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Genetic Resources and Domestication of Macadamia

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Horticultural Reviews, *Volume 35* Edited by Jules Janick

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I. INTRODUCTION

Macadamia F. Muell is a long-lived evergreen tree of subtropical and tropical origin (Maiden 1888; Cheel and Morrison 1935; Stephenson 1990a; Nagao and Hirae 1992). The embryo of the mature fruit produced by two of the Australian species (*M. integrifolia* Maiden & Betche and *M. tetraphylla* L.A.S. Johnson) is a high-valued edible kernel that is the basis of an expanding world industry. Macadamia kernels are consumed as roasted snack food, chocolate-coated confectionary, in bakery products and ice cream, and as oil (Cavaletto 1981; Stephenson 1990b; Stephenson 2005) and fit the characteristics of a luxury good, where demand is elastic with income (Osman 1982; Surono 1987). Macadamia is the only member of the Australian flora to have been domesticated as an internationally commercial food crop.

Knowledge of genetic resources has important consequences for management, crop development, and breeding. However, this knowledge is not well documented for macadamia. In this review, we collect and evaluate literature from disparate sources to describe the distribution, structure, and status of the wild germplasm and the origin, important selection criteria, and utilization of the domesticated resource.

A. Botany

The fruit of the macadamia is described as a follicle (Francis 1928; Hartung and Storey 1939); being a ''dry dehiscent fruit formed from one carpel and having a longitudinal line of dehiscence'' (Strohschen 1986).

It is composed of an inner kernel, comprising a small subglobose embryo and two large semiglobose cotyledons, encased by a thick and woody outer testa (shell) and a fibrous outer pericarp (husk) (Strohschen 1986). The shell is usually extremely hard (Jennings and Macmillian 1986; Naimi-Jamal and Kaupp 2007). Parenchyma cells in the mature embryo contain abundant oil bodies (Walton and Wallace 2005), and the oil content of fresh mature kernels is around 76% (Saleeb et al. 1973; USDA 2006), making macadamia the highest oil-yielding commercial nut (Strohschen 1986). Most of the oil is composed of monounsaturated fats (78% of total lipids), primarily oleic (18:1, 58% of total lipids) and palmitoleic (16:1, 17% of total lipids) acids (Cavaletto et al. 1966; Saleeb et al. 1973; USDA 2006). This is the highest concentration of palmitoleic acid in any natural food (Bridge and Hilditch 1950; Cavaletto 1980; Colquhoun et al. 1996). Saturated fats comprise 16% of the total lipid component. Sugar content at maturity is around 5%, with most (97 to 99% of total sugars) being nonreducing sugars (Cavaletto et al. 1966; USDA 2006; McConchie et al. 2007b; McConchie et al. 2007a; Wall and Gentry 2007).

Mature embryos of *M. ternifolia* F. Muell. contain high levels of cyanogenic glycosides at maturity (Dahler et al. 1995). In contrast, the levels of cyanogenic glycosides are high in the developing embryos of *M. integrifolia* prior to shell hardening, but decline by fruit maturity. Cotyledons of germinating seeds and the tissues of young seedlings of *M. integrifolia*, *M. ternifolia*, and *M. tetraphylla* also contain very high levels of cyanogenic glycosides (Dahler et al. 1995) and may be adaptations to reduce herbivory (Dahler et al. 1995; O'Neill 1997).

Macadamia flowers are borne on a rachis that may contain 100 to 300 flowers, each approximately 10 mm in length (Urata 1954; Ito 1980). Mature trees (>15 years of age) may produce approximately 10,000 racemes. Anthesis in the main production areas of Australia occurs over a period of approximately 5 weeks (depending on cultivar) from early September to early October (Moncur et al. 1985; Boyton and Hardner 2002). In contrast, the period of flowering in Hawaii extends over a protracted period of up to 30 weeks between November and May with three distinct peaks that are distinguishable between late January and early April (Nagao and Sakai 1988; Nagao and Sakai 1990; Nagao et al. 1992; Nagao et al. 1994). Flowers are pollinated by insects—in Australia, primarily European honeybees (*Apis mellifera*) and native bees (*Trigona* spp.) (Heard 1994; Wallace et al. 1996). About 10% of the flowers set fruit (Sakai and Nagao 1985), and cross-pollination increases initial set (Sedgley et al. 1990) and generally

final yield (Ito and Hamilton 1980; Trueman and Turnbull 1994a; Wallace et al. 1996; McConchie et al. 1996).

During a short period 2 to 3 weeks after anthesis, developing fruit abscise at a high rate, coincident with a high rate of growth in the size of remaining fruit (Sakai and Nagao 1985; Trueman and Turnbull 1994b). High rates of abscission are also observed 5 to 7 weeks and again around 10 weeks after anthesis (Sakai and Nagao 1985; Trueman and Turnbull 1994b). Generally, only low rates of abscission occur after this period and appear to be a consequence of pest or disease attack (Sakai and Nagao 1985; Trueman and Turnbull 1994b).

Growth in fruit size continues to approximately 12 to 15 weeks after anthesis (Sakai and Nagao 1985; Nagao and Hirae 1992; Trueman and Turnbull 1994b) with shell hardening also complete by this time (Jones 1937, 1939, 1994b; Trueman and Turnbull 1994b). Fruit mass continues to increase to approximately 23 weeks after anthesis (Trueman and Turnbull 1994a; McConchie et al. 1996). Oil content of the developing embryo is initially low until 12 to 15 weeks, after which the rate of oil accumulation increases rapidly, reaching a plateau at approximately 23 to 25 weeks after anthesis (Jones 1937, 1939; Baigent 1983; McConchie et al. 1996; Trueman et al. 2000).

Initial studies appear to have assumed that splitting of the husk indicated fruit maturity (Cheel and Morrison 1935; Wills 1939; Leverington 1958); however, more recent studies indicate that the husk dehiscence occurs well after maximum oil content of the kernel has been reached and generally after the fruit have abscised from the tree (Trueman et al. 2000). The period of mature fruit drop in Australia is between March and July (approximately 24 to 46 weeks after anthesis), although this may extend to overlap with flowering in September (Nagao and Hirae 1992; Boyton et al. 2002; Hardner 2005). Fruit abscission in Hawaii occurs between August and April (Ito 1984; Nagao and Hirae 1992). This, combined with the extended flowering period, leads to the presence of fruit at different development stages on the tree at the same time in this environment.

B. Horticulture

Macadamias were recognized by aboriginal culture prior to colonization. The name *goojabarigh* (Bailey 1901) is the local aboriginal name of the species indigenous to northern Queensland. Farther south, the local aboriginal name for the macadamia species that occurs in the Mount Bauple area is *jindilli* (Gross 1995); *kindal kindal* is the term used by the Aborigines for the macadamia that grows in the northeast of New South

Wales (Maiden 1888; Cheel and Morrison 1935). In the Pine Rivers, north of Brisbane where two species co-occur, *burrwang* is reportedly the local indigenous people's name for macadamia (Wagner-Wright 1995). Common European names for macadamia include smooth shell macadamia, rough shell macadamia, Queensland nut, Bopple nut, bauple nut, popple nut, Australian nut, bush nut, and gympie nut (Francis 1928; Cheel and Morrison 1935; Wills 1939; Hamilton and Storey 1956; Leverington 1958, 1971).

Although macadamias used in commercial plantations are derived from species indigenous to Australia (Gross 1995), the crop was initially commercialized in Hawaii (Wagner-Wright 1995). Currently, macadamia is produced in several tropical and subtropical regions, primarily Australia, Hawaii, southern and central Africa (South Africa, Kenya, and Malawi), and Central and South America (Guatemala and Brazil) (Piza et al. 2006), with some development in southeast Asia (Thailand and China) (Supamatee et al. 1992; Xiao et al. 2002b; Venkatachalam and Sathe 2006). World production of macadamia kernels in 2005 was estimated at 28,000 tonnes(t) (Piza et al. 2006), up 115% from 13,000 t in 1995 (USITC 1998). Currently, macadamia represents 1.3% of the world nut meat market (INC 2006).

Macadamia trees are commonly propagated by grafting selected scions onto seedling rootstocks (Stephenson 1990a; Nagao and Hirae 1992), although cuttings and clonal rootstocks have also been used (Stephenson 1990a; Trochoulias 1992; Wiid and Hobson 1996; Bell 1996). However macadamia propagated as cuttings are less stable in the field than plants on seedling rootstocks (Hamilton and Fukunaga 1959; Hobson 1971; Phiri 1985; Nagao and Hirae 1992; Trochoulias 1992). Similar observations have been reported for tissue-cultured plants (Xiao et al. 2002a). Orchards are generally established with selected cultivars grafted onto seedling rootstocks at densities between 100 to 350 trees/ha (Stephenson 1990a; Nagao and Hirae 1992), although higher densities of 667 trees/ha have been used (Trochoulias and Burnside 1987). In contrast, the Kenyan macadamia production system is characterized by many small land owners each growing only a few trees (Gathungu and Likimani 1975; Onsongo 2006).

Grafted trees usually begin bearing between 3 and 6 years of age (Stephenson 1990a; Oosthuizen 1992; Nagao and Hirae 1992) and may be commercially productive for at least 40 to 60 years (Hamilton and Fukunaga 1959). Common horticulture practices of fertilization, weed, pest and disease control, and canopy management are implemented (Stephenson 1990a; Nagao and Hirae 1992; Stephenson and Trochoulias 1994; Hardner et al. 2006). In some areas irrigation is applied, but

this is not a universal practice (Trochoulias and Johns 1992; Stephenson and Trochoulias 1994).

In commercial orchards, mature fruit are generally allowed to abscise and fall from the tree for harvesting. Fruits are either mechanically or hand-harvested from the ground at regular intervals to reduce the incidence of kernel deterioration (Leverington 1962a; Mason 1983; Mason and Wells 1984; Liang et al. 1996). After harvesting, the husk is mechanically removed, and, prior to processing, nuts are dried to around 1.5% kernel moisture content using a regime of initially low temperature ($<40^{\circ}$C) to reduce kernel browning (Prichavudhi and Yamamoto 1965; Mason and McConachie 1994; Mason 2000). Dried nuts are mechanically cracked to extract the kernel (mature embryo). The term *kernel recovery* refers to the mass of kernel extracted per mass of nut in shell (NIS). Sorting pre- and postcracking is used to remove unacceptable product and to grade kernels into product styles (Mason and McConachie 1994; Mason 2000). Raw kernel may be further processed using oil or air-dry roasting (Moltzau and Ripperton 1939; Leverington 1962a; Winterton 1966; Mason 1987; Mason and McConachie 1994). Consumer surveys have indicated a strong preference for roasted kernel as snack food compared to raw kernel (O'Riordan et al. 2005).

Macadamia production requires a large initial investment in terms of land, purchase of grafted trees, farm machinery, infrastructure, and in some areas, irrigation (Hardner et al. 2006). The major costs of production are land rental (38%), general fixed costs (20%), and orchard establishment (9%) (Hardner et al. 2006). The major costs of processing nuts to raw kernel are cracking (30%), sorting (20%), and packing (22%).

II. WILD GENETIC RESOURCES

A. Taxonomy

1. Families, Tribes, and Gondwanan Origin. The ancestors of *Macadamia* can be traced to a group of primitive rain forest plants ancestral to the modern Proteaceae Juss. family. These first appear in the palynological record during the late Cretaceous, around 100 million years ago, when Australia was still part of the great southern landmass, Gondwanaland (Ramsay 1963; Johnson and Briggs 1963; Johnson and Briggs 1975; Boland 1984). Despite having their evolutionary roots in the rain forest, the Proteaceae is now not well represented in these ecosystems, with most species being adapted to dryer, fireprone habitats (Johnson and Briggs 1963).

The Proteaceae is part of an ancient group of angiosperms (flowering plants) in subclass Magnoliidae (dicotyledons) that comprises approximately 1,500 species in 80 genera, of which 900 species in 50 genera are found in Australia (Harden 1990). The center of diversity of the family appears to be have been in the part of Gondwanaland that is now Australia (Johnson and Briggs 1975). Other well-known Proteaceae genera include *Grevillea* R.Br. ex Knight, *Banksia* L.f., *Hakea* Schrad. & J.C. Wendl., *Protea* L., and *Leucadendron* R.Br., all of which are cultivated for their inflorescences (Harden 1990; Criley 1998; Sedgley 1998; Coetzee and Littlejohn 2001; Ben-Jaacov and Silber 2006).

In a recent classification of Proteaceae (Weston and Barker 2006), the genus *Macadamia* is located in the tribe Macadamieae, together with several other Australian genera, including *Athertonia* L.A.S. Johnson & B.G. Briggs, *Catalepidia* P.H. Weston, *Gevuina* Molina and *Hicksbeachia* F. Muell., many of which also produce sizable nuts (Stace et al. 1998). Although *Floydia* L.A.S. Johnson & B.G. Briggs had been included in Macadamieae (Johnson and Briggs 1975), it has been moved to the tribe Roupaleae Meisn. (Weston and Barker 2006), which is in the same subfamily of Proteaceae. The center of origin of this tribe is probably eastern Australia and neighboring landmasses that once formed part of eastern Gondwanaland (Johnson and Briggs 1975). The present-day distribution of the tribe includes Australia, some Pacific islands, South America, and South Africa (Venkata Rao 1970; Johnson and Briggs 1975). *Macadamia* is closely aligned with two other genera, *Brabejum* L. (1 species endemic in southern Africa) and *Panopsis* Salisb. (11 species endemic to tropical and subtropical America) in the subtribe Macadamiinae (Johnson and Briggs 1963, 1975; Venkata Rao 1970; Gross 1995; Weston and Barker 2006).

2. Morphology and Phylogenetics. Species of *Macadamia* have been informally grouped into two clades based on morphological and geographic affinities (Johnson and Briggs 1975). A recent classification of Proteaceae that also incorporates molecular data (Weston and Barker 2006) suggests the genera is paraphyletic and includes the other genera from the subtribe *Panopsis* and *Brabejum* as subclades. Six species from New Caledonia described as *Macadamia* (Virot 1968; Hamilton 1970) have since been placed in *Virotia* L.A.S. Johnson & Briggs, within the subtribe Virotiinae of Macadamieae (Weston and Barker 2006).

The ''southern clade'' (coastal central and southern Queensland and northern New South Wales) comprises four species, and the ''northern clade'' has five species, distributed in northern Australia and Sulawesi, Indonesia. All *Macadamia* species generally have the form of a small to

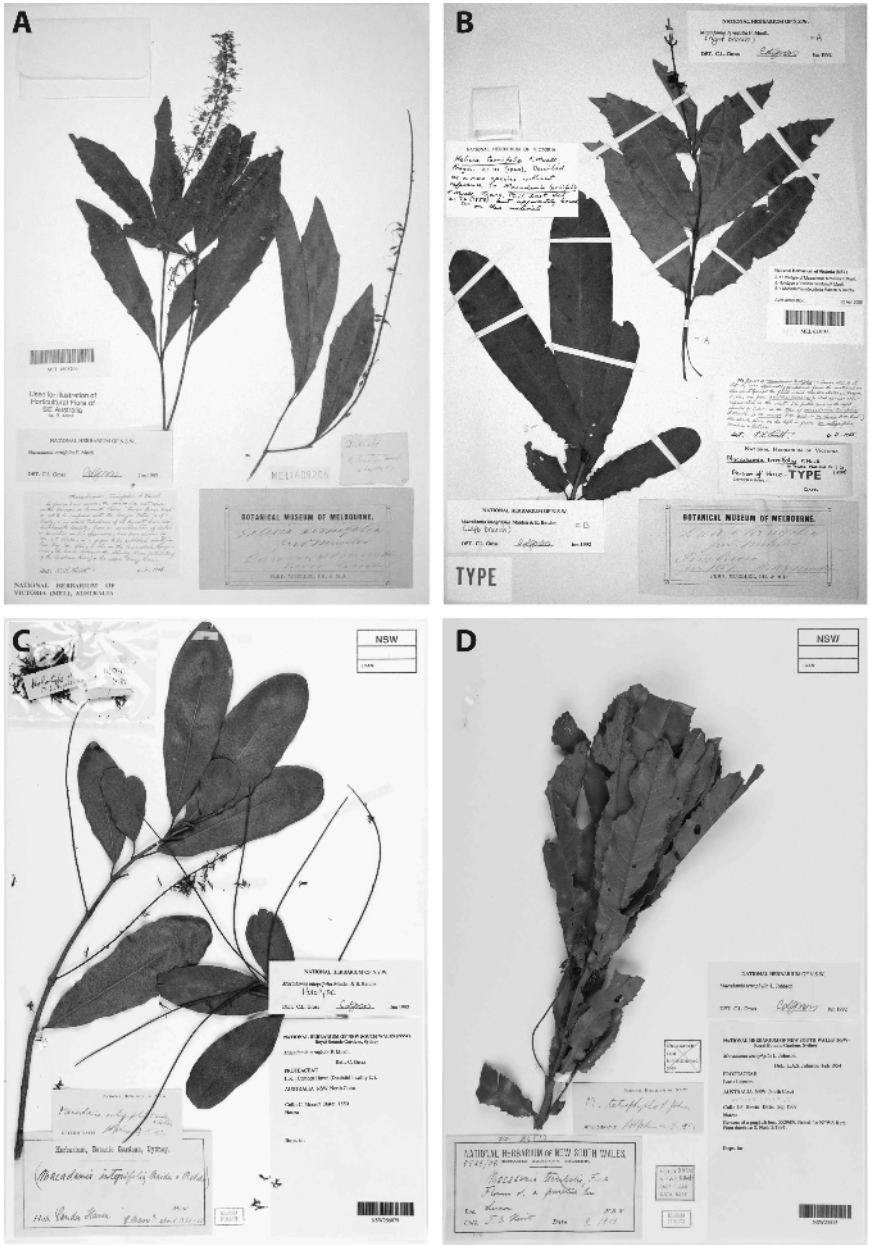
medium-size tree, up to 40 m (Gross 1995). The leaves are simple and sclerophyllous with or without spinose margins. Flowers are formed as a conflorescense and the fruit is a globular follicle.

The Southern Clade. The four species of the ''southern clade,'' *M. integrifolia, M. tetraphylla, M. ternifolia,* and *M. jansenii* C.L. Gross & P.H. Weston, are naturally found in a narrow region along the eastern coast of Australia, between 152 and 154°E longitude and 25 and 29°S latitude.

The first botanical specimens were of *M. ternifolia* (Fig. 1.1A) collected by the Australian explorer Ludwig Leichhardt in 1843 (Smith 1956) from the Conondale Range region. Despite earlier awareness, *Macadamia* was not formally described until 1857 by Ferdinand von Mueller, based on material collected with Walter Hill from the Pine River valley north of Brisbane (Fig. 1.1B). The genus was dedicated to John Macadam, the honorary secretary (and later president) of the Philosophical Institute of Victoria (von Mueller 1857). John Macadam is also famous for his role as one of the umpires in the first recorded game of Australian Rules Football (Blainey 1990). Mueller called the taxon ''*Macadamia ternifolia*''; however, his type specimen included material of both *M. ternifolia* and what was subsequently classified as *M. integrifolia* (Fig. 1.1B), which lead to much subsequent confusion (Smith 1956). This herbarium sheet does not include any fruit, and although a drawing of the fruit is presented in the formal description of the species (von Mueller 1857), it appears more like the fruit of a *Grevillea* species than that of any macadamia.

Several taxonomic treatments of the group followed (Storey 1959). Maiden and Betche classified the smooth-leafed variant as *M. integrifolia* in 1897 (Maiden and Betche 1897) (Fig. 1.1C). This holotype was described as being collected from Camden on the central coast of New South Wales (NSW), although this is well outside the natural range of the species and may have come from a cultivated individual (Johnson 1954). Two years later they revised it

Fig. 1.1. Herbarium sheets of *Macadamia* species. (A) Herbarium specimen of the then-unnamed *M. ternifolia* collected by Ludwig Leichhardt in 1843. Reproduced with permission from the archives of the Royal Botanic Gardens, Melbourne. (B) Herbarium specimen used to describe *Macadamia ternifolia*, including the Holotype (upper right) and a second specimen (lower left) later identified as *M. integrifolia*. Reproduced with permission from the archives of the Royal Botanic Gardens, Melbourne. (C) *Macadamia integrifolia* holotype. Reproduced with permission from the archives of the Royal Botanic Gardens, Sydney. (D) *Macadamia tetraphylla* holotype. Reproduced with the permission of the Royal Botanic Gardens, Sydney.


A
B
C
D
TYPE
NSW
NSW

to *M. ternifolia* var. *integrifolia*, having observed ''all degrees of transition between the two leaf forms'' (Maiden and Betche 1899). Up until 1954, specimens of *M. tetraphylla* were considered as either *M. integrifolia* or *M. ternifolia* (Smith 1956) due to their spinose leaf margins, which was the major character for species resolution at the time. *Macadamia tetraphylla* was eventually classified as a separate species in 1954 (Johnson 1954) (Fig. 1.1D). Finally in 1956, the species was resolved into the three taxa recognized today, *M. integrifolia*, *M. tetraphylla*, and *M. ternifolia* (Smith 1956). Two previously described species, *M. lowii* F.M. Bailey and *M. minor* F.M. Bailey, are recognized as synonyms of *M. ternifolia*. The fourth species of the southern clade, *M. jansenii*, was discovered more recently by Ray Jansen (Gross and Weston 1992) and therefore was not involved in the earlier taxonomic confusion of the genus.

