–2.2	4.5–11.5	
<i>A. fulvicoma</i> var. <i>hirsuta</i>	157	10	1.0	2.6	
<i>A. grandiflora</i>	56–214	4–15	1.2–2.4	4.5	5.62
<i>A. hemsleyana</i>	12–80	8–10	0.8–1.7	5.1	
<i>A. henryi</i>	4.4	6	0.8		
<i>A. hubeiensis</i>	51–60	14	1.2	8.5	2.04
<i>A. indochinensis</i>	17–41.5	7–14	1.4–2.0	5.7–6.4	
<i>A. lanceolata</i>	33	12	1.2		
<i>A. latifolia</i>	671–2140	10	1.1–1.9	3.14	6.10
<i>A. liangguangensis</i>	10–56	7	1.0	2.2	
<i>A. lijiangensis</i>	60	14	1.1	7.4	5.1
<i>A. macrosperma</i>	28.8	10	0.6–1	5.9	9.0
<i>A. melanandra</i>	203	14	0.9	7	8.9
<i>A. melliana</i>	45	8.5	2.5	1.5	
<i>A. persicina</i>	314	14.5	1.6	5.4	4.2
<i>A. polygama</i>	58–87	11–17	0.2–1.1	11.2	
<i>A. rubricaulis</i>	17	8	2.6	2.7	
<i>A. rubus</i>	30	7	0.6		

(continued)

Table 2.2 (continued)

Species	Vitamin C (mg/100 g)	Soluble solids concentration (%)	Titrateable acidity (%)	Total sugars (%)	Amino acids (% W/W)
<i>A. rudis</i>	5	5	1.0		
<i>A. rufotricha</i> var. <i>glomerata</i>	42	6.5	1.2	2.2	
<i>A. sabiifolia</i>	68	12.4	1.0	3.1	
<i>A. sorbifolia</i>	42	11	1.8		
<i>A. styracifolia</i>	642	9	1.1	5.8	4.0
<i>A. tetramera</i>	107	11–15	0.2	7.8	
<i>A. valvata</i>	62–92	8	0.2–1.4	3.3–6	4.65
<i>A. zhejiangensis</i>	289–371	10–12	1.4–1.7	6.4	

^aData source Database of *Actinidia* Research Center, Wuhan Institute of Botany, CAS; Cui et al. (2002)

(Cheng et al. 2004). Similarly, published values for ascorbate concentrations in fruit of *A. chinensis* var. *deliciosa* range from 30 to 400 mg/100 g FW (Ferguson 1990b), and in a population of 65 female vines of *A. eriantha* raised from the one collection of seed, the ascorbate content was 195–720 mg/100 g FW (Bank and Ferguson 1986). Existing commercial kiwifruit cultivars were selected on attributes other than vitamin C content but show considerable variation. Some of the widely grown *A. chinensis* var. *chinensis* and *A. chinensis* var. *deliciosa* cultivars, such as ‘Jinyan’ and ‘Jinkui’ in China, contain twice as much ascorbate as ‘Hayward’ fruit (Li et al. 2010). However, even *Actinidia* cultivars with relatively low contents are still very good sources of vitamin C. Selection for high vitamin C in new cultivars should be feasible as, at least in *A. chinensis* var. *chinensis*, ascorbate content had high narrow-sense heritability (Cheng et al. 2004). Fortunately, selection for increased sugar content or soluble solids content should lead to a simultaneous increase in ascorbate content (Cheng et al. 2004).

Fruit of *Actinidia* species vary greatly in ascorbate concentrations, from as low as 4–5 mg/100 g FW in fruit of *Actinidia henryi* and *Actinidia rudis* to the astonishing levels, enough to account for more than 1 % of the fresh weight, in *Actinidia latifolia* (671–2140 mg/100 g FW) and *A. eriantha* (500–1379 mg/100 g FW) (Huang et al. 2004; Nishiyama et al. 2004; Du et al. 2009; Latocha et al. 2010; Table 2.2). Fruit of some genotypes *A. kolomikta* likewise contain

high amounts of ascorbate, up to 1 % fresh weight (Chesonienė et al. 2004). These differences in vitamin C would account for much of the variation observed between *Actinidia* species in antioxidant activity (Du et al. 2009). When fruit size is taken into account, the best sources of vitamin C in the genus are the fruit of *A. chinensis* var. *chinensis*, *A. chinensis* var. *deliciosa*, and especially *A. eriantha*.