In broad terms, the cultivated species *M. integrifolia* and *M. tetraphylla* are medium-size trees (attaining heights of 6 to 18 m and 3 to 18 m respectively) (Gross 1995), and bear large edible nuts. In contrast, the wild relatives *M. ternifolia* and *M. jansenii* are smaller trees (up to 8 m and 6 to 9 m, respectively) (Gross 1995), with small, bitter, inedible nuts, attributable to the presence of cyanogenic glycosides (Dahler et al. 1995).

Several morphological characters can be used to distinguish between the four southern clade species (Table 1.1), although the description of a shell thickness of up to 1 cm for *M. integrifolia* seems a little excessive compared to Leverington (1962a), who reports a maximum shell thickness of 0.7 cm across 94 genotypes. The major advantage of morphological descriptors lies in their ease of detection. However, some of these traits are visible only at certain times of the year (e.g., leaf flush color, floral and fruit descriptors) or at reproductive maturity (floral and fruit descriptors). Considerable morphological variation within each species, and overlap between them, can make visual classification difficult (Johnson 1954). Most of the leaf descriptors are not valid for identifying young seedlings, as juvenile states for most characters are similar across the species. In the adult form also, leaves of *M. integrifolia* may have spiny margins and leaf dimensions resembling those of *M. ternifolia* or hybrids of *M. integrifolia* and *M. tetraphylla*. Environmental effects can cause large variation in some characters, such as leaf and nut size. Specimens of *M. tetraphylla* with white flowers instead of the characteristic pink-red hue are occasionally observed (McConachie 1980; Gross 1995). Overlap in other characters is also observed, including leaves per whorl, leaf dimensions, nut size, and shell thickness (Johnson 1954).

Table 1.1. Morphological differences between the four *Macadamia* species of the Australian southern clade. These characters are for mature specimens.[a]

Character	*M. integrifolia*	*M. tetraphylla*	*M. ternifolia*	*M. jansenii*
Leaf				
No. per whorl	Usually 3	Usually 4	Usually 3	3
Dimensions (cm)	6.5–14 × 2–6.5	7–30 × 1.4–6	9–12.5 × 2–3.5	10–17.5 × 2.5–5
Ratio length: width	Low	High	Medium high	Medium
Shape	Ovate to obovate	Oblong to oblanceolate	Narrowly ovate	Oblanceolate
Margin spines	Few or none	Always many	Few	None
Apex	Acute to obtuse	Acute or subacute	Acute, mucronate	Acute to attenuate
Base	Very shortly attenuate	Truncate, attenuate	Attenuate	Attenuate or cuneate
Petiole length (mm)	6–18	0–4	4–10	2–14
Flush color	Green	Pink to red	Pink to red	Green
Floral				
Flower color	Creamy white	Pink	Pink	Creamy brown
Fruit				
Nut dimensions (cm)	2.5–3.1 × 2.4–3.0	2.6–3 × 1.6–2.4	~1.6 × ~1.2	1.4–1.8 × 1.1–1.6
Shell texture	Smooth	Pebbled/rough	Smooth	Smooth
Shell thickness (mm)	6–10	2–6	1	0.8–1.5

[a]Etymology: *Macadamia*: after John Macadam (1827–1865), secretary of the Philosophical Institute of Victoria; *integrifolia*: ''entire leaves''— leaf margins not (as) spinose as in *M. tetraphylla*; *tetraphylla*: ''four leaves''— leaves in whorls of four; *ternifolia*: ''three leaves''— leaves in whorls of three; *jansenii*: after R.C. Jansen (1941–1997), a naturalist who first collected the species.
Source: Descriptions from Gross (1995), Stanley and Ross (1986), and Storey (1959).

A potential cause of the considerable morphological variation observed is interspecific hybridization (Johnson 1954; Smith 1956). The morphological state of F_1 *Macadamia* hybrids is typically intermediate for most characters (Storey and Saleeb 1970). Some individuals may be later-generation hybrids or backcrosses, from natural hybrid zones or from sites of cultivation. Extensive interspecific hybridization renders the species status of many individuals highly ambiguous when assessed solely by morphology. The gradation of leaf forms observed by Maiden and Betche (1897) in *M. integrifolia* to *M. ternifolia* may have been due to the presence of natural hybrids of the two species (Storey 1965b).

No clear relationships between the four southern clade species are obvious from morphological comparisons (see Table 1.1). While *M. ternifolia* and *M. jansenii* are often considered similar because their small bitter nuts are not suitable for cultivation and because of their relatively smaller height, other features group the species in different ways. *M. ternifolia* and *M. tetraphylla* share a common feature in their pink-red leaf flushes and flowers. All but *M. tetraphylla* have whorls usually of three leaves. All but *M. jansenii* and some specimens of *M. integrifolia* have some degree of spines on their leaf margins.

Molecular marker studies have shed further light on genetic affinities and phylogenetic relationships between southern clade species. In an isozyme study, Sharp and Playford (1997) found *M. ternifolia* and *M. jansenii* to be relatively closely related, as were *M. integrifolia* and *M. tetraphylla*. However, the inclusion of interspecific hybrids between the latter pair of species probably confounded the relationships among the species. Another isozyme study by Aradhya et al. (1998) concluded that *M. ternifolia* is either a conspecific variant or a close relative of *M. integrifolia* but that *M. tetraphylla* was more closely related to *M. integrifolia* than to *M. ternifolia*. Unfortunately, this analysis probably was compromised by the inclusion of hybrids and the omission of *M. jansenii*. At the very least, the results clearly demonstrated that the three species form a species complex.

Results from a combined randomly amplified DNA fingerprinting (RAF; Waldron et al. 2002) and sequence tagged microsatellite site (STMS) marker study (Peace et al. 2002) suggested that *M. integrifolia* and *M. tetraphylla* were sister species, and there was greater affinity between *M. ternifolia* and *M. jansenii* than with the other two species. This work was extended to include a wider range of germplasm for the four main species of the southern clade and was careful to exclude hybrids from the analysis (Peace 2005). The most closely related species pair in this analysis was *M. integrifolia* and *M. tetraphylla*, with *M. ternifolia* being

more closely related to this species pair than to *M. jansenii*, which was the genetic outlier of the four species. However, this study included *M. ternifolia* accessions from only half the known natural range of the species and only two specimens of *M. jansenii*. A more comprehensive survey of germplasm of these two species is required to definitely resolve relationships between the four species of the southern clade.

The Northern Clade. The ''northern clade'' of *Macadamia* includes five species. Three species are native to far north Queensland: *M. whelanii* F.M. Bailey, *M. claudiensis* C.L. Gross & B. Hyland and *M. grandis* C.L. Gross & B. Hyland (Gross 1995). Two other species have been reported from the tropical island province of Sulawesi, Indonesia, where *M. hildebrandii* Steenis has a wide distribution and *M. erecta* has been recorded at high altitude (Sleumer 1955; McDonald and Ismail 1995).

A major distinction between the southern and northern clade macadamias is the branched conflorescence of the latter (Gross 1995; McDonald and Ismail 1995). In addition, adult leaves of the far north Queensland and Sulawesi species occur in whorls of four or more, and leaf margins are always spineless (Gross 1995; McDonald and Ismail 1995). Nuts of these five species tend to be larger than those of the southern clade species (Gross 1995; McDonald and Ismail 1995). Kernels of *M. whelanii* are known to contain cyanogenic glycosides (Gross 1995), similar to *M. ternifolia* and *M. jansenii*. However, this characteristic is not shared with *M. claudiensis*, *M. hildebrandii*, and *M. erecta* (McDonald and Ismail 1995). For example, *M. hildebrandii* reportedly produces fruit with edible kernels that have good eating qualities (Sleumer 1955). Such information is not available for *M. grandis* (Gross 1995). The size of *M. grandis* trees in the wild are similar, or larger, than for *M. integrifolia* and *M. tetraphylla* (Gross 1995; McDonald and Ismail 1995).

Johnson and Briggs (1975) suggested that the Sulawesi species evolved from an Australian progenitor around 15 million years ago when the two landmasses were still connected. Such a progenitor is likely closely allied to the northern clade of Australian macadamias, given the close morphological similarities between members of this group compared to the southern clade taxa.

Limited isozyme evidence suggests that *Hicksbeachia pinnatifolia* (which belongs to a different subtribe) is more closely related to the southern clade *Macadamia* than is *M. hildebrandii* (Aradhya et al. 1998). If so, it brings into question affinities between *Macadamia* and genera such as *Panopsis* and *Brabeium* that are within the same subtribe as *Macadamia.*

A molecular marker analysis (RAF) of several Proteaceae species (Peace 2005) confirmed that the northern clade species, *M. whelanii* and *M. claudiensis*, are not closely related to the southern clade *Macadamias* or to each other. In accordance with current taxonomy, but in contrast to the above-mentioned isozyme results, the RAF study indicated that other species from the Macadamieae tribe, including *Hicksbeachia pinnatifolia*, which is native to southeast Queensland and northern NSW, are no more genetically similar to the southern clade *Macadamias* than are *M. whelanii* and *M. claudiensis* (Peace 2005). A further more detailed phylogenetic investigation of the tribe is warranted. The remainder of this review focuses predominantly on the commercially developed *Macadamia* species and their close relatives in the southern clade.

B. Cytogenetics

All *Macadamia* species surveyed to date are reported to be diploid with a haploid chromosome number of 14: *M. integrifolia* (Ramsay 1963; Storey and Saleeb 1970); *M. integrifolia*, *M. tetraphylla*, and *M. ternifolia* (Storey 1965b); and *M. integrifolia*, *M. tetraphylla* (Storey and Saleeb 1970). A single report of polyploidy has been made (IPBGR 1986), but no details were provided to enable verification. Hybridization between *M. tetraphylla* and *M. integrifolia* does not appear to disrupt normal chromosome pairing or disjunction, and the chromosome number of F_1 progeny remains $n = 14$ (Storey and Saleeb 1970).

In the most recent review of the cytological data for 188 species in 65 genera of Proteaceae, Stace et al. (1998) suggests that the genera of subfamily Grevilleoideae are almost entirely diploid, with chromosome base numbers of $n = x = 10$, 11, 12, 13, and 14 and with two observed instances of triploidy. They argued against an earlier hypothesis that this chromosome series represented ''paleo-polyploidy'' from an ancestral genome of $x = 5$ or 7 (e.g., Venkata Rao 1970; Johnson and Briggs 1975) and instead suggested that members of the Proteaceae are derived from an ancestral genome of $x = 12$ or 21, with 24 chromosome arms (fundamental number [FN] = 24).

The ancestral grevilleoid genome of $x = 14$ is probably of Gondwanan origin, and consists of 10 metacentric and 4 short telocentric chromosomes (Stace et al. 1998). Many members of the tribe Macadamieae appear to have retained this original genome: $n = x = 14$ for *Macadamia*, *Brabeium*, and *Floydia*, with $n = x = 13$ (fusion of a telocentric and a metacentric chromosome) for *Hicksbeachia* and *Gevuina* (Stace et al. 1998). However, they also suggest that

additional chromosomal evolution subsequent to this origin is possible.

Chromosome numbers for *Athertonia*, *Panopsis*, and several other members of tribe Macadamieae have not yet been reported. While information on chromosome size in *Macadamia* is not available, five other genera surveyed from subfamily Grevilleoideae have relatively small chromosomes (Stace et al. 1998). In particular, the genome size of *Brabeium stellatifolium*, in the same subtribe as *Macadamia*, was the smallest reported (mean chromosome length of 1.0 μm; (Stace et al. 1998). Having such small grevilleoid chromosomes is evidence against a paleo-polyploid origin, as is the lack of additional isozyme loci in Australian genera of Proteaceae (Stace et al. 1998). The number of isozyme loci in *Macadamia* reported by Vithanage and Winks (1992) and Aradhya et al. (1998) also appears consistent with a diploid rather than ancient tetraploid origin. Stace et al. (1998) suggest that if paleo-polyploidy has occurred in ancestral Proteaceae, molecular genetic investigation in genera such as *Macadamia* may reveal (extensive) gene silencing, which would have occurred through the process of ''diploidization.''

C. Species Distributions and Hybrid Zones

The most up-to-date information on the distribution of southern clade *Macadamia* species is provided by a recent field collection for ex situ conservation and assessment that was based on initial surveys of Queensland's Environmental Protection Agency databases and herbarium records (Hardner et al. 2004). With the exception of *M. jansenii*, which occurs at a single site in the Bulburin State Forest near Miriam Vale, central east Queensland (Gross and Weston 1992), the southern clade *Macadamia* are distributed in a narrow band parallel to the coast between Lismore in northern NSW and Mount Bauple in southeast Queensland (Hardner et al. 2004; Peace 2005) (Fig. 1.2). Within this natural range, the clade occurs in lowland subtropical rain forest among coastal valleys and foothills. The three southern species occupy separate though overlapping parts of this geographic range. The natural distribution of *M. ternifolia* and *M. integrifolia* is confined to southeast Queensland, and *M. tetraphylla* mainly occurs in northern NSW, extending into the coastal valleys of the Gold Coast hinterland in southern Queensland (Barry and Thomas 1994; Hardner et al. 2004; Peace 2005).

1. *Macadamia integrifolia*. This is the most widely distributed of the southern *Macadamia* species (Barry and Thomas 1994) (Fig. 1.2).

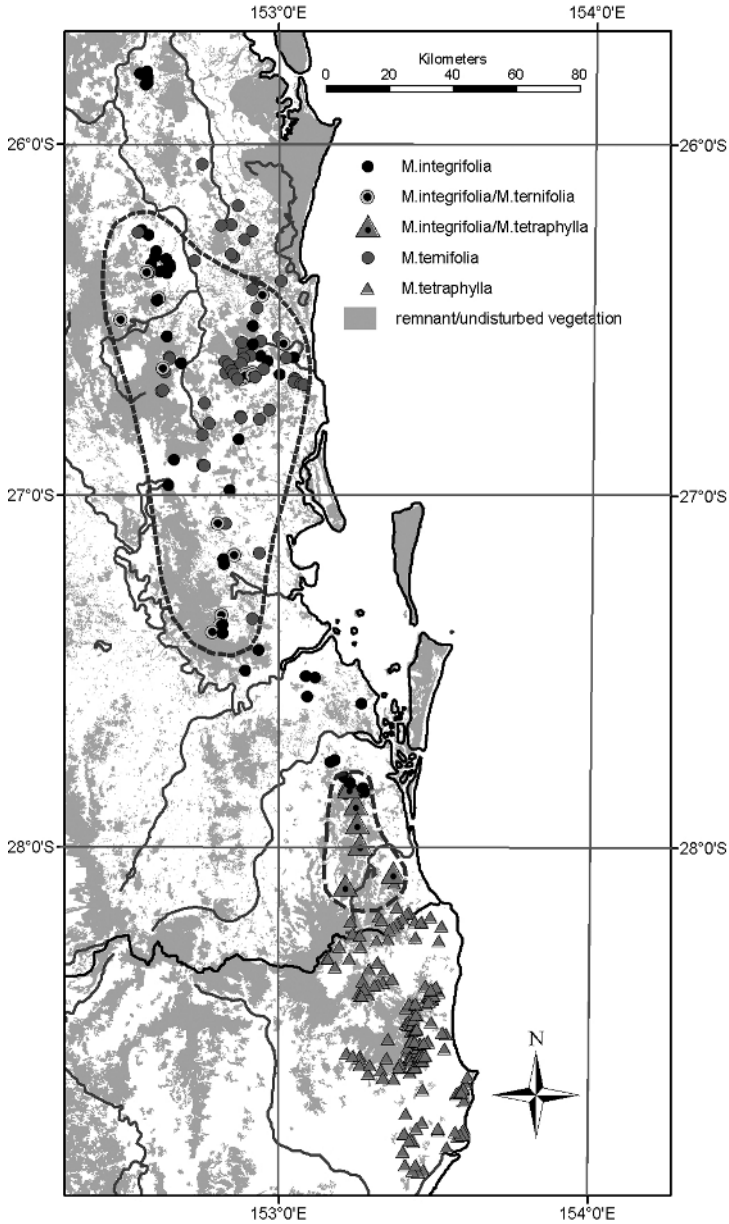


Fig. 1.2. Natural distribution of southern species of *Macadamia* and natural hybrids. Dotted lines indicate the extent of hybrid zones.

It occurs parallel to the coast extending from Mount Bauple near Maryborough in the north to the NSW–Queensland border in the south (Hardner et al. 2004; Peace 2005), a linear distance of approximately 275 km. Frequently sympatric with *M. ternifolia* and occasionally *M. tetraphylla*, *M. integrifolia* occurs in subtropical lowland rainforest communities (Harden 1990), ranging from complex to simple notophyll vine forest and microphyll-notophyll vine forest (Barry and Thomas 1994, Table 2).

2. *Macadamia jansenii*. This species is known from a single site in the Pine Creek catchment of Bulburin State Forest, in central eastern Queensland (Gross and Weston 1992), and is over 150 km north from the nearest population of any other southern clade species of *Macadamia*. The population comprises approximately 30 individuals, located on the moderately graded lower slopes of a narrow gully containing an intermittently running tributary (Barry and Thomas 1994).

3. *Macadamia ternifolia*. This species extends from Goomboorian approximately 18 km northeast of Gympie, to Mount Nebo approximately 10 km west-southwest of Samford in southern Queensland (Hardner et al. 2004; Peace 2005). *Macadamia ternifolia* occurs across approximately 150 km from north to south and, in its southern range, overlaps with the northern range of *M. integrifolia* (Fig. 1.2).

4. *Macadamia tetraphylla*. *M. tetraphylla* occurs in the coastal rain forests of the Richmond and Tweed River catchments in northeast NSW, and extends north to Mount Wongawallan in southeast Queensland (Barry and Thomas 1994). In its northern range its distribution overlaps *M. integrifolia*, where hybrids are frequently found at sympatric sites (Peace 2003) (Fig. 1.2). This species is often found in small remnants of the former Big Scrub (Holmes 1987; Lott and Duggin 1993), albeit as small populations, and has also been recorded in riparian rain forest in this region (Pisanu 2001). Northern outlier records of *M. tetraphylla* on the Sunshine Coast may be historical plantings (Hardner et al. 2004; Peace 2005). It may be that before wide-scale clearance of the Big Scrub, *M. tetraphylla* had a more continuous and higher-density distribution than today. Certainly the species is frequently found in a myriad of small remnant patches that now comprise less than 1% of the landscape (Pisanu 2001).

5. Interspecific Hybridization. Hybridization between *M. integrifolia* and *M. tetraphylla* readily occurs both in cultivation, and naturally

where the species co-occur (Storey 1959; Barry and Thomas 1994; Hardner et al. 2000; Peace 2005). Natural hybrids between *M. integrifolia* and *M. ternifolia* have also been widely found in areas of sympatry (Peace 2005). Originally evidence for hybridization was based on observations of trees with intermediate morphology (Smith 1956; Storey 1959). More recently, however, DNA marker analysis has confirmed that natural hybrids do occur (Peace 2005). Due to allopatry, hybrids between other species pairs in the southern clade have not been recorded in the wild, although hybrids between all pairs of species have been synthesized artificially (Hardner et al. 2000).

Natural populations of the two cultivated species, *M. integrifolia* and *M. tetraphylla*, are sympatric south of Brisbane in southeast Queensland, and it is common to find trees displaying intermediate morphologies. However, in no cases have specimens of both pure species been found in the same population, and in the middle of the natural hybrid zone is a small region where only hybrids occur (Peace 2005). This natural hybrid zone was believed to be restricted in area of only a few square kilometers (Storey and Saleeb 1970; McConachie 1980; Hardner et al. 2000), but a more recent survey has determined that the zone extends over at least 20 km, and perhaps much farther (Peace 2005). It is possible that the zone has been extended by human disturbance, such as the removal of a 10-km-wide eucalypt belt in the Gold Coast hinterland in the early 1900s that acted to promote increased pollen flow between populations and species (Wills 1961).

DNA analysis (RAF) of individuals in this hybrid zone has identified a full range of potential genotypic combinations between the two species, with a clear gradation from pure *M. integrifolia* to pure *M. tetraphylla* types from north to south (Peace 2005). Such a pattern of variation indicates that interspecific hybrids are fertile and have been segregating as later-generation hybrids and/or backcrossing to pure species types for many generations. The genetic distinctness of *M. integrifolia* and *M. tetraphylla* means that they should continue to be recognized as sound species, and F_1 (and later-generation hybrids) between the two can be identified easily using multilocus DNA analysis (Peace 2005).

The hybrid zone between *M. integrifolia* and *M. ternifolia* is similar, although hybridization between these species may not be so extensive and was identified only recently. Even though the two species were known to coexist over a greater geographic range than *M. integrifolia* and *M. tetraphylla*, trees with intermediate morphology had not been reported (Storey 1965b; McConachie 1980). However, a recent survey located several macadamia populations that included both *M. ternifolia*

and *M. integrifolia* trees and at least one possible hybrid, all in the Pine River/Samford Valley area (Hardner et al. 2004; Peace 2003). DNA analysis of these trees with species-specific markers (Peace 2005) confirmed the existence of several interspecific hybrids, and the co-occurrence of specimens of the pure species, in contrast to that found for the *M. integrifolia*/*M. tetraphylla* hybrid zone. Although fewer individuals were analyzed than from the *M. integrifolia*/*M. tetraphylla* hybrid zone, a range of intermediate genotypes was identified including F_1, later-generation segregants, and/or backcrosses (Peace 2005). This further indicates that F_1 hybrids are fertile and that hybridization between the two species has occurred over many generations in this zone.

Controlled crosses between *M. ternifolia* and *M. jansenii*, and *M. ternifolia* and *M. integrifolia* have produced viable progeny (Hardner et al. 2000). No attempts were made to cross *M. tetraphylla* with either *M. ternifolia* or *M. jansenii*, as flowering times did not overlap. However, given the cross-compatibility among the other pairings of species in the southern clade, it is likely that *M. tetraphylla* completes the group of fully cross-compatible species. Attempts to hybridize *M. integrifolia* with the northern clade species *M. whelanii* or *M. claudiensis* were unsuccessful (Hardner et al. 2000). Pollen from the northern clade species appeared to germinate on *M. integrifolia* styles, but pollen tube growth was arrested before reaching the ovule. Graft compatibility within, but incompatibility between, has been demonstrated for the southern and northern clade species (Storey and Frolich 1964), further evidence that the northern clade macadamia species are closely allied with each other but not with the southern clade species.

The high degree of reproductive compatibility among the southern species suggests that hybridization may pose a threat to the integrity of the pure species in the wild, particularly considering that the cultivated germplasm in Australia largely coincides with the native distribution of three main species of the southern clade.

D. Ecology

1. Habitat and Structural and Floristic Characteristics. The southern clade *Macadamia* species are native to the subtropical lowland rain forest of northern NSW and southeast Queensland. In Queensland, Webb's (1968) structural-physiognomic classification (e.g., Sattler and Williams 1999) is mainly used to describe plant communities; Floyd's (1990) structural-physiognomic-floristic classification is often used in NSW. Some reports of *Macadamia* habitat refer to both systems (e.g., Barry and Thomas 1994).

Table 1.2. Common rain forest types associated with three common southern clade *Macadamia* species.

Macadamia spp.	Structural classification	Subtropical rainforest floristic alliance
M. integrifolia	Complex Notophyll Vine Forest	*Argyrodendron trifoliolatum dominant*
	Notophyll Vine Forest	*Argyrodendron actinophyllum* dominant
	Araurcarian Notophyll Vine Forest	*A. actinophyllum* and *Araucaria cunninghamii*
M. tetraphylla	Notophyll Vine Forest	*A. trifoliolatum* dominant
	Mixed Notophyll Vine Forest	*Cupaniopsis anacardioide Acmena spp.*
M. ternifolia	Complex Notophyll Vine Forest	*A. trifoliolatum dominant* or *Argyrodendron trifoliatu* and Dissilaria *baloghioides* alliance
	Araurcarian Notophyll Vine Forest	*A. actinophyllum* and *Araucaria cunninghamii*
	More rarely in notophyll gallery rain forest or complex notophyll riparian vine forest	

Source: Structural classifications after Webb (1968) and subtropical rain forest subformation floristic alliances after Floyd (1990).

Tropical and subtropical rain forest of the lowlands typically have three or more tree layers, with or without emergents, whereas at higher altitudes and latitudes, one or two distinct vegetation layers are more common (Webb and Tracey 1994). Under the classification of Floyd (1990), rain forests where *Macadamia* is most common are subtropical types, usually dominated by *Argyrondendron* species (Booyongs), coastal rain forest on basalt dominated by *Cupaniopsis anacardioides* (Tuckeroo), and rain forest with *Araucaria* (Hoop Pine) as an emergent tree (Table 1.2).

Floyd's (1990) floristic alliances are equivalent to a number of types defined on the basis of structure (various forms of notophyll vine forest) (Table 1.2). Notophyll rain forests contain species where the majority of leaves are approximately 6 to 8 cm long. Tropical rain forest tends to be comprised of species with mesophyll leaves (12.7 cm long or larger) compared to subtropical forms, and temperate rainforests typically have smaller leaves (on the order of 2.5 cm long, after Webb 1968). A variety of plant lifeforms and features are characteristic of subtropical rain forest. These include a multilayered billowing

canopy, stranglers, palms, plant buttressing, epiphytes, woody vines, large-leaved herbs, and ground vines (Floyd 1990; Hunter 1991).

Dryer subtropical rain forests generally have two tree strata, an upper layer with scattered emergents such as hoop pine and a lower continuous stratum. Leaves are commonly compound, thick and hard, and usually less than 7.5 cm long (microphyll, after Webb 1968). Stranglers and woody vines are common, but plant buttressing and large epiphytes are rare. The shrub layer is well developed and prickly, and the herb layer is sparse (Floyd 1990; Hunter 1991).

2. Rainfall, Climate, and Soils. The subtropical rain forest in which the southern clade *Macadamia* typically are found occurs in warm, humid locations, where annual rainfall is high (>1300 mm), reliable and uniformly distributed or with summer maxima. The wettest months in northern NSW and southeast Queensland are January, February, or March. The driest months are August or September. Average annual rainfall is between 1120 and 2351 mm. Temperatures in the region tend to be moderate, with average minima between 13 and 16.4°C and maxima between 22.4 and 27.1°C. January is generally the hottest month and July the coolest (Commonwealth Bureau of Meteorology 2003).

Subtropical rain forests are found below 600 m elevation on Cainozoic igneous rocks, especially on basalt and rhyolite in the McPherson and Main ranges of southern Queensland (Sattler and Williams 1999) and on the volcanic geology of the Tweed shield (RACAC 1996). Rain forest is mostly found at low altitude and is replaced with warm-temperate rain forest with increasing altitude or latitude (Floyd 1990). Rain forest is common on high-fertility soils such as red krasnozems and brown prairie soils that are rich in nutrients like phosphorous and calcium, essential for rain forest growth (Floyd 1990).

Occurring over a range of substrates and topographic positions where there is high soil nutrient status and good drainage (Barry and Thomas 1994), *M. integrifolia* has the largest geographic range and may also have the greatest environmental amplitude of the southern *Macadamia* species. *M. integrifolia* is most commonly found on high-nutrient volcanic (basalt and diorite) and alluvial soils that are slightly acid (pH 5.5 to 6.5) and has been recorded at altitudes between 5 and 340 m, on slopes ranging from steep to level (Barry and Thomas 1994), and on north, southeasterly, and west aspects.

Found on high-fertility volcanic soils, *M. tetraphylla* also occurs to a lesser extent on alluvial deposits (e.g., upper Mullumbimby Creek) or weathered volcano-lithic rocks in the Burringbar Range (Pisanu 2001). Within the Tweed and Richmond River catchments, *M. tetraphylla*

occurs at the base of the rhyolite cliffs of the border ranges, on the lower south- and east-facing slopes of Mount Warning (Pisanu 2001). Soils are well drained (Barry and Thomas 1994), with textures from clayey sand to loams or silty clay, and soil pH between 4.98 and 5.87 (Pisanu 2001). The species is found at altitudes between 10 and 460 m (Barry and Thomas 1994) but mostly around 150 m (Gross 1995), and on moderate to steep slopes on north, south, east, and west aspects (Pisanu 2001).

Generally found on soils derived from volcanic parent material, mostly basalt but also trachyte, andesite, tuff, and rhyolite, *M. ternifolia* is also known to occur at the interface between sandstone and basalt (Barry and Thomas 1994). Soils tend to be well-drained sandy loams to light clays, and pH ranges between 5.5 and 7.0 (Barry and Thomas 1994). This species is found at altitudes between 100 and 320 m but mostly below 200 m, usually on moderate to steep hill slopes and foot slopes (Barry and Thomas 1994). It may have a more restricted habitat preference than the other two species as it has mostly been recorded in south-facing gullies.

Macadamia jansenii is found in a single moderately steep gully at 350 m elevation with east-southeast aspect. The geology is Muncon volcanics, a mixed intermediate and basic lava volcanic/sedimentary complex. Soils are dark brown sandy clay loams with good drainage, about 40% rock fragments on the surface, and pH 7.0 (Barry and Thomas 1994).

3. Abundance and Population Dynamics. Patterns of abundance within populations of *Macadamia* species appear to vary. *Macadamia integrifolia* and *M. ternifolia* occur sparsely in their natural habitat, with individual plants widely separated (Barry and Thomas 1994; Neal 2007). In contrast, *M. tetraphylla* distribution is described as clumped, with very few individuals dispersed between clumps (Pisanu 2001). It is not clear, however, whether these patterns are natural phenomena or an artifact of clearing and habitat fragmentation.

Several studies on the population dynamics of wild *Macadamia* suggest that mature populations are demographically stable, having low rates of mortality and recruitment, with recruitment increasing in response to disturbance. Pisanu (2001) found that survivorship within *M. tetraphylla* populations was high at all growth stages with low mortality at mature stages, suggesting that populations have some level of resilience to periodic disturbance. Populations in small fragments were found to be increasing at slow rates, whereas populations within contiguous forest did not change over a three-year period (Pisanu 2001). Similarly, an investigation into the population dynamics and

demography of *M. integrifolia* (Neal 2007) observed increased site-level fecundity and recruitment in small and medium-size habitat fragments compared to larger remnants. No evidence of differences in mortality levels between fragment sizes was found, suggesting stronger population growth in the smaller fragments compared to the more intact sites.

E. Genetic Structure and Dynamics of Native Populations

1. Genetic Structure of Natural Populations. Molecular marker studies have provided insights into the patterns of genetic diversity in remnant wild populations of *Macadamia*. The first survey of genetic diversity used isozymes (Sharp and Playford 1997), and clustered southern *M. integrifolia* and northern *M. tetraphylla* populations together and separately from northern *M. integrifolia* and southern *M. tetraphylla* populations. The authors concluded that this pattern was caused by the inclusion of hybrid populations in the southern *M. integrifolia* region, which confounded the true relationship between the species regions.

As part of a more recent molecular marker study, 165 genomic loci (RAF) were screened (Peace 2005) for 274 accessions of the National Macadamia Germplasm Collection, comprising most of the geographic range of the four southern clade species (Hardner et al. 2004). The four species could be clearly distinguished using this marker set, and hybrids were removed from the analysis of the pure species.

M. integrifolia populations exhibited a significant isolation-by-distance effect over the range of the species. (Proximate populations were more genetically similar than more distant populations.) Populations from a northern *M. integrifolia* group around the Mary River valley (including the Mount Bauple and Amamoor regions) were partially differentiated from a southern group of populations from the Pine Rivers district south to the Gold Coast hinterland. However, the overall measure of genetic differentiation between populations was moderate ($Gst = 0.233$) and indicates historical gene exchange between proximate populations (Peace 2005). *M. tetraphylla* populations overall exhibited lower regional differentiation ($Gst = 0.143$), indicating higher levels of historical gene flow between populations (Peace 2003). No significant isolation-by-distance effect was observed.

In the regions sampled for *M. ternifolia*, this species exhibited greater regional and population differentiation, but less diversity within populations, than *M. integrifolia* sampled in the same region (Peace 2005). However, approximately two-thirds of the natural distribution of *M. ternifolia* (mostly the northern range) were not surveyed and so remain uncharacterized. Little is known of genetic character of the only

known population of *M. jansenii*. However, the two accessions of this species that were assessed in the RAF marker analysis were as genetically distant as any two *M. ternifolia* accessions, and not particularly closer than any two accessions within the other two species, suggesting that the single known population of *M. jansenii* contains appreciable genetic diversity (Peace 2005).

Two microsatellite marker studies have recently been completed independently for *M. tetraphylla* and *M. integrifolia*. A study of *M. tetraphylla* (Spain 2006) screened six populations from the Mount Warning caldera to the Lennox Head area of NSW for four microsatellite loci (Schmidt et al. 2006). Moderate to high levels of genetic diversity ($He = 0.422$) and low adult population differentiation ($\theta = 0.016$) were found, indicating high historic gene flow between populations. Four microsatellite loci (Waldron et al. 2002; Peace et al. 2003; Schmidt et al. 2006) were used to screen 10 populations of *M. integrifolia* in the Amamoor and Samford regions of Queensland (Neal 2007). High levels of adult tree diversity ($He = 0.77$) and low genetic differentiation between populations at Amamoor ($Fst = 0.069$) and Samford ($Fst = 0.047$) were also evident in this species.

2. Mechanisms of Gene Flow. The low population differentiation observed in the above molecular marker studies of *M. integrifolia* and *M. tetraphylla* suggests that gene-flow mechanisms are sufficient to have maintained a network of interbreeding populations over a large area of suitable habitat (Spain 2006; Neal 2007). Considering the difference in scale of sampling between the microsatellite studies and the RAF marker studies, the levels of gene flow are comparable, and indicate high historical gene flow for both species between proximate populations (5 to 50 km) but more restricted gene flow among more dis- tant populations (> 50 km). In general, mid- to understory shrubs and trees are expected to have effective gene-flow mechanisms to maintain genetic contact between disparate individuals (Ward et al. 2005). This hypothesis could be explored further in macadamia by using biparental markers to assess the relative contribution of pollen and seed dispersal. Certainly, *Macadamia* species appear adapted to low-density living.

Although most current knowledge of the reproductive biology of *Macadamia* is based on cultivated trees growing within the natural range, it probably closely approximates that occurring in the wild. However, it is likely that individuals within natural populations are influenced by a wider range of complex ecological factors (Neal 2007), and thus the actual reproductive behavior of these plants may be quite different from that of the relatively precocious individuals growing in

commercial plantations that have been developed through selection and horticulture inputs.

In orchard studies, *M. integrifolia* has been observed to possess a partial gametophytic self-incompatibility mating system (Sedgley et al. 1990). This should effectively promote outcrossing and limit self-fertilization in natural populations. As predicted, a survey of open-pollinated progeny arrays from two remnant *M. integrifolia* stands (Neal 2007) confirmed that progeny are almost solely the result of outcrossing, with no selfing or biparental inbreeding observed. Outcrossing experiments in orchards observed higher rates of fertilization and nut set when cultivars were outcrossed, though some viable seed is still produced after selfing (Sedgley et al. 1990; Meyers 1997; Vithanage et al. 2003). However, in natural populations of *M. integrifolia*, no optimal crossing distance or effect of genetic relationship (including selfing) on fruit set was observed, suggesting that fruit set in wild *M. integrifolia* populations is likely to be resource limited rather than pollen limited (Neal 2007).

Similar to that in cultivated orchards (Heard and Exley 1994; Wallace et al. 1996), both introduced honey bees and native stingless bees have been observed visiting *M. integrifolia* flowers in natural populations (Neal 2007). However, in *M. tetraphylla*, only honey bees were observed foraging flowers at nine sites over a three-year period (Pisanu 2001). Studies of pollen flow in orchards suggest that cross-pollination can occur over hundreds of meters across rows (Vithanage et al. 2003). In natural populations, pollination distances over several kilometers have been observed using paternity analysis (Neal 2007). Despite concerns that the introduced honeybee *A. mellifera* may pose a threat to many native plant species by altering pollination and increasing inbreeding (Gross 2001), this hypothesis is not supported in *M. integrifolia* given that almost complete outcrossing was observed in the wild (Neal 2007). It may be that the stronger flight and increased potential for pollen carryover of *A. mellifera* (Ghazoul et al. 1998) can even lead to increased pollination distances compared to native pollinators.

Water, gravity, and animals have also been proposed as potential dispersal vectors of *Macadamia* fruit (Pisanu 2001; Peace 2005). Pisanu (2001) found that dispersal of *M. tetraphylla* seeds was linked to slope angle with distinctive seedling shadows down-slope of large trees and with a mean distance of seedlings to adults of 3.81 m. All seed germination occurred in close proximity to adult trees, with 77% of seeds germinating within two meters of an adult during the three-year period of study (Pisanu 2001). The presence of small *M. tetraphylla* populations and individual plants along creek beds downstream of large populations of these species in the upper catchments suggests that

limited dispersal by flood events may occur (McConachie 1980; Pisanu 2001; Peace 2005). Gallery notophyll vine forest has been identified as habitat for *M. integrifolia* and *M. ternifolia* (Environmental Protection Agency 2005b), and a significant number of *Macadamia* population records are located adjacent to watercourses, providing support for this hypothesis (Pisanu 2001). However, the commercial practice of using water to separate mature nuts (sinkers) from low-quality nuts (floaters) does not suggest that mature viable fruit float in water. It may be that swift floodwaters are the only effective mechanism by which macadamia seeds are carried downstream.

Rodents (*Rattus rattus*, *Uromys caudimaculatu*) are predators of *Macadamia* seeds in Australian orchards (Horskins and Wilson 1999), with significant levels of nuts removed to adjacent habitats (Elmouttie and Wilson 2005), suggesting that rats may have a role in the dispersal of nuts in the wild. Pisanu (2001) found evidence of rodent seed predation at all *M. tetraphylla* study sites with 25 to 100% of seeds taken in a field seed removal trial. However, there is little evidence of hording of nuts by rats, as almost all nuts found in rat burrows in native habitat adjacent to commercial orchards were damaged (Elmouttie and Wilson 2005). There is limited information of the role of birds and other mammals in the dispersal of macadamia fruit in natural populations (McConachie 1980; Peace 2005).

The role of humans in the precolonization dispersal of *Macadamia* is unknown. *Macadamia* nuts were a food source for indigenous peoples both in Indonesia and Australia (Gross 1995; Hill and Baird 2003). *M. hildebrandii, M. integrifolia, M. tetraphylla*, and *M. whelanii* are all recorded as being eaten or used for their oil (Gross 1995), and it has been suggested that Aborigines may have transported *Macadamia* nuts over long distances (McConachie 1980).

F. Conservation Status of Wild Populations

1. In Situ Conservation

Status of Macadamia Habitat. Protection of habitat is critical to *Macadamia* conservation. The region that contains the southern *Macadamia* clade is currently experiencing sustained growth in both the agriculture and urban-industrial sectors, with increasing pressure on remaining areas of native vegetation and wildlife populations (Hardner et al. 2004). A high proportion of the former extent of lowland subtropical rain forest throughout the range of southern *Macadamia* has been cleared. For example, in the combined Tweed, Byron Coast,

Richmond River administration areas, less than 30% of the original land cover comprises undisturbed native vegetation (NSW Parks and Wildlife Service 1993). Much of the central and eastern part of this region was formerly covered by the ''Big Scrub,'' an area of continuous subtropical lowland rain forest extending from the townships of Bryon Bay to Lismore (Holmes 1987). Currently less than 1% of the Big Scrub remains, comprising a disjunct network of small remnants totaling 550 ha across the Lismore Plateau (Lott and Duggin 1993). Similarly, in southeast Queensland, approximately 40% of the original extent of subtropical rain forest remains (WWF Australia 2004; Accad et al. 2006).

In southeast Queensland, one of the four regional ecosystem types described as habitat for southern *Macadamia* (12.3.1) (Environmental Protection Agency 2005b) is represented by less than 10% of its original extent and is classified as Endangered (Accad et al. 2006). Loss of *Macadamia*-suitable habitat has been greatest on private property, where less than 24% of the original extent remains (Accad et al. 2006). As of 2003, 37% of remnant *Macadamia* habitat was located on private property, with a further 41% located within relatively unprotected state forests (subject to timber exploitation). Currently, 21% of remnant *Macadamia* habitat is located within conservation areas (Accad et al. 2006).

Impact of Habitat Fragmentation. Much of the remnant wild *Macadamia* occurs as small (< 50 individuals) fragmented populations surrounded by cleared habitat (Hardner et al. 2004; Neal 2007). The impact of habitat fragmentation on the population demography, associated community diversity, and genetic diversity of *Macadamia* has been examined recently. Spain (2006) surveyed six fragmented populations of *M. tetraphylla* of varying size and disturbance. The genetic diversity of seedling cohorts within stands was positively correlated with population size. However, while there was no correlation with population inbreeding and population size, level of inbreeding was significantly correlated with density of adult trees. This may indicate a potential biparental inbreeding effect, as spatial genetic structure (where proximate individuals are more genetically similar than those farther away) was evident at all sites. Compared to mature trees, genetic differentiation in the seedling cohort increased (from 0.016, $p = 0.23$, to 0.061, $p < 0.0001$, respectively), indicating increased genetic drift due to a reduction in gene flow of the seedling cohort compared to mature trees, a probable consequence of the fragmentation process. Diversity of the floristic community associated with *M. tetraphylla* was not significantly related to fragment size, but a

significant correlation between disturbance level and species paucity and the incidence of invasive species was evident. No correlation was found between the community diversity of species and the genetic diversity of *M. tetraphylla*.

A second study (Neal 2007) surveyed 10 plots of *M. integrifolia* within rain forest patches of varying size and isolation. Rather unintuitively, stronger population growth rates were evident in small fragments compared to plots located in medium- and large-habitat blocks, as a result of increased site-level fecundity and recruitment, but with no apparent change in short-term mortality. Resource availability, particularly increased lights levels in small fragments, is the most likely cause of this observed effect. Population viability may also benefit from the long life span of the species and observed resilience of adult plants to disturbance, potentially buffering populations against stochastic events (Neal 2007).