Vitamin C content of fruit can be affected by many preharvest and postharvest factors (Lee and Kader 2000). Ferguson and MacRae (1992) found little loss of vitamin C in ‘Hayward’ kiwifruit stored for many months, but in some cultivars under some conditions, it seems that there can be losses on storage (Cotter et al. 1991; Tavarini et al. 2008; Oz 2010).

2.4.9 Other Fruit Characteristics

Other important fruit characteristics such as time of maturity and ripening, handling and storage responses, and yield potential are discussed in Ferguson (1990b). Fruit of *A. chinensis* var. *chinensis* and *A. chinensis* var. *deliciosa* have a particularly long growing season from flowering to harvest maturity, and there is an incentive to select for early maturity, especially for planting in districts that suffer early autumn frosts.

The good storage life of *A. chinensis* var. *deliciosa* ‘Hayward’ fruit is one of the main reasons for the eventual reliance of the New Zealand

kiwifruit export industry on this cultivar (Ferguson 2011). ‘Jintao’ has a better storage life than most other *A. chinensis* var. *chinensis* selections (Huang et al. 2002), possibly because of its thicker fruit skin. Storage life, as assessed by general fruit softening, by tissue breakdown, or by the development of off-flavors, must remain an important criterion in the selection of new cultivars.

2.5 Further Exploration of Wild Genetic Resources

The future sustainability of the world kiwifruit industry will largely depend on *Actinidia* genetic resources native to China and on the wisdom of kiwifruit breeders. The past century of kiwifruit domestication, even if very successful, is really just the beginning because our present cultivars are only one to three generations away from wild genetic resources. To make further progress, it is necessary to understand the underlying natural diversity in *Actinidia* and to study new theories and new methods to explore and then exploit more effectively the useful genotypes from the wild.

Firstly, the breeding and genetic improvement of dioecious plants are still very difficult for plant breeders because blind choice of the male parents normally means that it is unlikely that superior genotypes can be selected from crosses. Progeny testing of male parents requires a large investment in money, labor, and land even if it can be justified because it allows for more focused and efficient breeding programs. In contrast, the exploration of wild genetic resources leading to the selection of superior genotypes from natural populations is still a very effective and straightforward approach to the genetic improvement of kiwifruit. Continued investigation of the wild *Actinidia* resources in China is therefore essential.

Secondly, *Actinidia* species are polyploid perennial plants: Controlled, systematic breeding is difficult, because of the complexity that is due to the large number of chromosomes, the existence of ploidy races, and the lack of understanding the nature autopolyploidy versus allopolyploidy in the genus. Diploid *Actinidia* plants are $2n = 58$, but

are themselves probably palaeopolyploids, while octoploids have chromosome numbers as high as $2n = 232$. Nevertheless, ploidy variation provides *Actinidia* breeders many opportunities to discover and select from a wealth of genotypic and phenotypic variation which is the product of long-term adaptive evolution driven by ploidy variation and genomic complexity in nature. Interspecific hybridization among *Actinidia* species also creates possibilities for genetic improvement of *Actinidia*. Planned or targeted selection of various ploidy races, even cryptic ploidy races, from wild populations would be of additional advantage to kiwifruit breeders. Continued investigation of ploidy races in the wild, together with better formulated strategies for the exploitation of the diversity in ploidy and its effective use, should be one of the important approaches for cultivar development.

Thirdly, reproductive isolation of the various *Actinidia* species is not absolute, and in the wild, there are many interspecific, introgressed heterozygotes. Continuous variation of different gender types and morphological traits is found in wild populations of *Actinidia* (Huang et al. 2000). This rich genetic variation provides tremendous potential for selection from the wild and for the formulation of breeding strategies for kiwifruit cultivar improvement.

Finally, in China, *Actinidia* species, especially natural populations of horticulturally important species, are distributed widely across very different geographic and climatic regions particularly in hybrid zones where different species overlap where rich macro- and microhabitats support many different unique genotypes and/or phenotypes. Such hybrid zones of wild sympatric populations not only are ideal plots for the theoretical study of evolutionary biology, but also can be thought of and effectively used as natural breeding orchards. By taking advantage of newly available data of well-saturated genetic maps based on genotype-by-sequencing together with resequencing of a large number of genotypes of different species, kiwifruit breeders should be able to exploit such natural areas for targeted gene or genotype discovery to explore new useful genes and/or genotypes that can be used in the development of new cultivars.

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