In contrast to the study of *M. tetraphylla* (Spain 2006), Neal (2007) found that heterozygosity estimates in *M. integrifolia* were comparable across sites and cohorts, independent of fragmentation status. However, allelic diversity was correlated with fragment size. In addition, small *M. integrifolia* sites displayed increased differentiation, decreased interpopulation gene flow, and higher genetic similarity between individuals compared to plots in medium and large fragments. At two study sites where open-pollinated progeny arrays were surveyed, there was little evidence of inbreeding, and paternity analysis of open pollinated progeny arrays demonstrated long-distance gene flow between sites that were separated by 2.8 km, suggesting that despite fragmentation, *M. integrifolia* can maintain genetic connectivity over a wide geographic area (Neal 2007). Pollination by introduced honeybees in small fragments may actually facilitate gene flow across the landscape due to increased foraging distances and greater capacity for pollen carryover compared to native pollinators, an effect observed in other species (Dick 2001).

In summary, both studies identified detrimental genetic effects of fragmentation for two *Macadamia* species that are likely to be shared by all species demonstrating similar life history characteristics. These impacts include decreased genetic diversity within fragments and decreased gene flow between fragments. In both studies, a potential effect of intrapopulation genetic structure was identified as a potential inbreeding threat to small populations. However, despite these findings, species of *Macadamia* appeared to maintain high levels of genetic diversity even within small fragments, indicating that small fragments retain conservation value. In addition, smaller fragments exhibited increased demographic growth and potential for long-distance gene flow.

Supplementary planting in small fragments, or increasing connectivity between remnants through habitat restoration, is expected to reverse some of the observed fragmentation impacts and would be among the best strategies to preserve the species in situ, particularly in highly fragmented landscapes (Neal 2007).

Legislative Protection. At the national level, Australian legislation and policies define measures for the conservation of species and communities under the Environment Protection and Biodiversity Conservation Act 1999 (Department of Environment and Heritage 2006). The country is further obligated as signatory to treaties under the Convention on Biological Diversity 1992, which requires consideration of a global strategy for plant conservation, protection of ecosystems, natural habitats, and the maintenance of viable populations of species in natural surroundings (Secretariat of the Convention on Biological Diversity 2005). At the global level, the conservation status of species is assessed and defined under the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (Standards and Petitions Working Group 2006). The southern *Macadamia* species are not currently red-listed because most plant taxa listed in the 1997 IUCN Red List of Threatened Plants (Walter and Gillett 1998) have not yet been evaluated against the revised Red List Criteria (IUCN 2006).

At the regional level, southern *Macadamia* species are listed under the Queensland Nature Conservation Act 1992 (Environmental Protection Agency 2005a) and the NSW Threatened Species Conservation Act 1995 (Department of Environment and Conservation 2006). Under relevant Australian jurisdictions and the 1997 IUCN Red List, *M. jansenii* is classed as Endangered, because it is known only from a very small population with very restricted distribution. The remaining three species are classed as Vulnerable because of population declines attributed to clearing and fragmentation of lowland subtropical rain forest throughout their geographic range.

2. Ex Situ Conservation. A collection of cuttings from over 370 trees across more than 70 sites (including native populations, old planted populations, and stands of unknown origin) has been used to establish the National Macadamia Germplasm Collection as an extensive core collection of the major species of the southern *Macadamia* clade (Hardner et al. 2004; Peace 2005). This collection has been planted in orchard trials to conserve a large sample of the genetic variation and evaluate the material for introduction into future breeding programs. An obvious exclusion is *M. jansenii*, although the small size of the only

known population of this species may limit collection through conventional methods.

III. GERMPLASM DOMESTICATION

Genetic improvement in macadamia has delivered long-term commercial gains to macadamia production (Hamilton and Ito 1984; Stephenson and Gallagher 2000) and has underpinned the success and expansion of the industry throughout the world (Hamilton and Ito 1984; Stephenson 1990a; Nagao and Hirae 1992; Allan 1993). However, as the crop has only recently been domesticated, with cultivars only a few generations from the wild, macadamia germplasm is relatively underdeveloped, and much potential for genetic improvement appears to exist.

Detail of the origin and pedigree of domesticated germplasm is scant with most only available in industry publications. Recent development of DNA marker methodology (Aradhya et al. 1998; Steiger 2003; Steiger et al. 2003; Peace 2005; Peace et al. 2005; Schmidt et al. 2006) has assisted with the elucidation of genetic relationships in the domesticated germplasm. A review of published and unpublished literature identified over 900 cultivar names representing 500 apparently distinct genetic entities (Hardner and McConchie 1999). However, only selections that have had some commercial or historical significance are considered here.

A. Hawaii

Despite the Australian origins of the plant, macadamia was initially commercialized in Hawaii, and germplasm improvement is considered as having played a major role in this development (Hamilton and Storey 1956; Shigeura and Ooka 1984; Hamilton and Ito 1986; Nagao and Hirae 1992; Wagner-Wright 1995). In addition, Hawaiian cultivars are responsible for much of the current world production (Hamilton and Fukunaga 1970; Allan 1989; Ito and Hamilton 1989; Stephenson 1990a; Peace et al. 2005; Tay 2006).

1. Initial Introductions. The first introduction of macadamia to Hawaii was on the island of Hawaii by William Herbert Purvis sometime between 1881 and 1885 (Hamilton and Storey 1956; Hamilton and Fukunaga 1959; Shigeura and Ooka 1984; Wagner-Wright 1995) (Fig. 1.3). The origin of these seeds is uncertain, although DNA profiling suggests that the germplasm was sourced from the Mount Bauple region (Peace 2005).

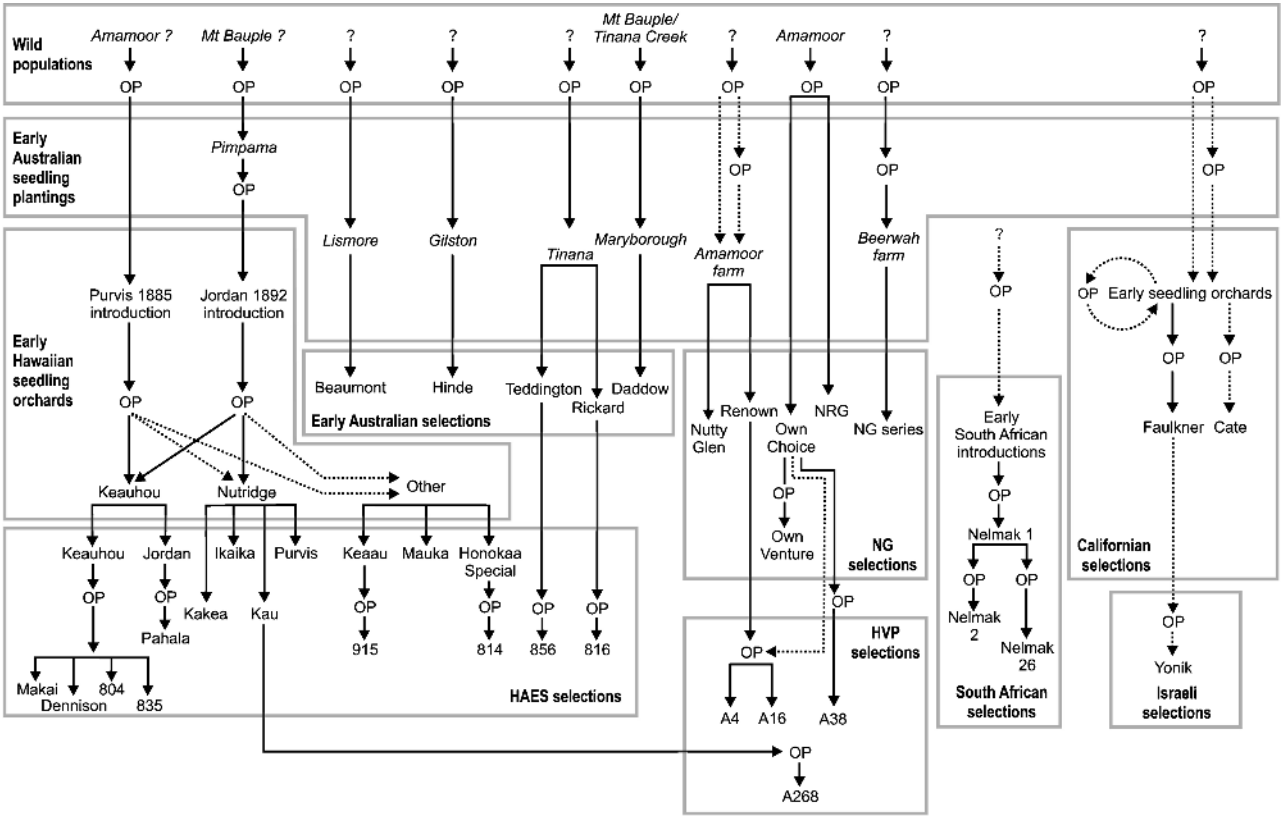


Fig. 1.3. Recorded origins of domesticated macadamia germplasm. Dotted lines represent uncertainty of lineage, and OP signifies open pollination. Horizontal relationships are not necessarily reflective of chronological order of selection.

It is also reported that this sample contained germplasm producing small bitter nuts (Shigeura and Ooka 1984), although it is unknown if these represented what is known today as *M. ternifolia*.

A second independent introduction of *M. integrifolia* was made in 1892 to the island of Oahu by Captain Robert Alfred Jordan, who reportedly was given some locally collected seeds during a visit to a friend in Pimpama, south of Brisbane (Shigeura and Ooka 1984; Wagner-Wright 1995). However, recent DNA profiling suggests that wild origin of this germplasm is from populations around the Amamoor region (Peace 2005), approximately 300 km north of Pimpama (Fig. 1.3) (see later discussion). This introduction reportedly produced six trees (Wagner-Wright 1995) and was considered the principal source of the first of the Hawaiian commercial cultivars (Storey 1965b), although both the Purvis and Jordan germplasm sources appear to have given rise to important cultivars (Peace 2005).

M. tetraphylla was used in reforestation plantations on the island of Hawaii in 1892 to 1894 by the Territorial Board of Agriculture and Forestry and thus represents a third early introduction of macadamia into Hawaii (Shigeura and Ooka 1984; Wagner-Wright 1995). No details of the source can be found, but it is has been suggested they came from the Murwillumbah area in northeast NSW (McConachie 1980; Wagner-Wright 1995). There are suggestions of other introductions of macadamia in the early 20th century (Wagner-Wright 1995), but no other information confirming this could be found.

2. First Orchards. From 1910, the potential of macadamia as a crop was considered in Hawaii, and by 1912, the Hawaii Agricultural Experiment Station (HAES) had begun distributing seedlings for commercial plantings (Wagner-Wright 1995). The first commercial orchards were established in the 1920s by the Honokaa Sugar Company at Mauka Kea on the island of Hawaii and by the Hawaiian Macadamia Nut Company (HMNC) in 1925 at Nutridge on the island of Oahu and Keauhou on the island of Hawaii (Ito 1983; Shigeura and Ooka 1984; Wagner-Wright 1995). The orchard at Mauka Kea was reportedly established with seed collected from the Purvis introduction of *M. integrifolia* (Shigeura and Ooka 1984) (Fig. 1.3). Some authors suggest the Nutridge orchard was planted with both the Jordan and Purvis seedlings (Shigeura and Ooka 1984; Wagner-Wright 1995), although others (Urata 1954) record that only the Purvis germplasm was used. The Keauhou orchard was planted with over 7,000 seedlings of both *M. tetraphylla* and *M. integrifolia*, although the *M. tetraphylla* trees were later removed (Shigeura and Ooka 1984;

Wagner-Wright 1995). Numerous other small orchards were also established (Wagner-Wright 1995).

From the early development of the industry in Hawaii, *M. integrifolia* was the preferred species (Ripperton et al. 1938; Cavaletto 1983; Shigeura and Ooka 1984). *M. tetraphylla* trees were considered to bear spasmodically and be more susceptible to insect attack. The shape of nuts was considered to be unsuitable (oblong) and shells harder and denser than *M. integrifolia*. The quality of kernels was reportedly more variable after oil roasting, although the taste was considered sweeter and more pronounced (Ripperton et al. 1938; Cavaletto 1983; Shigeura and Ooka 1984; Wagner-Wright 1995). In contrast, *M. integrifolia* nuts were considered to have thinner shells and more consistent response under oil roasting (Wagner-Wright 1995). No *M. tetraphylla* trees have been planted in Hawaii since about 1939 (Hamilton and Storey 1956), and existing *M. tetraphylla* trees were either eliminated or top-worked (Wagner-Wright 1995).

3. Scion Selection Program. The development of reliable grafting technology (Jones and Beaumont 1937; Shigeura and Ooka 1984) created the possibility of reducing the variability of seedling material and exploiting the full genetic variation available. This is considered to be one of the turning points in the history of the crop (Hamilton and Fukunaga 1973; McConachie 1980; Shigeura and Ooka 1984; Wagner-Wright 1995). It has been suggested that clonal orchards produce three to five times that of seedling orchards (Hamilton and Fukunaga 1959).

A scion selection program was initiated by the Hawaiian Agricultural Experiment Station (HAES) between 1934 and 1936 by surveying existing commercial seedling orchards to identify elite trees for further testing (Hamilton and Storey 1956; Hamilton and Ito 1984; Shigeura and Ooka 1984; Wagner-Wright 1995). Initial selection of promising orchard seedlings was based on observations of tree structure and vigor, production, apparent pest and disease resistance, nut characteristics, kernel recovery, and kernel characteristics (Beaumont 1937; Hamilton and Fukunaga 1973; Shigeura and Ooka 1984), although there is little detail on how these were assessed and integrated to compare candidates.

In 1935 and 1936, the HAES made the first selections from seedling orchards, all *M. integrifolia* by morphology (Hamilton and Storey 1956; Wagner-Wright 1995). By 1938, nuts from 19,000 trees had been evaluated to select 41 promising cultivars (Wagner-Wright 1995). This was reduced to five selections for establishment of clonal orchards over six sites for evaluation of productivity (Hamilton and Fukunaga 1959,

1973; Shigeura and Ooka 1984; Wagner-Wright 1995). Approximately 8,000 seeds were also collected from these selections for establishment of progeny trials (Wagner-Wright 1995). In 1948, five cultivars were released and given Hawaiian names to associate them with their origin (Hamilton and Ito 1984; Shigeura and Ooka 1984; Wagner-Wright 1995) (Fig. 1.3). 'Keauhou' (HAES 246) is the oldest Hawaiian cultivar, first selected in 1935. The others were 'Pahau' (HAES 425), 'Nuuanu' (HAES 336), 'Kohala' (HAES 386), and 'Kakea' (HAES 508).

Following the release of the first set of cultivars, the selection program was continued and expanded to the screening of seedlings in orchards or progeny plantings (Hamilton and Ito 1976). Between 1934 and 1984, an estimated 120,000 orchard seedlings and progeny plantings had been surveyed to give over 900 selections (Hamilton and Ito 1976, 1984). Most of these were discarded after what is described as preliminary screening and evaluation procedures (Hamilton and Fukunaga 1973; Hamilton and Ito 1976). While some selections have proved commercially valuable, the shortcomings of this process have been described (Hamilton and Fukunaga 1973); standards used for macadamia selection were later considered variable and arbitrary, were based mainly on superficial observation of the original seedling trees and nuts produced, and testing for yield, quality and suitability was often incomplete.

The most promising selections were grafted and established in trial plantings to objectively evaluate their productivity under orchard conditions (Hamilton and Fukunaga 1973; Hamilton and Ito 1976). Released cultivars were also planted as checks. Selections were assessed for vigor, tree habit, presence of stick-tights, number of fruit per raceme, productivity on favorable and unfavorable sites, nut size, kernel recovery, percentage of first-grade kernel, and raw kernel appearance (Hamilton and Ito 1976). Details of these selection criteria are discussed later.

Techniques for controlled crossing to produce full-sib families were developed in Hawaii (Urata 1954); however, it has been reported that while 300 crosses were made, they failed to produce progeny with desirable characteristics (Stephenson 1990a). By 1990, a total of 14 cultivars had been named and released by HAES (Nagao and Hirae 1992). In addition to the initial five cultivars, 'Ikaika' (HAES 333) and 'Wailua' (HAES 475) were released in 1952, 'Keaau' (HAES 660) in 1966, 'Kau' (HAES 344) in 1971, 'Mauka' (HAES 741) and 'Makai' (HAES 800) in 1977, and 'Purvis' (HAES 294) and 'Pahala' (HAES 788) in 1981 (Hamilton et al. 1981; Hamilton and Ito 1984; Shigeura and Ooka 1984). The final named cultivar from the program 'Dennison' (HAES 790) was released in 1990 (Hamilton and Ito 1990).

Two HAES selections have been named by others. 'HAES 791', which was rejected in Hawaii because of poor structure and prolonged flowering under tropical conditions, was found to be suitable to South African conditions (Blight 1989). It was originally given the name 'Richard' in South Africa (Blight 1989) but later named 'Fuji' in Hawaii (Peace et al. 2005). 'Jordan' (HAES 426) was named as an ornamental cultivar in California (Brooks and Olmo 1978). Other selections made in Hawaii outside the HAES evaluations are also recorded (Urata 1954; Hamilton and Ito 1976; Shigeura and Ooka 1984; Wagner-Wright 1995), in particular 'Honokaa Special', 'Chong 3', and 'Bond 23'. There has been no release of cultivars since 1990, although promising later selections have been made available for commercial utilization without official release and are commonly known by their HAES selection number (Ito and Hamilton 1989; Stephenson et al. 1995; Nagao et al. 2003). Few new seedlings have been planted out for evaluation (Mehlenbacher 2003).

4. Further Introduction of Australian Germplasm. A second wave of introductions was made from the 1940s through the 1950s (Hamilton and Fukunaga 1962). These authors record that the first successful importation of scion wood was made in 1949 by the University of Hawaii of a reputedly highly productive clone from a grower in southern Queensland. This, however, was of *M. tetraphylla* type and not productive in Hawaii. A further six clones were imported from Australia in 1950 and 1951, and one *M. tetraphylla* and two *M. integrifolia* types were imported from Queensland in 1952. In 1954, Dr. Beaumont of the HAES visited Australia and collected 34 scions of which 24 were successfully propagated in Hawaii. A further 24 scions were imported after 1955 (Hamilton and Fukunaga 1962). By 1962, 30 of the introductions had fruited, with 21 being of *M. tetraphylla* or hybrid type. Of those fruiting, 'HAES 685' ('B21' and 'Teddington' in Leverington 1962a) was the only introduction listed as a promising variety, and 'HAES 666' ('B5' or 'Rickard' in Leverington 1962a) was kept for further observation. This group also included 'HAES 695' (or 'NSW-44'), which although discarded in Hawaii (Hamilton and Fukunaga 1962), would later be taken to California and named as 'Beaumont'. It has been suggested that the Australian *M. integrifolia* selections introduced into Hawaii had a tendency to bear earlier than the introduced *M. tetraphylla* selections (Hamilton and Fukunaga 1962). However, there has been little impact of these introductions on the Hawaiian breeding program (Hamilton and Fukunaga 1973), apart as parents for several newer selections (see below).

Table 1.3. Summary of HEAS cultivars.

Name	HAES no.	Source	Release year	Reference[a]
Keauhou	246	Keauhou orchard	1948	1,2
Pahau	425	Keauhou orchard	1948	1,2
Nuuanu	226	Keauhou orchard	1948	1,2
Kohala	386	Keauhou orchard	1948	1,2
Kakea	508	Nutridge orchard	1948	1,2
Ikaika	333	Nutridge orchard	1952	3,4
Wailua	475		1952	5
Keaau	660	Glaisyer Orchard, Kauai	1966	4, 6
Kau	344	Nutridge orchard	1971	3, 4, 7
Mauka	741	Glaisyer orchard, Kauai	1977	4, 5
Makai	800	OP progeny of 'Keauhou'	1977	4, 8
Purvis	294	Nutridge orchard	1981	7, 9, 10
Pahala	788	Originally reported as OP progeny of 'Jordan'	1981	9, 10, 11
Dennison	790	OP progeny of 'Keauhou'	1990	9

[a]1 = Storey 1963; 2 = Shigeura and Ooka 1984; 3 = Hamilton and Ito 1984; 4 = Aradhya et al. 1998; 5 = Hamilton and Storey 1956; 6 = Steiger et al. 2003; 7 = Wagner-Wright 1995, 8 = Ito and Hamilton 1989; 9 = Ito and Hamilton 1990; 10 = Brooks and Olmo 1983; 11 = Hamilton et al. 1981.

5. Summary of Pedigree Relationships. The historical records and known pedigrees of the cultivars suggest they may be between two and four generations from the wild (Table 1.3, Fig. 1.3). 'Kakea', 'Ikaika', 'Kau', and 'Purvis' were selected from among seedling planted in the Nutridge orchard (Shigeura and Ooka 1984; Wagner-Wright 1995). Recent DNA marker studies indicates that 'Kakea', 'Ikaika', and 'Purvis' share greater affinity among themselves compared to 'Kau' (Peace 2005). 'Keauhou' was selected from the Keauhou orchard (Shigeura and Ooka 1984; Wagner-Wright 1995). 'Keaau' and 'Mauka' were selected from the Glaisyer orchard in Lawai valley on the island of Kauai (Hamilton and Ito 1977a; Vithanage and Winks 1992; Wagner-Wright 1995; Aradhya et al. 1998) (Table 1.3) and appear closely related from molecular marker analysis (Peace 2005). No record of the germplasm used to establish these orchards is available.

Several of the Hawaiian cultivars are advanced generation selections from open-pollinated progeny of early cultivars. The cultivar 'Keauhou' is reported as the seed parent 'Makai', which was selected from open-pollinated progeny planted at the Waiakea Experimental Farm (Hamilton and Ito 1977a; Ito and Hamilton 1989; Aradhya et al. 1998), and 'Dennison', which was selected from similar progeny planted at the University of Hawaii Waimanalo Research Station (Hamilton and Ito

1990). 'HAES 804' and 'HAES 835' are also reported as open-pollinated progeny of 'Keauhou' (Ito and Hamilton 1989). DNA marker analysis (Peace 2005) has confirmed all of these cases of 'Keauhou' parentage and has identified other undescribed progeny from this parent ('HAES 783' and 'HAES 828').

'Pahala' was originally reported as an open-pollinated progeny of 'Jordan' (Hamilton et al. 1981; Brooks and Olmo 1983). The parentage of 'Jordan' is not recorded; however, it appears to have been originally selected from the Keauhou orchard (Brooks and Olmo 1978). Others (Aradhya et al. 1998; Steiger et al. 2003) may have misunderstood this description, as they have attributed the parentage of 'Pahala' to the cultivar 'Keauhou'.

'Honokaa Special' is reported as the seed parent of 'HAES 814' (Vithanage and Winks 1992). There is little detail on the orchard origin of the maternal parent, although it was most likely selected from the Mauka Kea planting of the Honokaa Sugar Company (Wagner-Wright 1995), which was established with predominately Purvis germplasm (Urata 1954; Shigeura and Ooka 1984). 'HAES 816' is an open-pollinated progeny of 'HAES 666' (Ito and Hamilton 1989), which is identified by others (Hamilton and Fukunaga 1962; Leverington 1962a) as the Australian selection 'Rickard'. and 'Teddington' ('B21' or 'HAES 685') is reportedly the mother of the open-pollinated selection 'HAES 856' (Aradhya et al. 1998). 'Keaau' is reportedly the maternal parent of the open-pollinated 'HAES 915' (Ito and Hamilton 1989).

B. Australia

1. Early Seedling Orchards. Until the mid-1960s, orchards in Australia were established with seedling material (Wills 1961; Leverington 1962a, 1971). Planting of macadamia in Australia reportedly began around the 1860s in areas coincident with the natural distribution of the species, with seed most likely sampled from the surrounding natural populations (McConachie 1980) (Fig. 1.3). The world's first commercial macadamia orchard was of *M. tetraphylla* and was planted sometime between 1878 and 1888, at Rous Mill, near Lismore, NSW (McConachie 1980). By 1900, there were five *M. tetraphylla* orchards in NSW but no recorded orchards in Queensland, but many specimen trees in parks and gardens (McConachie 1980). The first orchard in Queensland (of 30 *M. tetraphylla* trees) was planted in about 1910, while the first large commercial orchard in Queensland was planted in 1917 (McConachie 1980). Orchard plantings increased in both NSW and Queensland through the 1910s to 1930s (Wills 1939; Willis 1961; McConachie

1980). NSW orchards were entirely of the local *M. tetraphylla* species until about 1931, whereas both species were planted in Queensland before this time (McConachie 1980). A high proportion of selections from a survey of Australian orchards in the early 1950s were *M. tetraphylla* types (Leverington 1962a), consistent with a bias toward this species in these early plantings.

It has been suggested that the first Australian orchard at Rous Mill was the source of much of the seed for these early orchards (McConachie 1980). The presence of old *M. tetraphylla* seedling plantings north of Brisbane (Hardner et al. 2004; Peace 2005), distant from wild populations of this species but within the natural distribution of natural *M. integrifolia* populations, illustrates the wide distribution of the germplasm.

Nurseries in the early 1900s may have played a major role in the distribution of genetic material, although few records are available that trace the origin of germplasm. By the mid-1930s, a nurseryman in Brisbane, Walter Petrie, had selected and named some of his parent trees (including 'Smooth Queen', 'Eggshell', 'Pearl', 'Comet', 'Rough King', 'Planet', 'Large Everbearer', and 'Large Queen') (Petrie 1935; Trochoulias et al. 1989) and seedling trees were sold under the name of their seed parent (Ian McConachie pers. comm.). The cultivar 'Don' may be a synonym of Petrie's 'Large Queen' (Trochoulias et al. 1989), although it could also be a seedling selection from this parent. The origin of this early nursery material is unclear, but it probably encompassed both species and may be hybrids (Trochoulias et al. 1989). It is unlikely these original parental selections have survived (Storey 1963), although there are later reports in the literature of 'Eggshell' (Trochoulias et al. 1989) and an accession 'Smooth Queen' is reported in the USDA Germplasm Repository in Hawaii (Aradhya et al. 1998).

2. 1950 Seedling Surveys. Australian attempts at clonal grafting were not succ-essful until the mid-1950s (Leigh 1968; Leverington 1971; McConachie 1980). The poor uniformity in Australian seedling orchards and the success of the Hawaiian industry stimulated an interest in discovering elite genetic material in Australian orchards (Leverington 1962a). Evaluation of seedling trees in Australia reportedly began in 1948 (Storey 1963), with Leverington (1962a, 1971) reporting a survey of Queensland and NSW orchards being undertaken in 1952 by state Agriculture departments to identify elite individuals based on observed tree vigor, growth characteristics, cropping habit, potential yield, and nut quality/shape, although no detail of how these criteria were assessed or integrated is given. It is also reported (Hamilton and Fukunaga 1962)

that Dr. J.H. Beaumount from HAES further encouraged these surveys during a visit to Australia in 1954.

Ninety-four individuals were selected for further evaluation based on nut characteristics including: (1) shape and size, (2) thickness of shell wall, (3) kernel diameter, (4) kernel color, (5) quality of kernel after the removal of mould and insect damage, and (6) palatability after oil roasting (Leverington 1962a). Forty Queensland selections were given a prefix to identify the origin of the material, which ranged from Maryborough to the Gold Coast Hinterland (I and T—Currumbin; X—Victoria Point; S—Manly; H and P—Gilston, J—Flaxton, G—Eight Mile Plains, N—Tamborine; B—Maryborough; M—Maleny; D—Greber at Amamoor). Most of the selections were identified as *M. tetraphylla* (only 'H2', 'B5', 'B6', 'B10', and 'B22' were identified as *M. integrifolia*).

Fifty-four NSW selections were identified only by a number, including 'NSW-44', which was a hybrid selection from a property at Highfields (Vithanage and Winks 1992), west of Casino, outside the natural distribution of the species. This selection would later be named in California as 'Beaumont' (Storey 1965a). Other NSW selections were from Carool and Stokers Siding (Leverington 1962a).

The number of selections was reduced by rejecting candidates with small kernel diameter, then using kernel recovery and percentage first-grade kernel (Leverington 1962a). The processing properties of the roasted and salted kernels were also evaluated (Leverington 1971).

Names were given to several of the initial selections (Anon 1961): 'Ardrey' ('J4'), 'Amamoor' ('D8'), 'Collard' ('L4'), 'Colliston' ('H1'), 'Elimbah' ('F1'), 'Flaxton' ('J3'), 'Greber' ('D1') (different from the Malawi selection, 'D1', as assessed by Peace 2005), 'Hinde' ('H2'), 'Howard' ('L1'), 'Maroochy' ('J6'), 'Oakhurst' ('B20', identified as *M. integrifolia* type in Anon. 1961 but as *M. tetraphylla* in Leverington 1962), 'Rickard' ('B5'), 'Stephenson' ('H3'), 'Sewell' ('N3'), 'Teddington' ('B21' in Leverington 1962a or 'HAES 685' in Hamilton and Fukunaga 1962, described as *M. integrifolia* × *M. tetraphylla* by Storey (1963) and *M. tetraphylla* by Leverington 1962a and Hamilton and Fukunaga 1962), and 'Tinana' ('B6'). 'Renown' ('D4' in Leverington 1962a but linked to this name by Storey and Hopfinger 1974) was also included in this list. The cultivar 'Powell' or 'Powell's Pride' ('P1' in Leverington 1962a) is recorded as an Australian selection by Dr. J.H. Beaumont when he visited Australia in 1954 (Storey 1963).

These selections are probably only one to three generations from the wild, depending on the sources of the seeds for the establishment of the original orchards (Fig. 1.3). 'Hinde' is the only cultivar of this program currently in commercial use; it is the preferred rootstock in the Australian

industry (Stephenson 1990a; Trochoulias 1992b). Details are not available on the source of the germplasm used to establish the Gilston orchard where this cultivar was selected, but DNA marker analysis identified this cultivar as pure *M. integrifolia*, apparently originating from the southern part of the range of this species (Peace 2005).

3. Norm Greber Selections. In addition to the selections made by the Queensland Department of Agriculture and Stock in the mid-1950s from his property, selections undertaken by Norm Greber form another major group of Australian germplasm (Fig. 1.3). These were derived from open-pollinated seed collected from wild populations and from his, and others', seedling orchards and backyard trees (Trochoulias et al. 1989; Vithanage and Winks 1992).

Historical records suggest that selections 'Own Choice', 'NRG', and 'Greber' originate from the same seed lot collected from nearby wild *M. integrifolia* populations in the Amamoor Creek valley near Gympie (Trochoulias et al. 1989; Vithanage and Winks 1992). It is unknown how many maternal trees comprised this wild seed lot. 'Renown' and 'Nutty Glen' are recorded as being selections from Norm Greber's farm in Amamoor; however, as these are hybrid types, the seed for these selections could not have come entirely, if at all, from local populations. It has been suggested that seedlings for the Amamoor orchard were supplied by Walter Petrie (Peace 2003). Other cultivars of Norm Greber, 'Greber Hybrid' and 'Own Venture', are recorded as full sibs, with 'Own Choice' and 'Renown' as parents (Trochoulias et al. 1989), although it is unknown if and how hybridization was controlled. A series of selections assigned 'X' also originated from progeny plots planted in Norm Greber's backyard at Beerwah, although the source of seed is unclear (Trochoulias et al. 1989). This is not to be confused with the 'X' prefix used for earlier selections from Victoria Point (Leverington 1962a). The prefix 'NG' has also been used to identify these selections (e.g., Stephenson et al. 1995). Storey (1965b) also recorded 'Eggshell' ('D3'), indicating this was a selection from the Greber property; however, there are no records of how this relates to the nursery seed parent tree of the same name listed by Petrie (1935).

Parentage analysis using DNA markers (Peace 2005) has been used to disentangle some of the relationships within the Greber germplasm. An identical DNA profile across a large number (over 100) of dominant and codominant markers and multiple genotypes suggests that the germplasm tested as 'Own Choice' may be the same as that of 'HAES 772'. This is supported by reports that these two cultivars have similar morphology (Vithanage and Winks 1992). While 'Own Choice' is of

M. integrifolia type, 'NRG' has been classified as of hybrid type according to morphology and DNA marker assessment of species composition (Peace 2005). This fact suggests that, if this cultivar had indeed been sampled from nearby wild populations, the seed tree was pollinated by foreign germplasm, possibly from the nearby orchard of the breeder Norm Greber, most likely 'Renown' (Peace 2005). Percentage analysis also confirmed that 'Own Venture' is probably a seedling of 'Own Choice' but not 'Renown', and 'Greber Hybrid' is probably not a direct seedling of either (Peace 2005). From a dendrogram based on DNA markers, 'X3', 'X4', and 'X8' clustered in a hybrid group that included 'Beaumont' but separate to another hybrid group containing 'Renown', 'NRG', 'Greber Hybrid', and known progeny of Renown (Peace 2005), indicating a different genetic background. Historical records suggest that 'X4' is a hybrid selection from Walter Petrie (Trochoulias et al. 1989).

4. Miscellaneous Australian Selections. There are records of several miscellaneous cultivars in Australia from the 1940s to the 1990s (Trochoulias et al. 1989; Vithanage and Winks 1992). 'Kopp', 'Heilscher', and 'Daddow' are recorded as selections from backyard or farm plantings around the Maryborough region propagated from *M. integrifolia* seed collected from wild populations around Mount Bauple or the headwaters of Tinana Creek (Fig. 1.3), although there are some reservations that *M. integrifolia* occurs naturally in this area (Ian McConachie pers. comm.). According to DNA marker analysis, 'Heilscher' most likely did originate from natural populations of this region. However, 'Kopp' appeared to have a mixed heritage, and 'Daddow' was determined to be derived from more southerly native *M. integrifolia* populations, one of the few cultivars identified as such, and more related to 'Hinde' than any other cultivar (Peace 2005). 'Release' and 'Mason 97' were from separate properties near Gympie, 'Armanasco' is recorded as from a property to the south of Brisbane, and 'Probert' is from near Mapleton (Vithanage and Winks 1992). 'McGregor' is an obscure Australian selection (Storey 1963) with little information of its origin.

Numerous other Australia selections have been described. 'HAES 680' was selected by Dr. J.H. Beaumont on a trip to Australia in 1954 (Hamilton and Fukunaga 1962; Wagner-Wright 1995). 'Rickard selection' ('HAES 687') was also collected on this trip, presumably from Rickard's property in Maryborough identified in the 1950 Australian survey (Leverington 1962a). No details are available on selections identified as 'Imbil' and 'Jackman' (Hamilton and Fukunaga 1962).

Several cultivars were recorded as selections by Dr. W.B. Storey from the University of California when he visited Australia in 1960. 'Currumbin' (Z1), 'Tomewin' (Z2), and 'Taylor's Triumph' (Z3) were selected from a property in the Currumbin valley (Storey 1963, 1965b; Storey and Hopfinger 1974). Other Australian selections include 'Collins' from Redland Bay, 'Duranbah 95' from northern NSW, 'Mammoth' (I1 in Leverington 1962), 'Nelson' (also ARN) from Stokers Siding (reported in Leverington 1962 but not given a designation), 'Tallebudgera' (T) from along Tullebudgera creek, and 'Wilson-10' from Mount Tamborine (Storey and Hopfinger 1974). 'Rankine' (also known as 'HY') is considered a hybrid type, and 'The Pocket' is *M. integrifolia* (Storey 1965b).

5. Hidden Valley Plantations Program. A breeding program was initiated at Hidden Valley Plantations in 1972 (Bell and Bell 1987) (Fig. 1.3). Early in the program, seedlings produced from open-pollinated seeds from high-yielding seedling parent trees were evaluated, but the program has progressed to evaluation of open-pollinated progenies from named cultivars and preliminary selections, through to progenies from semicontrolled crosses of certain cultivars. More than 25 characteristics are included in a weighted selection scheme. These include resistance to husk spot, kernel mass, tree structure, cropping, shape of kernel, color of kernel, and kernel sticking (assumed adherence to shell). The performances of standard cultivars are used as checks for evaluation (e.g., 'Keauhou' for field and 'Makai' for kernel characteristics, Bell and Bell 1987). Much of the assessment of these characters relies on visual assessment by trained operators; some characters are not well defined, some confound measurement and importance, and in some cases the relationship between the character and importance is not linear.

Several cultivars from this program have been released. 'A4' and 'A16' were the first plants to achieve Plant Breeders Rights (PBR) in Australia (Bell et al. 1988). These are both open-pollinated progeny from 'Renown', and recent DNA marker analysis has indicated that they are full sibs, with 'Own Choice' as the pollen parent (Peace 2005) (Fig. 1.3). A third cultivar, 'A38', has also been given PBR status and is the open-pollinated progeny of 'Own Choice' (Hidden Valley Plantations 1994).

Other cultivars have been released and used in commercial orchards without PBR. 'A29' (Bell and Bell 1987), 'A104', and 'A199' are open-pollinated progeny of 'Renown' (Vithanage and Winks 1992), not 'Own Choice' as reported by Aradhya et al. (1998) (H. Bell pers. comm.), although A199 appears to be a seedling of both 'Renown' and 'Own Choice' from DNA marker analysis (Peace 2005). 'Own Choice' is the

mother of open-pollinated progeny 'A90' (Vithanage and Winks 1992) and 'A203' (Aradhya et al. 1998), and 'A268' is an open-pollinated seedling of 'Kau' (H. Bell pers. comm.), the latter confirmed by DNA marker analysis (Peace 2005).

6. Australian Macadamia Breeding Program. A major breeding program was initiated in 1996 to produce cultivars suited to Australian conditions (Hardner and McConchie 1999; Mehlenbacher 2003; Hardner et al. 2005). This program is based on a quantitative genetic approach, where pedigree relationships and experimental design are used to increase accuracy of predicted genetic values and a formal selection index is used to trade off differences in multiple traits across multiple candidates (Hardner and McConchie 1999). Candidate cultivars identified in the program are vegetatively propagated for further testing in regional cultivar trials (Hardner and McConchie 2003; Hardner et al. 2005).

The major selection objectives of this program are tree size, precocity, average rate of yield increase, proportion of reject NIS, total kernel recovery, proportion of reject kernel, proportion of marketable whole kernel, and marketable kernel size (Hardner and McConchie 1999, 2003; Hardner et al. 2005, 2006). Elite selections are identified using a selection index, with an index value calculated for each candidate as a linear combination of the genetic value of the individual for each selection objective, weighted by the importance of the trait (Hardner et al. 2006). Trait weights are derived as the change in a profitability index (i.e., profit/costs) for an economic model due to a unit change in the level of the trait. This model includes the costs of production of a 100-ha orchard over a 20-year planning horizon from orchard establishment, the cost of processing the nuts, and the price of a range of raw kernel styles sold by the factory (Coverdale et al. 1999; Hardner et al. 2006). Net present value is used to account for the timing of costs and income over a long planning horizon.

These economic weights are based on current production systems that may not be applicable in 10 to 20 years when trees come into commercial production. However, the future can be uncertain, and models of current production systems provide a useful structure for examination of future scenarios. A linked pedigree also enables the breeding program to respond quickly to changes in the relative importance of selection objectives, as elite genotypes can be quickly identified under alternative scenarios (Hardner and McConchie 1999).

Genetic values of the breeding objective traits are predicted using genetic correlations with the traits that have been directly assessed on

the progeny (Hardner and McConchie 1999). Juvenile-mature correlations for different objectives indicate that selection can be made for kernel recovery, percentage whole kernels, and kernel size within two years of the first crop, but several years of yield are required to select for yield (Hardner et al. 2001, 2002). These results support selection for long-term yield by eight years after planting.

Two cycles of crossing have been undertaken (1993–1994 and 1997–1999) among 40 Hawaiian and Australian cultivars, and about 5000 seedlings have been planted across 14 sites in three of the major growing areas in Australia (Hardner and McConchie 2003; Mehlenbacher 2003). Mixed-model statistical methods (Henderson 1984) will be employed to combine data across sites and years and predict the genetic values of individuals across or within growing regions (Hardner and McConchie 1999).

Release of cultivars from the first breeding cycle is predicted for 2012 (Mehlenbacher 2003), 15 years after the planting of the first progeny trials. In comparison, the initial cultivar release in Hawaii (in 1948) was 23 years after the initial seedlings had been planted in the production orchards (1925, Shigeura and Ooka 1984). The quantitative genetic approach, where gain is achieved by increasing accuracy of selection, also contrasts with previous strategies adopted in macadamia, where gain was achieved through large population size and high selection intensity but low accuracy.

This quantitative approach is not well suited to traits that are vaguely defined or rely on personal judgments. Nevertheless, a formal quantitative approach enables all available information to be combined objectively for prediction of genetic value and identifies gaps in knowledge and assumptions that are made to fill these gaps. This approach also provides a comprehensive structure for review and modification, which is important for institutional breeding programs.

C. Other Programs

1. California. The origins of Californian cultivars are relatively obscure. *M. integrifolia* was reportedly introduced into California in about 1879, with other introductions in following years and the introduction of *M. tetraphylla* in the early 1890s or 1900s (Storey 1957, 1965b; Ferguson and Arpaia 1990) (Fig. 1.3). Both species were used in ad hoc plantings from San Francisco to the Mexican border prior to 1946. Early Australian selections (described in Leverington 1962a) were introduced in the early 1960s (Storey 1964). There has been no comprehensive program to develop new cultivars for

California (Ferguson and Arpaia 1990), although by the 1950s several local cultivars of *M. integrifolia* ('Arcia', 'Faulkner', 'Parkey') and *M. tetraphylla* ('Burdick', 'Hall', 'Santa Ana') types had been identified (Storey 1963; Steiger et al. 2003). Other local Californian cultivars include 'Pierce', 'Kirsch', 'Tanner', 'Bays', and 'Limonera' (Schroeder 1994). The cultivar 'Cate' is a *M. tetraphylla*–type selection that was propagated from a seedling growing in Malibu in 1958 and was planted in California during the 1970s (James 1978). 'Beaumont' and 'Jordan', originally selected in Australia and Hawaii respectively, were named in California as cultivars for ornamental use (Storey 1965a; Brooks and Olmo 1983).

2. South Africa. South African macadamia germplasm can be traced back to cultivated germplasm from Australia, Hawaii, and California (Fig. 1.3). The seed used to establish the first orchards in 1930s were reportedly imported from Hawaii (Peace et al. 2005). This seed gave rise to an indigenous selection, 'Nelmak 1', which is of hybrid type, and it is believed that other South African cultivars, 'Nelmak 2' and 'Nelmak 26', are progeny of 'Nelmak 1' (Peace et al. 2005). *M. integrifolia* and *M. tetraphylla* seeds were also imported from Australian nurseries (Petrie and others) in 1935 and used to produce seedlings for orchard establishment. The South African selections 'R14', 'W148', and 'W266' are reportedly derived from these introductions (Peace et al. 2005). Seeds of the Californian *M. integrifolia* selection 'Faulkner' were reportedly introduced from Hawaii in the 1970s and were the source of a series of 'F' selections (Peace et al. 2005).

3. Kenya. Macadamias were introduced into Kenya in 1946, and plantations in Kenya prior to 1973 were established with seedling material (Gathungu and Likimani 1975). A selection program was initiated in 1971 to identify superior trees for grafting. Criteria for selection were: (1) vigorous growth, (2) spreading structure with wide crotch angles, (3) consistent yields, (4) short ripening period, (5) resistance to pest and diseases, (6) nut size, (7) kernel shape, (8) kernel recovery, (9) oil content, and (10) health implications (Gathungu and Likimani 1975). The preference for a spreading habit is in contrast to the Hawaiian preference for an upright form. The authors suggested that hybrids could also be used to reduce oil content but increase sweetness. Seven Kenyan selections have been published: 'Kiambaa T22', 'Chania H28' and 'H29', 'BHL 1', 'BHL 2', 'BHL 3', and 'BHL 6' (Gathungu and Likimani 1975). The extent of adoption of this material is unclear. These selections have an average oil content between 76.5% and 82%,

between 80% and 100% first-grade kernel, average kernel recovery between 33% and 36%, average nut diameter between 23 and 27 mm, average kernel diameter between 17 and 21 mm, and sucrose content between 1.68% and 2.64% (Gathungu and Likimani 1975).

4. Others. A number of cultivars have been developed in several other countries. The cultivar 'Yonik' (13/3) was selected in Israel from progeny raised from seeds described as 'Kona-778' type that were introduced from Hawaii in 1966 (Kadman and Slor 1982). 'HAES 778' is the *M. integrifolia* selection 'Faulkner' from California (Aradhya et al. 1998), but further research is required to confirm the relationship between these two cultivars.

A series of Brazilian selections has been recorded in the literature. The selections 'Keaudo' (IAC 2-23), 'Keaufa' (IAC 4-21), 'Keaumi' (IAC 4-20), and 'Keaure' (IAC 4-18) are reported as open-pollinated sibs from 'Keauhou' (Ojima et al. 1976; Barbosa et al. 1991). 'Kakea' is reportedly the seed parent of 'Kakedo' (IAC 4-10) and 'Kakere' (IAC 5-10) (Ojima et al. 1976). No details are reported for the parentage of the Brazilian selections 'Aloha', 'Campinas A', 'Campinas B', 'Campinas F', 'Campinas H' and 'Waiado' (Barbosa et al. 1991; de Sa 1991; Aradhya et al. 1998; Sacramento et al. 1999).

Seeds were introduced into Thailand in 1953 (Supamatee et al. 1992) from unknown sources. Several selections from Thailand ('Kau Kor #1' and 'Kau Kor #2') have been recorded (Steiger et al. 2003). Two indigenously developed cultivars have been reported from Mexico (Quintas 2006) without further detail of parental origin. Macadamia seed was introduced into New Zealand in the 1890s, and a range of cultivars was introduced in the 1970s (Richardson and Dawson 1991). A private company has made a number of local selections, which are given prefixes 'PA' and 'PB'. A breeding project is reportedly under way in the Panxi region of China, with particular emphasis on *M. tetraphylla* germplasm for cold resistance (Xiao et al. 2002b).

D. Genetic Structure of Domesticated Germplasm

1. Use of Molecular Markers. Molecular marker technology is a power- ful tool for analyzing genetic relationships among cultivars. Several markers systems have been used to quantify genetic diversity within sets of macadamia cultivars, enabling comparisons of relatedness between various domesticated origins and determination of the likely causes of cultivars gene-pool differentiation.

Isozyme Marker Studies. The first molecular study in macadamias employed nine isozyme loci to survey 74 cultivars that were placed into 10 groups based on the combinations of four alleles detected at the phosphoglucoismerase (pgi) locus (Vithanage and Winks 1992). However, the distribution of cultivars from different selection origins and species type among these groups was not consistent.

Germplasm analysis was extended using 16 isozyme loci to group 40 cultivars into seven apparent groups (Aradhya et al. 1998). At the highest level of organization, the cultivars grouped clearly as either *M. integrifolia* or *M. tetraphylla*, but several known hybrid-type cultivars ('Renown', 'Beaumont', and 'A16') complicate the further detail of the organization. Five groups (1a to 1e) were relatively closely associated and together were classified as *M. integrifolia*, although one of these groups (1c) contained mostly hybrids. The two *M. integrifolia* groups with the largest number of individuals, and mostly of Hawaiian selection origin (1a and 1b), were very closely related compared to the other groups. The authors used this apparent separate grouping as evidence that the two early introductions of *M. integrifolia* to Hawaii (by Purvis and Jordan) were from genetically distinct ancestral populations. However, this is not convincing, given the little diversity and subjective demarcation between the two groups. Alternative interpretations are that the close affinity between the two groups suggests that cultivars were derived from only one of the germplasm sources ('Purvis' or 'Jordan'), or that the two sources were not from distinct natural origins. The authors also asserted that Australian selections probably represent a different genetic background (natural origin) and selection history to Hawaiian selections. However, several Australian cultivars clustered within groups 1a and 1b, while groups 1c, 1d, and 1e included many hybrids and other cultivars with ambiguous species status, indicating that at least some of the differences between groups were due to the inclusion of *M. tetraphylla* germplasm ancestry in cultivars.

DNA Marker Studies. In a third marker study (Vithanage et al. 1998), 76 mostly *M. integrifolia* genotypes were screened with random amplified polymorphic DNA (RAPD) and codominant STMS markers, although no clear arrangement was observed other than single accessions of *M. tetraphylla*, *M. ternifolia*, and *M. jansenii* each appearing very distinct from the *M. integrifolia* and hybrid cultivars, similar to observations in the isozyme studies. Cultivars domesticated within Hawaii and Australia were distributed throughout the dendrogram. A survey with 105 amplified fragment length polymorphism (AFLP) markers of 24 accessions of the cultivated species (and three

accessions of related species) identified two distinct groups of Hawaiian cultivars within *M. integrifolia* (Steiger et al. 2003). However, the specific cultivar composition of these groups was different to the isozyme study of Aradhya et al. (1998). The authors compared the overall diversity in the macadamia germplasm with coffee and papaya, finding it higher in macadamia (Steiger et al. 2003), although it is likely the diversity among the macadamia cultivars was inflated by the inclusion of multiple species.

Thirty cultivars were separated into four groups using a principal component analysis of the allelic variation of 175 RAF (randomly amplified DNA fingerprinting) and STMS codominant marker alleles and 230 dominant RAF markers (Peace et al. 2002). Species composition weighted % of species specific markers was calculated using 134 alleles specific to *M. integrifolia* and 34 specific to *M. tetraphylla* (Peace et al. 2004). Species specificity of a marker was determined by surveying the frequency of the markers in groups of cultivars that had been characterized as pure species from morphology (Peace 2005). Using this methodology, the four groups of cultivars corresponded to *M. integrifolia*—Hawaiian selection origin; *M. integrifolia*—Australian selection origin; hybrids—Australian selection origin; and *M. tetraphylla*—Australia selection origin. Species status (*M. integrifolia*, hybrid, or *M. tetraphylla*) was clearly the major determinant of genetic differences (Peace et al. 2002).

This methodology was improved (Peace 2005) by determining species specificity of markers from the National Macadamia Germplasm Program collection (Hardner et al. 2004) of 274 accessions from 58 wild populations. Individual genotypes were initially assigned to one of six species types based on morphology (*M. integrifolia*, *M. tetraphylla*, *M. jansenii*, *M. ternifolia*, *M. integrifolia* × *M. tetra-phylla* hybrid, *M. integrifolia* × *M. ternifolia* hybrid), and species-specific markers were then identified as those that were only represented in wild populations of one of the species but not in those of other species or in hybrid populations. This separates classification of marker species specificity from their implementation in the study of species relationships in the domestication germplasm. The species-specific markers were then used to survey the genetic diversity of 83 cultivars and selections (Peace 2005). Cultivars were distributed in eight distinct clusters—four of *M. integrifolia*, three clusters of hybrids, and one *M. tetraphylla*, with six to 26 individuals per group. Principal component analysis with separation of cultivars in two dimensions was also used to display this grouping arrangement (Peace 2005). The species specificity of the markers allowed the species composition of the genotypes to be quantified

(Peace et al. 2001, 2005; Peace 2005). A study of South African cultivars (Peace et al. 2005) was a subset of this larger study.

The two RAF primers used for the cultivar and wild germplasm survey (Peace 2005) were chosen for their ability to amplify at least one microsatellite marker, and thus the information generated by these primers were RAMiFi markers (randomly amplified microsatellite fingerprinting, Peace et al. 2004). In total, 165 dominant markers and nine codominant microsatellite markers were used (Peace 2005). These markers were also employed to verify/deduce the parentage or identity of certain cultivars within the 85-cultivar set (Peace et al. 2002; Peace 2005; Peace et al. 2005), the results of which are described within the domestication history sections. For this purpose, the microsatellite markers were the most useful, while the accompanying dominant markers provided abundant accessory information (Peace 2005).

The Hawaiian *M. integrifolia* cultivars formed two distinct clusters. Cluster 1 contained 'Keauhou' and its known offspring, 'Ikaika' and 'Kakea', and 'HAES 816', a Hawaiian selection from open-pollinated progeny of an Australian selection introduced into Hawaii. Cluster 2 contained 'Kau', 'Keaau', 'Mauka', 'HAES 814', and an old Australian selection, 'Own Choice'. Aradhya et al. (1998) also found 'Kau', 'Keaau', and 'Mauka' to have very similar genetic profiles.

Clusters 3 and 4 contained a range of Australia *M. integrifolia* selections. Clusters 5, 6, and 7 contained cultivars that are mixtures of the two species, including the Australian cultivars 'A4' and 'A16' with their maternal parent 'Renown'. Cluster 7 appeared to share greater affinity with *M. tetraphylla*. The last cluster contained cultivars of pure *M. tetraphylla* origin.

Comparison of Marker Results. Clustering of macadamia species and cultivars from the various marker systems studies was compared by Peace et al. (2004). Six sets of marker data (two isozyme, two of STMS, and one each of RAPD and RAMiFi) were obtained for a common set of 14 macadamia individuals. These individuals consisted of nine cultivars typically regarded as *M. integrifolia* (the Hawaiian-bred 'Keauhou', 'Ikaika', 'Kau', 'Kakea', 'Keaau', 'Mauka', 'Makai', and 'HAES 816' and the Californian-bred 'Faulkner'), three regarded as *M. integrifolia* × *M. tetraphylla* hybrids ('A4', 'A16', and 'Beaumont'), and one accession each of *M. tetraphylla* and *M. ternifolia*. The exact accessions used for the latter two species varied for some of the marker studies. Matrices of pairwise genetic distance were calculated, dendrograms were produced, and the matrices were compared using Mantel matrix correlation (Peace et al. 2004).

The six dendrograms revealed some overall trends. Most marker systems identified the *M. tetraphylla* and *M. ternifolia* accessions as the most distantly related individuals. The three hybrid cultivars tended to cluster together and separately to the *M. integrifolia* cultivars. The *M. integrifolia* 'Faulkner' appeared distinct from the other cultivars of that species. The eight *M. integrifolia* cultivars of Hawaiian selection origin tended to form a separate cluster.

The correlation among the relationships of cultivars for three of the marker sets (isozyme from Aradhya et al. 1998; RAPD from Vithanage et al. 1998; RAMiFi from Peace et al. 2002) was significant and greater than 0.6 (Peace et al. 2004). These three sets of marker systems produced similar clustering arrangements of cultivars that were also consistent with expectations, and Peace et al. (2004) concluded that these markers were more robust. There was little correlation of the genetic relationships from each of the three other marker studies with any other study. For two of the other marker systems (isozyme from Vithanage and Winks 1992; STMS from Vithanage et al. 1998), the differentiation of individuals was more divergent, including intermixing in the dendrogram of individuals from different species. The STMS and RAMiFI marker data sets of Peace et al. (2002) produced the largest genetic distances and thus appeared to better be able to distinguish among genotypes (Peace et al. 2004).

2. Influences on Genetic Structure. The combined results of genetic marker studies, particularly where species status of cultivars was considered, suggest that germplasm organization of cultivated macadamia is determined primarily by species status (i.e., whether an individual is one of the pure species or a hybrid) and species composition (the proportion of each constituent species within a hybrid) (Peace 2005). Natural origin is considered the second most important factor followed by breeding/selection origin.

Species and Hybrids in Cultivation. In all marker studies to date, pure *M. integrifolia* and pure *M. tetraphylla* cultivars were observed to be the most genetically separated individuals, with hybrids (where identifiable as such) intermediate. Species composition calculations indicated that increasing amounts of one species over the other primarily determined the overall placement of hybrid cultivars (Peace 2005).

Cultivars all along the scale from pure *M. integrifolia* to pure *M. tetraphyll*a have been identified by genetic marker analysis (Peace et al. 2002, 2005; Peace 2005). This continuity in species composition of the domesticated germplasm suggests that hybrids are fully fertile in

cultivation. According to these analyses, and consistent with assessment by morphology, hybrid cultivars are particularly common in the Australian and South African macadamia industries (Peace et al. 2005; Peace 2005). However genetic marker analyses also suggest that the species type of many macadamia cultivars is misclassified by morphology, particularly those with small *M. integrifolia* or *M. tetraphylla* compositions, including several common cultivars of Australian selection origin (Peace 2005). Further research is required to determine the effects the various proportions of each species detected within cultivars might have on their performance.

Particular mention is made of the cultivar 'Fuji', which is the only macadamia genotype, cultivated or otherwise, identified as a trispecies hybrid (Peace 2005; Peace et al. 2005). Species composition calculations suggest that the *M. ternifolia* composition of 'Fuji' is approximately one-quarter, at least two generations removed from its *M. ternifolia* ancestor (Peace 2005). The *M. ternifolia* possessed by 'Fuji' is an unusual phenomenon for macadamia, and demonstrates the opportunities that may exist from greater exploration of the wild genetic resources of the genus. Several of the characteristics of this cultivar may have been derived from its *M. ternifolia* heritage (Peace 2005; Peace et al. 2005). In Hawaii and South Africa, 'Fuji' trees are reportedly small, spindly trees (Blight 1989), similar to the stature of wild *M. ternifolia* (Gross 1995). This supports the view that this cultivar is susceptible to wind damage in exposed areas but could be ideal for high-density planting (Blight 1989). The absence of bitter kernels (presence of cyanogenic compounds), which is normally found in wild *M. ternifolia*, is likely to be due to the recessive gene action of this trait (Hardner et al. 2000).

Native Origin of Cultivars. Peace (2005) deduced natural origins of cultivars by linking the presence of particular markers of apparent restricted geographic origin in wild populations with their presence in cultivars and identifying the most closely related wild populations and specific wild accessions for each cultivar from both cluster analysis and raw genetic distance values. Although there are limitations to this method, given the small population sizes sampled for the wild accessions included in the analysis and the difficulty, particularly for cluster analysis, in determining origins for cultivars derived from mixing between natural gene pools, the outcomes were clear for certain cultivar groups. The northernmost regions of the native range of *M. integrifolia* were implicated as contributing the most to the genetic background of cultivars of the world's macadamia industry, including the Hawaiian germplasm groups, many Australian cultivars, and cultivars from several

other countries (Peace 2005). In most cases, these assignments corresponded to the historical records of the source of these cultivars.

The evidence from the molecular studies in macadamia is in conflict with the generally accepted view that the Jordan germplasm is derived from the southern range of *M. integrifolia*. In the first instance, Hawaiian cultivars tend to cluster together in these marker studies, suggesting that only one or two germ pools were sampled in the initial introduction. Second, the results in Peace (2005) indicate that the two clusters containing the named Hawaiian selections from the original 1920s orchards are both associated with the northern range (Mount Bauple/Amamoor) of *M. integrifolia*, with cluster 1 sharing greater affinity with the Amamoor region and cluster 2 appearing to be more closely aligned with the Mount Bauple region. This is supported by the inclusion in cluster 2 of 'Heilscher', an Australian selection that reportedly came from the Mount Bauple area. Third, Pimpama, the reported origin of the Jordan collection, lies at the opposite end of the species range some 300 km to the south within the hybrid zone of *M. integrifolia* and *M. tetraphylla* (Fig. 1.3). Further work is required to reconcile this conflict. It may be that the seeds for the Pimpama trees were sourced from the northern distribution. Alternatively, none of the Jordan germplasm may be represented in the domesticated Hawaiian germplasm. It has been reported that the Purvis germplasm was collected from the Mount Bauple area (McConachie 1980). If this is correct, this germplasm may be represented by cluster 2 in Peace (2005).

The Australian cultivars 'Daddow' and 'Hinde' were the only pure *M. integrifolia* cultivars identified with natural origins entirely or predominantly in the southern *M. integrifolia* regions (Peace 2005). The Tweed River valley in the central part of the native range of *M. tetraphylla* was most implicated by RAMiFi markers as the source of cultivars of that species (Peace 2005). Hybrid cultivars from the three major cultivated hybrid germplasm did not appear to have arisen from any one region, suggesting that hybrids in cultivation are artificial species combinations and not directly sampled from the natural hybrid zone (Peace 2005).

Selection and Breeding. Breeding/selection origin clearly does not adequately describe the organization of genetic diversity in macadamia (Peace 2005). Cultivars of Hawaiian and South African origin were spread among four different clusters; three cultivars from Malawi were not particularly related and were each located in different clusters; Australian cultivars were in every major cluster; and even selections from the same Australian program of Norm Greber were in five different

clusters. Germplasm exchange in recent generations appears to account for the lack of geographical continuity in the clustering of macadamia cultivars. Breeding programs, such as those in Hawaii and Greber's, have included germplasm from several sources; this has resulted in some individuals having little genetic affinity despite undergoing a common selection regime. Intermixing of germplasm through domestication appears to have given rise to some groups of germplasm where cultivars within the groups are more closely related to each other than to any wild accession surveyed (Peace 2005). These represent novel germplasm that apparently does not occur in the wild. It is suggested that most of the widely planted cultivars in Australia, Hawaii, or South Africa are of this germplasm type (Peace 2005).

3. Wild Genetic Diversity Represented in Cultivation. Domestication appears to have captured a large proportion of the neutral genetic diversity present in recent collections from the remnant wild populations. Peace (2005) calculated that the 83-cultivar set surveyed contained half the genetic diversity (measured as the number of observed polymorphic dominant markers and codominant marker alleles) of the wild accessions of the National Macadamia Germplasm Collection from the three main species of the southern clade of *Macadamia*. Alternatively, the proportion is approximately two-thirds when measured as average heterozygosity of dominant markers, presumably higher due to the inclusion of many hybrid cultivars that arose in cultivation rather than being directly sampled from wild gene pools. More *M. integrifolia* diversity is represented in cultivation than for other *Macadamia* species (Table 1.4).

Table 1.4. Proportion of the genetic diversity contained with the National Macadamia Germplasm Collection that is represented within the 10 most-plant cultivars in the three largest macadamia-producing regions in the world.

	Proportion of wild germplasm diversity (%)					
	Average heterozygosity of dominant markers			Polymorphic markers and alleles		
Cultivar group	Hawaii	Australia	S. Africa	Hawaii	Australia	S. Africa
Pure *M. integrifolia*	15	79	89	28	50	46
Pure *M. tetraphylla*	0	18	30	0	12	19
Both cultivated species	25	47	57	15	31	34
All species	22	43	55	11	23	27

Source: Adapted from Peace 2005.

Low genetic diversity (average heterozygosity; number of polymorphic markers) was detected in the two clusters dominated by Hawaiian-derived cultivars (0.013 and 0.026; 18 and 23), compared to other clusters (0.050 to 0.083; 29 to 46). This supports the hypothesis of low genetic diversity within Hawaiian germplasm (Peace 2005), which is in contrast to the discussion in Aradaya et al. (1998). Interestingly, the introduction of new germplasm into the Hawaiian breeding program in the 1950s does not appear to have increased genetic diversity appreciably. For example, selections 'HAES 814', 'HAES 816', and 'HAES 856' were seedlings of trees other than the first-generation Hawaiian cultivars but were still very closely related to other Hawaiian cultivars, apparently due to a similar native region of origin (Peace 2005).

The diversity of germplasm utilized in commerical production is expected to be much less than that described by Peace (2005) for the large 83-cultivar set, as many of these are rare with very limited planting. Genetic diversity within only the most widely planted cultivars of the three largest-growing regions was calculated separately and found to be about between 40% to 80% less than that in the larger cultivar set (Peace 2005; Table 1.4). The most widely planted Hawaiian cultivars contain a low proportion of total available diversity, even for *M. integrifolia*. Although Hawaiian *M. integrifolia* cultivars form the bulk of the orchard trees in Australia and South Africa, genetic diversity in cultivation is considerably higher in these countries due to the popularity of cultivars from other sources. South Africa has the most diversity, as it incorporates the most *M. tetraphylla* germplasm and a minor amount from *M. ternifolia* (from the cultivar 'Fuji'). Given the short history of domestication in macadamia, it is unlikely that the domesticated germplasm represents the only source of elite genetic material in macadamia. There appears considerable opportunity to capture large gains through exploring the wider diversity available in the genus.

IV. GENETICS OF KEY SCION SELECTION TRAITS

There are many biological traits of interest for genetic improvement in macadamia (Bell 1983; Hardner and McConchie 1999, 2003; Stephenson and Gallagher 2000). However, often these traits are poorly defined, and there is limited information on their inheritance (Hardner and McConchie 1999; Hardner et al. 2001).

Response to selection is determined by the extent of genetic variation in a trait and the intensity of selection (Falconer 1989). There are a few reports of genetic parameters estimated from cultivar trials (Hardner

et al. 2001, 2002). However, because these cultivars have been selected, the magnitude of genetic variation may be underestimated compared to a progeny population (Falconer 1989).

Studies reporting significant differences between cultivars provide other sources of evidence for the existence of genetic variation. However, it is difficult to assess the importance of cultivar differences that are reported without significance testing. In addition, some studies report means for unbalanced designs that are biased due to the absence of information from particular sites. Reported observations of cultivar performance gained from familiarity with the crop are similarly difficult to evaluate but can provide additional information on possible extent of genetic variation.

In this review we examine a wide range of published data on cultivar performance. To assist with the summary and comparison of these results, data were accumulated across studies and analyzed using a mixed-model Restricted Maximum Likelihood (REML) approach to account for unbalance in the data (Patterson and Thompson 1971). Several publications have presented masses of data. These are obviously valuable for understanding the genetic data of macadamia; however, the analysis and summary of this information is beyond the scope of this publication.

A. Tree Structure

Tree structure has been defined in terms of vigor, habit, tree size, and canopy density, although methods for quantifying most of these characteristics have not been developed, and assessment relies on trained assessors (Stephenson et al. 1995). A set of standard descriptors for tree structure have been developed (e.g., Domingo et al. 2004), which could be used to assist consistency among studies.

Early selections in Hawaii favored vigorous trees with round or cone-shaped habit (Hamilton and Ito 1977a), and spreading habit was favored in a Kenya selection program (Gathungu and Likimani 1975). In contrast, an upright habit was favored in the later Hawaiian selections, as this was considered more suitable for higher planting densities and increased early returns (Hamilton and Fukunaga 1973; Hamilton and Ito 1977a; Hamilton et al. 1981). The preference for upright trees is also followed in Australia (Stephenson and Gallagher 2000). The economic effect of tree size has been modeled by linking planting density to canopy width at age 10 (Hardner et al. 2006). Cultivars with larger canopy width are planted at wider densities so that the age at which canopies touch is maintained at 10 years. This has a large negative

impact on profitability, given all other traits are unchanged. An alternative approach could be to assume a common planting density and let tree size determine timing of orchard operations, particularly canopy management. There is also an interest in ultra-high-density plantings (e.g., 5×3 m, Trochoulias and Burnside 1987; Stephenson 1990a); however, the relationship of tree size with profitability may not be the same as described above for orchards at coventional densities, due to differences in the production system and cost structures.

Individual broad sense heritability of canopy width is moderate ($H = 0.3$), and the correlation of cultivars across environments was high (Hardner et al. 2002). Canopy width was also genetically correlated with stem girth ($r_g = 0.6$). In Australia, 'A4' had the smallest predicted mean (4.2 m) for 40 cultivars over two sites compared to 'Keauhou' and 'Makai' (5.7m) (Hardner et al. 2002). 'A16', 'HAES 814', 'Daddow', 'NG18', 'Own Venture', 'HAES 849', 'Keaau', 'Mauka', and 'Kau' were intermediate. Cultivar means for canopy width at 10 years (Hardner et al. 2006) was correlated with width at 14 years averaged across four sites (Stephenson and Gallagher 2000) ($r_{cv} = 0.6$). Reports of tree structure from field observations indicate that 'Keauhou' and 'Kakea' are spreading trees with round canopies and 'Kau', 'Keaau', 'Mauka', 'Pahala', and 'Makai' are upright (O'Mara 1977; Hamilton et al. 1981; Hamilton and Ito 1984). It has also been suggested that 'Makai' requires a higher intensity of tree training at a young age to develop a good structured tree (Ito and Hamilton 1989).

Stem girth has been examined by some authors (Allan 1989; Supamatee et al. 1992; Stephenson et al. 1995). In Australia, heritability of stem girth calculated from a trial of 40 cultivars across four sites was low to moderate ($H = 0.2$), but cultivar performance was highly correlated across sites (Hardner et al. 2001). To account for unbalance, a-REML analysis was undertaken on data presented for stem girth of 10 cultivars across seven locations in Thailand with four replications at each location (Supamatee et al. 1992). This analysis indicated that 'Keaau' was significantly more vigorous than 'Own Choice' and an indigenous hybrid cultivar, but there was no significant difference among the other cultivars. The analysis could not test for genotype-by-environment interaction ($G \times E$) as no within-site error was reported. In Hawaii, 'Ikaika' and 'Kakea' are considered more vigorous than 'Kau' and 'Keauhou' based on general field observations (Hamilton and Fukunaga 1959; Hamilton and Ito 1984).

An open canopy density may be important for penetration of light (Huett 2004) and spray application; however, the density of canopies is difficult to quantify, and there is a lack of studies demonstrating a

measurable impact. Reports based on field observations classify the canopy of 'Kau' as dense and state that the canopy of 'Daddow' becomes 'denser with age'. 'Keaau', Mauka', 'HAES 816', and 'A16' are reported as having moderate-dense canopies, and 'Keauhou' as only having a moderate canopy density. Others (O'Mara 1977) describe the canopy of 'Hinde' as open.

Resistance to wind damage is also an important consideration in Australia (Stephenson and Gallagher 2000), China (Lu et al. 1998b), and Hawaii (Shigeura and Ooka 1984), where tropical cyclones and typhoons can cause severe damage. Spreading trees with wide crotch angles are considered more susceptible to wind damage (Hamilton and Ito 1984) although this has not been quantitatively demonstrated. Direct assessment of resistance of macadamia to wind damage was undertaken in southern China (Lu et al. 1998a, 1998b, 2004). For a wind strength between 7 and 9 on the Beaufort scale, there were significant differences in damage among cultivars with 'Own Choice' the most resistant, followed by 'Kau', 'Ikaika', 'Keauhou', and 'Makai'. Differences disappeared at wind strengths above 11. Strong wind can cause immediate loss of yield and long-term damage to the tree (Lu et al. 1998b). Yield was reduced by 60% to 70% in the years following wind damage, and yield recovered in only 50% of trees in the second year after damage. These quantitative differences among cultivars are supported by observations in Hawaii (Hamilton and Ito 1984; Ito and Hamilton 1989). 'Hinde' is also considered susceptible to wind damage (O'Mara 1977), and 'Fuji' is considered susceptible in exposed areas in Hawaii (Blight 1989).

B. Flowering Phenology

Genetic variation in the length of flowering period may have consequences for the opportunity for cross-pollination, and the extent to which indiscriminate environment events that are adverse for pollination (e.g., rain) may impact on the reproductive capacity of a tree. In Hawaii, an association between length of flowering period and length of harvest period has been suggested (Nagao and Hirae 1992). Individual broad sense heritability of individual trees calculated from a study of 20 cultivars at a single site over a single season in Australia indicated that there are strong differences among cultivars for the date of the commencement of flowering of individual racemes ($H = 0.87$) with lower genetic variation for duration of flowering of an individual raceme ($H = 0.53$) (Boyton and Hardner 2002). Early-flowering cultivars include 'HAES 842', 'HAES 814', 'Kau', and 'Keauhou', contrasted

with later flowering cultivars 'A4', A16, and 'NG8'. However, variability in timing of the commencement of flowering among individual racemes and the duration of flowering within a cultivar (within and between trees) is larger than the variability among cultivars, suggesting opportunity for overlap of flowering between cultivars. In Hawaii, 'Keaau' reportedly flowers over a tightly defined period compared to 'Kakea', which tends to have a diffuse pattern (Nagao and Hirae 1992). Further knowledge on the impact of pollination availability on productivity is required to investigate the implications of differences in flowering phenology among cultivars.

C. Fruit Set and Arrangement

The large number of flowers in a raceme provides the opportunity for multiple fruit per raceme. In Hawaii, there is a preference for fruits in clusters of 10 to 20 nuts (Hamilton and Ito 1977b), although the rationale for this is not apparent. Alternatively, a large number of fruit per raceme may reduce the effectiveness of spraying for pest and disease control. Differences among cultivars in the number of mature fruit set per raceme tagged at flowering have been reported under Australian conditions (McConchie et al. 1997; Boyton et al. 2002). Fruit set per raceme from controlled pollination was highest for 'HAES 849' (8.6) and 'Mauka' (8.2); intermediate for 'Kau' (5.8); lower for 'Keaau' (5.0), 'A16' (4.9), 'HAES 816' (4.6), 'HAES 814' (4.6); and lowest for 'Own Venture' (3.5), Daddow (3.3), 'Keauhou' (2.8), 'HAES 781' (2.8), 'HEAS 842' (1.7), and 'A4' (1.6) (McConchie et al. 1997; Meyers 1997). Differences among these groups were significant. In an alternative study under natural pollination (Boyton et al. 2002), fruit set ranged from 2.2 per raceme for 'Kau' to 0.3 for 'HAES 816', although this calculation also included racemes that failed to produce fruits (47% of racemes tagged at anthesis). However, the ranking of cultivars in these studies may be different from that for number of fruits per raceme at maturity where no account is made of the number of failed racemes. In Australia, 'A38' reportedly sets up to 30 mature fruit per raceme (Hidden Valley Plantations 1994).

D. Yield

Yield is one of the fundamental traits for selection in macadamia (Cull 1978; Winks 1983; Hardner et al. 2006). The general pattern of yield in macadamia is commencement of production between age three and six years, followed by a general increase with age, leveling to a plateau

at later ages (Nagao and Hirae 1992; Mayer et al. 2006). Results from several cultivar trials suggest that, in general, yield reaches a plateau around 12 years of age at densities of 8×9 m (Ito et al. 1983), 5×10 m (Ito et al. 1998), and 5×9 m (Nagao et al. 2003).

Planting density may affect yield (Oosthuizen 1992; Mayer et al. 2006), although there is little evidence to support a later age decline in yield in crowded orchards (Hardner et al. 2000; McFadyen et al. 2004). In addition, yields may vary by 60% due to seasonal influences (Hardner et al. 2000; Mayer et al. 2006). This complexity makes a quantitative definition of yield difficult (Winks et al. 1986).

Parameters that have been used to describe yield are: age of first crop (Hardner et al. 2006), NIS per tree at a certain age (Stephenson and Gallagher 2000; Hardner et al. 2006), and total or average yield over a particular period (Stephenson et al. 1999; Hardner et al. 2006). The linear rate of the increase in yield has been used to describe yield during the accumulation phase of production (Stephenson and Gallagher 2000; Hardner et al. 2006). The complexity of describing yield has led some (Stephenson 2001) to suggest that physiological studies may provide a better platform for understanding of the trait, thereby enabling in greater selection response.

There has been an interest in developing a productivity index that relates yield to tree size to enable the comparison of yield across different ages and management scenarios (Winks 1986) and identify trees with higher yield per hectare (Hardner et al. 2002). The best regression between tree size and yield was achieved by describing tree size as the vertically projected area of the canopy (Chapman et al. 1986; Winks et al. 1986). Hardner et al. (2002) reported a productivity index calculated as cumulative yield divided by the horizontal projection of canopy area at age 10. Use of a productivity index to select trees for yield per hectare or compare trees at different ages requires the assumption that the ratio between yield and tree size is constant across ages or sites, but this has not been verified.

For comparison across studies, care is also needed to understand exactly what is being reported for yield. Yield may be reported as wet nut in husk (e.g., Nagao et al. 2003) or wet nut in shell (e.g., Ito and Hamilton 1987) with moisture content of over 20% (Stephenson 1990a; Wall and Gentry 2007). Alternatively, yield may be expressed as nut in shell (NIS) at a constant moisture content of 10% or 1.5% kernel moisture content, as this is the level nuts are generally dried to for cracking and processing (Stephenson 1990a; Mason and McConachie 1994). In some studies, yield is assessed after nuts that have fallen prior to the completion of oil accumulation have been removed from the site (Hardner et al. 2002).

Alternatively, this material may be included and may lead to an overestimation of commercial yield (e.g., Piza et al. 2006). In other cases, the inclusion or exclusion of such material is not reported.

Some studies report yield estimates from single-tree plot designs (e.g., Stephenson et al. 1996). The competitive environment of these trials is likely to be highly variable compared to production orchards, which generally have a single cultivar planted along each planting row. Studies are required to verify the accuracy of these designs.

1. Age of First Crop. An earlier age of bearing is generally considered a desirable characteristic in a cultivar as it can increase early orchard returns (Hardner and McConchie 1999). Commencement of production at three to four years after planting is considered desirable in Australia (Stephenson and Gallagher 2000). However, there is little quantitative information on the genetic architecture of this trait in macadamia. There was little range in the predicted effects for age of first crop for 20 cultivars over two sites (−0.2 to −0.1) (Hardner et al. 2006). The authors note that there was a large interaction between cultivar and site for this trait although further detail was not presented. Field observations suggest that 'Ikaika' (Hamilton and Ito 1984) and 'Kakea' (Hamilton and Fukunaga 1959) are particularly precocious compared to other Hawaiian cultivars. This, however, was not observed for 'Ikaika' when trialed in the Panxi region of China (Xiao et al. 2002a). 'Beaumont', 'HAES 814', and particularly 'Fuji' are considered precocious cultivars in South Africa (Blight 1989; Allan et al. 1999).

2. NIS Yield Per Tree. The selection criteria employed in the early Hawaiian program prior to the mid-1980s for yield was a minimum annual production of 45 kg per tree at age 8 in favorable sites and 35 kg per tree in less favorable (e.g., high temperature or wind, soil and drainage problems) sites (Hamilton and Ito 1976). This threshold was later increased to 68 kg at year 10 in favorable sites (Hamilton and Ito 1986). In contrast, a consistent yield of two tonnes per ha at 10 years (16 kg per tree at 10×8 m spacing) has been recommended as the benchmark for cultivars in Australia (Stephenson and Gallagher 2000).

Broad sense individual heritability (H) for annual yield to 10 years of nut in shell at 10% moisture content ranged between 0.06 and 0.18 for a trial of 40 cultivars across four sites in Australia (Hardner et al. 2002), considerably lower than canopy width and nut and kernel characteristics (Hardner et al. 2001), which were also examined. This suggests that assessment of yield on trees outside controlled trials or using a low number of replicates may not accurately estimate genetic potential.

Genetic correlations were high (0.7 and 1.0) among yield in successive years (Hardner et al. 2001). Yield at age 4 was not highly correlated with yield from 6 to 10 years of age ($r_{cv} = 0.49$ to 0.11), although genetic correlations between years were greater in later years. Correlations were higher when yield was expressed as cumulative yield, due to an averaging over annual variation. A high correlation of cumulative yield to age 7 with cumulative yield to year 10 ($r_{cv} = 0.9$) has been used to develop strategies for early selection in macadamia (Hardner et al. 2001). This study also indicated that there was no genetic correlation between yield and tree size ($r_{cv} = 0.1$) although there was a high within-tree correlation. This result has also been observed in other studies (Chapman et al. 1986).

Several reports have demonstrated difficulty in finding significant differences in yield among cultivars (Ito et al. 1983; Winks et al. 1987; Stephenson et al. 1995; Nagao et al. 2003), supporting the observation of low heritability for this trait. There was no significant difference between the top 21 cultivars for cumulative yield from 4 to 8 years of age and no significant difference between the top 16 cultivars for average yield over the same period (Stephenson et al. 1995) in the same trial used by Hardner et al. (2002) to estimate genetic parameters for yield.

Higher heritability ($H = 0.5$) has been reported for a productivity index of cumulative yield to 10 years per square meter of projected canopy area (Hardner et al. 2002). In addition, significant differences were found between nine cultivars for the regression of vertically projected canopy area and yield (Winks et al. 1986). Cultivar means for the productivity index were highly correlated with estimates of intercept of the regression of yield on tree size ($r_{cv} = 0.99$) compared to those for slope ($r_{cv} = 0.33$).

There is little quantitative data on the presence of genotype-by-environment interactions for yield in macadamia. Genetic correlations of 40 cultivars over four sites were variable between years but were higher and more consistent for cumulative yield, except for correlations with one particular site (Hardner et al. 2002). In contrast, there was much lower $G \times E$ for the productivity index of yield per square meter of projected canopy area, suggesting this parameter may be more efficient for selection than yield per se. These data were also used to examine the stability of cultivar means across sites and years (Stephenson et al. 1995), where a general trend was reported for higher-yielding cultivars to be more variable across sites and years. However, this analysis does not account for the low accuracy of the predicted means, which are based on a maximum of four replications.

Differential response of cultivars to altitude has been reported for Hawaii (Hamilton and Ito 1984; Ito and Hamilton 1989; Nagao and Hirae 1992) and Kenya (Gathungu and Likimani 1975), although no data were presented. Yield data for several cultivars at different altitudes has been presented (Ito and Hamilton 1987); however, this was based on only one to three replications of each cultivar at each site and is likely to be highly inaccurate. The physiological basis of apparent differences in productivity with altitude is poorly understood.

A number of other studies have reported yield at younger ages during the accumulation phase of production (Winks 1983; Ito et al. 1991; Supamatee et al. 1992; McCubbin and Lee 1996; Swanepoel and Hobson 1999; Lu et al. 2004). However, the variability in the quality of the data makes it difficult to integrate the results for comparison. In particular, estimates of production based on results from a single year or from very early in the bearing life of a tree may not be indicative of tree performance at later ages.

Yield for trees that are reaching the mature phase of production have been reported for a number of cultivars across a number of studies (Ito et al. 1983; Winks et al. 1987; Phiri 1985; Stephenson et al. 1995, 1999; Nagao et al. 2003), although some results have been not been included here (e.g., O'Mara 1977; Ito and Hamilton 1987) as they were based on only two to three replications of each individual. The rank of cultivars tends to be similar across studies. In Hawaii, the average annual yield between 10 and 16 years was significant higher for 'Kau' (47 kg WNIS per year) and 'Keauhou' (46 kg) compared to 'Keaau' (38 kg) with 'Kakea' (44 kg) and 'Ikaika' (42 kg) intermediate (Ito et al. 1983). Similarly, in an Australian study of 40 cultivars (Stephenson et al. 1999), the cultivars with the highest average annual yield of NIS between 12 and 14 years were 'Kau' (21 kg NIS per year) and 'Keauhou' (20 kg NIS per year); 'Keaau' was one of the lower-yielding cultivars (16 kg) in Australia. Other low-yielding cultivars in the Australian study included: 'A4' (12 kg), 'A16' (13 kg), 'HAES 816' (14 kg), 'HAES 814' (15 kg), 'HAES 849' (15 kg), and 'HAES 835' (16 kg). 'Mauka' (19 kg), 'Daddow' (18 kg), 'Own Venture' (18 kg), and 'NG18' (17 kg) were intermediate. In a later Hawaiian study (Nagao et al. 2003), 'Kau' produced the highest average annual yield between 10 and 13 years (45 kg WNIS per year). In agreement with the Australian results, the lowest yields were for 'Mauka' (29 kg), 'HEAS 849' (27 kg), and 'Pahala' (25 kg). Other smaller studies in Malawi (Phiri 1985) and Australia (Winks et al. 1987) have also demonstrated the superior yield of 'Keauhou' and the relatively low yield of 'Keaau'. The ranking of cultivars for mature yield in Stephenson et al. (1999) is in general

agreement with average total yield of NIS to 10 years (Stephenson et al. 1995), although at earlier ages the yield of 'Daddow', 'NG18', and 'Own Venture' were equal to that of 'Kau' and 'Keauhou' and the yields of 'HAES 814' and 'HAES 849' were intermediate. However, this study also reported that there was no significant difference among the top 15 cultivars, suggesting more replication is required to accurately identify the relative yield of cultivars. Differences in absolute yield between Hawaii and Australia may in part be due to the difference in the production system between the two countries, in particular the extended flowering and harvest seasons in Hawaii, where nuts are present on the tree all year round (Nagao and Hirae 1992), or different methods of assessment. There seems little support for differential performance of cultivars in Hawaii and Australia as suggested by some authors (Cull 1978; Stephenson et al. 1995).

E. Nutrition Utilization

Field observations of variability in symptoms of nutrient deficiencies among cultivars have been used to suggest a genetic basis to the efficiency of nutrient utilization (Hamilton and Fukunaga 1959). However, no experimental data has been provided to offer strong support for this hypothesis. In a limited on-farm trial, no significant differences were found in leaf nutrient content of 12-year-old bearing trees of 'Keauhou', 'Ikaika', 'Kakea', and 'Keaau' (Pire et al. 2002). Yamaguchi (2003) suggest that 'Purvis' has a higher demand for nitrogen compared to 'Keauhou', 'Kakea', and 'Keaau', with 'Ikaika' and 'Kau' requiring less. A similar pattern is reported for phosphorus, although it is considered 'Kakea' and 'Keaau' have higher demands for this nutrient than 'Keauhou'. No genetic variation for potassium demand was suggested. In contrast, others (Stephenson and Cull 1986; Robinson et al. 1997; Huett and Vimpany 2007) suggest 'Kau' requires more nitrogen than 'A4', 'Kakea' 'Mauka', 'Keauhou', 'Hinde', and 'Keaau'. It has also been suggested that 'Own Choice' may be particularly susceptible to copper deficiency (O'Mara 1977). Further quantitative information on the interaction between nutrition and the physiological processes of the tree is required to build these results into a selection program.

F. Abnormal Vertical Growth

''Abnormal vertical growth'' is a term used to describe a disorder of excessive vertical growth and reduction or absence of flowering that has been reported in Australia, South Africa, and Costa Rica (O'Farrell and

Searle 2003). There is reportedly a higher frequency of the disorder in 'Kau' and 'Mauka', and symptoms have been observed in 'Keauhou', 'Kakea', 'Keaau', and 'Makai', although not in 'A4' or 'A16' (O'Farrell and Searle 2003). Further work is required to quantitatively describe the disorder, and assess its genetic basis and interactions with environmental factors, before genetic improvement can be attempted.

G. Phenology of Fruit Drop

Variability in the length of fruit drop may impact profitability of macadamia production where fruit are harvested from the ground following natural abscission. Harvesting is a major cost of production (Nagao and Hirae 1992; Hardner et al. 2006). As fruit are harvested at 2 to 6 weekly intervals to maintain quality (Leverington 1962a; Mason 1983; Mason and Wells 1984; Liang et al. 1996), increased length of the period over which fruit drop will increase these costs. It has also been suggested that lateness of fruit drop may affect ability to control pest and diseases (Stephenson and Gallagher 2000).

M. tetraphylla selections reportedly have a much shorter fruit drop season than *M. integrifolia* selections (Leverington 1958, 1962a). Fruit drop patterns have been quantified using a generalized logistic function (Hardner et al. 2005a), although the authors report convergence problems for a number of samples, suggesting that an alternative model should be explored. Stephenson et al. (1995) defined harvest period for selection as early (>90% of the crop dropped over first four months of mature nut drop), mid (>90% of nut dropped over the first six months), and late (>10 % of crop remaining in tree after six months). Based on field experience, 'Keaau' is described as having a short harvest period and 'Kakea' is considered to have a long drop period (Hamilton and Ito 1984; Ito and Hamilton 1989; Stephenson and Gallagher 2000). 'Own Choice' is reported to be a late-dropping cultivar (O'Mara 1977).

The phenology of fruit drop in macadamia can be manipulated through the use of ethephon (Jones et al. 1996; Trueman et al. 2002). Differential response among five cultivars to application of ethephon approximately nine months after anthesis has been reported, with greater fruit drop in cultivars that had commenced natural abscission by the time of application ('HAES 814', 'HAES 842', and 'HAES 849') compared to 'A16' and 'Own Venture' (Salter et al. 2003). The authors suggest that the impact of ethephon is related to the phenological stage of the cultivar, although ethephon was applied only at a single date in this study. This study also reports a significant effect of cultivar on leaf

loss after ethephon application, but this was unrelated to the effect on fruit abscission.

H. Pest and Disease Resistance

Numerous pests and diseases appear to have coevolved with *Macadamia* in its natural habitat. However only a small number affect cultivation in Australia. For example, of the 150 or more insect species that are hosted by *Macadamia* (Gallagher et al. 2003), fewer than 10 are regarded as orchard pests of economic importance (Huwer and Maddox 2003). Pests and diseases may account for substantial crop losses through fruit abscission prior to the completion of kernel development or direct damage to the kernel (Leverington 1958; Waite et al. 1999; Jones 2002), and there is an interest in developing resistance in cultivars as part of an integrated pest management strategy (e.g., Jones and Caprio 1992). In contrast, some studies imply pest damage is unrelated to genotype and is mainly a consequence of variable management (Leverington 1962a; Stephenson 2001).

A full understanding of the pest and disease cycles is required to develop resistant cultivars. In Australia, nut-borer (*Cryptophlebia ombrodelta*, also called litchi fruit moth, Jones 1994a) is a major pest and can cause premature fruit drop prior to completion of shell hardening and oil filling (Ironside 1982; Waite et al. 1999). Tropical nut borer (*Hypothenemus obscurus*) causes kernel damage by attacking abscised fruit on the ground (Jones and Caprio 1992; Jones et al. 1996). Attack to developing fruit by fruit spotting bug (*Amblypelta nitida*) can lead to abortion of the immature fruit or kernel damage if it occurs later in the season (Waite et al. 1999; Gallagher et al. 2003). In Hawaii, the koa seedworm (*Cryptophlebia illepida*) can cause fruit drop prior to completion of oil accumulation (premature fruit drop) if attacked prior to shell hardening, although little actual kernel damage has been reported (Jones and Caprio 1992; Nagao et al. 2003). Southern green stink bug (*Nezara viridula*) is capable of piecing the shell during any stage in fruit development and after abscission, resulting in damage to the kernel (Nagao and Hirae 1992; Jones and Caprio 1994; Shearer and Jones 1996; Wright et al. 2003; Golden et al. 2006). Experimental evidence suggests that fruits that are mature or near mature do not necessarily abscise following feeding by *N. viridula* (Jones and Caprio 1994).

The actual extent of crop loss due to pest and disease attack may depend on timing of attack in the crop cycle (Waite et al. 1999). In a study in Hawaiian orchards, macadamias appeared able to compensate for the removal of up at least 30% of fruit prior to 150 days postanthesis

(Tobin et al. 1997). Crop loss due to insect attack, however, may be underestimated if based on the proportional mass of kernels that are damaged; this ignores the amount of kernel that otherwise would be produced if the kernel had developed normally (Jones and Caprio 1992). Measurement of damage levels as the proportion of nuts with damaged kernel may present a more realistic measure of the impact of pest damage (Jones and Caprio 1992; Golden et al. 2006).

Genetic variation in the extent of nut borer damage has been reported (Villiers 1977) (Table 1.5). Timing and degree of husk and shell hardness is thought to be related to the penetration ability of the larvae (Jones et al. 1992; Campbell et al. 2005). Genetic variation for husk hardness has been demonstrated, with hardness being highest for 'Ikaika', 'HAES 816', and 'Fernleigh Special' (Campbell et al. 2005). Differential rates of shell hardening among cultivars have also been observed (Jones 1994b), suggesting possibilities for manipulation through selection. However, alternative methods (e.g., parasitoids, Waite et al. 1999) may be more efficient than genetic improvement for managing the impact of this pest.

Cultivar differences in kernel damage from tropical nut borer have been reported (Jones and Caprio 1992; Jones et al. 1996) (Table 1.5). Kernel damage was significantly higher for 'Keaau' (26% after four

Table 1.5. Susceptibility of macadamia cultivars and selections to insect pests and tendency for stick-tights in Hawaii.

Cultivar	Tropical nut borer	Southern stinkbug	Koa seedworm	Stick-tights
Keauhou	Medium	Medium		Low
Purvis	High	Low	Medium-high	High-very high
Ikaika	Low	Low		Low-high
Kau	Medium	Medium	High	Low-medium
Kakea	Medium	Medium		High
Keaau	High	High		Low-medium
Mauka	High	Medium	Medium-high	Low-high
Pahala	High	Medium	Low	Low-very high
Makai	Low	Low	Medium-high	Low
816	High	High	Low	High
835	Medium	Medium		Low-medium
849				Low-high
856	Low	High	Medium-high	Low-medium
A4	High	High		Very high
A16	Medium	Medium		High
A38				High

Source: Hamilton and Fukunaga 1973; Hamilton and Ito 1984; Ito and Hamilton 1989; Jones et al. 1996; Jones 2002; Nagao et al. 2003.

weeks on the ground) and 'Kau' (18%) than 'Ikaika' (9%) and 'Mauka' (5%). The percentage damage of kernel from 'Keauhou' (12%) was not significantly different from that for the other cultivars. However, at high pest pressures, all cultivars experienced similar high levels of kernel damage (Jones et al. 1996). There is good evidence that shell thickness is the causal mechanism of resistance as there was a good fit of a power relationship between these two variables ($R^2 = 0.84$) (Jones et al. 1996). In contrast, the Pearson correlation coefficient between values of insect (and mold) damage and shell thickness reported for 94 Australian selections (Leverington 1962a) was not significant ($r = -0.28$), although this analysis confounds genetic and nongenetic effects.

No experimental evidence has been published to verify a differential response of cultivars to fruit spotting bug in macadamia. Waite et al. (1999) observed no difference in response of 'Kau' and 'Makai' to fruit spotting bug exposure. However, variation in damage for the related *Amblypelta l. lutescens* among cashew cultivars (Peng et al. 2005) suggests that further investigations could uncover genetic variation for this trait in macadamia.

In Hawaii, variation among cultivars has been observed for the percentage of kernels with damage from southern green stink bug (Jones and Caprio 1992) (Table 1.5). The cultivars 'Purvis' and 'Makai' had significantly less damage than the average; 'Kau', 'Mauka', and 'Pahala' did not differ significantly from the average level of damage; and 'HAES 816' and 'HAES 856' exhibited significantly more damage. It has been suggested that shell thickness and the rate of shell hardening may contribute to resistance (Jones and Caprio 1992; Nagao et al. 2003).

Based on field observations and experience, the susceptibility of 12 common cultivars to the three major insects in Hawaii has been reported (Table 1.5); however, these observations suggest that susceptibility for the different pests is not genetically correlated. However, the use of general terms and descriptive language makes further analysis difficult. Observations of high incidence of kernel damage in 'HAES 816' appear to confirm its susceptibility (Nagao et al. 2003).

Anthracnose is a disease of the husk and leaves (Hamilton and Storey 1956) and can be a particular problem in humid areas and when annual rainfall is greater than 1800 mm (Hamilton and Fukunaga 1959). A suggestion has been made that cultivars that are resistant to anthracnose have low stick-tights (Hamilton and Fukunaga 1970; Hamilton et al. 1981; Ito and Hamilton 1989). The cultivars 'Keauhou', 'Kakea', 'Ikaika', and 'Wailua' are considered to have good to excellent resistance to anthracnose (Hamilton and Storey 1956). 'Pahala' is considered to have moderate resistance (Hamilton et al. 1981).

Husk spot is considered a significant disease of macadamia in Australia, causing premature nut drop prior to completion of oil filling (Stephenson 1990a; Mayers 1991). There are no reliable figures for the economic impact of the disease, although some estimates range from 30% to 40% of crop loss. It is difficult to evaluate the accuracy of reported cultivar differences in disease susceptibility/tolerance without a clearer understanding of the relationship between disease severity and economic impact (Drenth 2004).

I. Stick-tights

Stick-tight nuts is a condition where the connective tissue between the stem and the fruit dies and nuts remain on the tree after the end of the harvest season until the husk rots and the old nuts fall (Nagao and Hirae 1992; Jones 2002). A link between stick-tights and high levels of pest and disease loads has been suggested (Jones and Caprio 1992; Jones et al. 1992, 1996), apart from the direct impact of crop loss. Absence or a very low occurrence of these nuts is preferred in Hawaiian (Hamilton and Ito 1984; Nagao and Hirae 1992; Jones 2002) and Australian (Stephenson and Gallagher 2000) selections. There is little information on the biology of this condition, and no studies have assessed the extent of stick-tights. A role for anthracnose has been suggested, but data are not available to establish this link.

Reports of differences among cultivars suggest a genetic basis for this trait (Table 1.5), although the apparent large variability within a cultivar also suggests an environmental component to variation. Cultivars that have been described as producing stick-tights are ‘Pahala’, ‘Kakea’, ‘Ikaika’ (Hamilton et al. 1981) ‘Own Choice’, and, to some extent ‘Hinde’ (Stephenson 1990a), although stick-tights have not been observed for ‘Own Choice’ in trials in China (Lu et al. 2004). A clearer understanding of the condition, how it can be objectively measured, and the impact on the production system are required to enable inclusion in selection decisions.

J. Nut Characteristics

1. Nut Size. Several nut characteristics have been considered as selection criteria in the development of macadamia germplasm. The Hawaiian program preferred cultivars that produced uniform medium-size nuts with 140 to 150 nuts per kg (6.5–7.0 g per nut) (Hamilton and Ito 1976, 1977b), although a wider range of nut size (130–190 nuts per kg) was considered acceptable in later selections (Hamilton and Ito

1984, 1986). The importance of nut size may be related to cracking efficiency, although this could be because crackers are designed for a particular size range, so that a higher frequency of damage may occur in consignments where the range of nut size is large (Liang 1980). Sorting prior to cracking, or an improvement in cracker technology, may reduce the importance of this trait. Based on commercial experience, it is also suggested that nuts smaller than 19 mm are difficult to handle, resulting in higher labor costs (Leverington 1958, 1962a, 1971; Gathungu and Likimani 1975).

Nut size has been found to be a highly heritable trait (individual broad sense heritability, $H = 0.63$), with little $G \times E$ across locations or ages (Hardner et al. 2001). A significant genetic correlation between nut and kernel mass is also reported. Others (Beaumont 1937) report a significant phenotypic correlation between nut size and kernel mass. High heritability of nut size is supported by field observations that seedlings germinated from seed selected for their small size produce a high proportion of small fruits (Gathungu and Likimani 1975). Cultivars with small nut sizes are 'HAES 814' (5.0 g), 'Keaau' (5.5–5.7 g), and 'NG18' (5.8 g); cultivars with large nuts include 'Own Venture' (8.1 g), 'A4' (7.1 g), 'Makai' (7.1 g), and 'Kau' (7.0–7.6 g) (Hamilton and Ito 1984; Stephenson et al. 1995). 'Purvis' is reported as having a average size nut (6.5 g) in Hawaii (Hamilton and Ito 1984), although in Australia this cultivar produces large nuts (7.2 g), similar in size to 'Makai' (Stephenson et al. 1995).

2. Nut Shape. Round nuts are considered easier to crack and grade than ovoid nuts (Leverington 1962a, 1971; Winterton 1968). Twin nuts, where two hemispherical nuts are formed, are considered rejects as they do not crack well (Cavaletto 1981). However, no studies quantify these characteristics or the impact of variation on costs of production. *M. tetraphylla* reportedly produces a higher frequency of ovoid nuts (Leverington 1958), but little is known of the extent of genetic variation within the species.

3. Nut Defects. Nuts that exhibit signs that the process of germination (i.e., opening of the suture in the shell) has commenced represent a source of crop loss, as the appearance and taste of germinating kernel is considered unacceptable, and the opening in the shell may permit entrance of disease organisms. Fruit may germinate on the tree or after the fruit has dropped to the ground, prior to harvesting. Germination in susceptible cultivars has been linked to the occurrence of wet weather; however, it has also been suggested that increased harvesting

frequency may minimize the occurrence of this defect (Hamilton and Ito 1984). A variability in nursery germination percent may be correlated with susceptibility to germination prior to harvesting (Hardner and McConchie 2006). Field experience suggests that 'Keaau', 'Pahala', and 'Beaumont' are prone to germination, particularly in wet weather (Hamilton and Ito 1984; Allan 1989; Ito and Hamilton 1989; Hardner and McConchie 2006).

Open microplyes are also considered unacceptable. At anthesis in macadamia, the nucellus is incompletely surrounded by the outer integuments, and a micropyle is formed 10 to 11 weeks later (Strohschen 1986). Usually a white enamel micopylar plug forms as the shell hardens (Francis 1928; Strohschen 1986); however, in some genotypes, the micropyle can be open at maturity (Stephenson 1990a; Nagao and Hirae 1992). This opening can allow entry of insects, molds, and moisture, thereby making the kernel unacceptable. It has been reported that 10% of nuts from 'Keauhou' may be affected by this defect (Stephenson 1990a).

4. Kernel Recovery. Kernel recovery, or kernel percent, is one of the easiest traits to assess and one of the most commonly reported. It can be defined simply as the percentage mass of nut that is the kernel (i.e., the embryo) and is used to calculate the expected mass of kernel from a given mass of nuts. Kernel recovery has a direct impact on the production system as fixed costs of production and processing per unit weight of kernel are lower with higher kernel recovery (Hardner et al. 2006). However, it has been suggested that cultivars with high kernel recovery have thinner shells, and, as discussed, thin-shelled cultivars are more susceptible to insect damage, preharvest germination, insect and rat damage, and kernel damage during cracking (Leverington 1958, 1962a, 1971; Gathungu and Likimani 1975).

The actual detail of how the trait is assessed, and therefore its meaning, may vary among studies. The mass of nuts may be wet NIS at field moisture (e.g., Ito et al. 1983; Nagao et al. 2003), 10% moisture content (e.g., Hardner et al. 2002), or NIS dried to 1.5% kernel moisture content (e.g., McCubbin and Lee 1996; Swanepoel and Hobson 1999). It has been reported (Leverington 1962a) that kernel recovery assessed from wet nuts may be higher than kernel recovery assessed after dehydration. Although the variability in assessment methods differences may affect absolute values, a study with 14 commercial cultivars indicated that the genetic correlation among kernel recovery calculated from wet NIS and NIS at 1.5% kernel moisture content is high (0.95) (Hardner et al. 2005b). In other studies, reject (e.g., mold and insect) nuts may be removed prior to assessment of nut mass (Leverington 1962a;

Stephenson 2000). Kernel recovery will tend to be higher in this case if reject nuts have a lower kernel recovery than the sample average.

The status of kernels included in numerator of the kernel recovery equation may also differ among studies. Some studies use the total mass of kernel (Stephenson et al. 1995; Hardner et al. 2001), while others (e.g., Leverington 1962a) remove unsound kernel, including those affected by insects, mold, or germination, prior to measurement of kernel mass, as these defects are not considered to be under genetic control. However, sound kernel recovery may not accurately represent kernel recovery in the absence of these defects, particularly if the levels of unsound kernel are high, as nuts containing unsound kernel are included in the denominator. Adherence of pieces of kernel to the inside of the shell after cracking may occur (Leverington 1958), and whether or not this is included in the assessment of kernel mass may affect how kernel recovery is calculated. Kernel recovery of 36% was recommended as the minimum for selecting cultivars in Australia (Stephenson and Gallagher 2000), while in Hawaii the selection threshold ranged between 34% (Cavaletto 1983), and 37% or 38% (Hamilton and Ito 1977b).

Several studies report higher kernel recovery of nuts collected from *M. tetraphylla* compared to *M. integrifolia*. In a sample of 94 selections from Australian orchards, the average kernel recovery for *M. tetraphylla* selections was 37% compared to 30% for *M. integrifolia* selections (Leverington 1962a, 1971). Saleeb et al. (1973) reported kernel recovery of 45% for *M. tetraphylla* and 39% for *M. integrifolia* selections and cultivars, some of which were a subset of the previous study. These authors also reported the shell of the nuts was significantly thinner in the middle and top for *M. tetraphylla* cultivars. Whether these results are affected by selection is difficult to determine.

Total kernel recovery was found to be highly heritable in a trial of 40 cultivars assessed over four sites in Australia analyzed using a mixed model approach ($H = 0.6$, Hardner et al. 2001). This study also observed no detectable $G \times E$ with site or age for kernel recovery. In contrast, a stability analysis (*sensu* Pritts and Luby 1990) with an extended data set (two additional sites) suggested the kernel recovery of some cultivars was unstable across sites and ages (Stephenson et al. 1999). The difference between these studies may be that the regression approach used in the stability analysis did not take into account the error of prediction of the cultivar mean.

To summarize and compare published kernel recovery for cultivars across a range of studies from Hawaii (Ito and Hamilton 1983; Ito et al. 1983; Ito and Hamilton 1989; Ito and Iyo 1992; Ito et al. 1998; Nagao

et al. 2003), Australia (Winks et al. 1987; Stephenson et al. 1999; Stephenson 2001), South Africa (Allan 1989; Oosthuizen et al. 1989; McCubbin and Lee 1996; Swanepoel and Hobson 1999), Brazil (Barbosa et al. 1991; Sacramento et al. 1995; Piza et al. 2006), Malawi (Phiri 1985), and China ((Xiao et al. 2002b), a REML analysis (as described earlier in this section on selection criteria) was undertaken. Sites across the different studies were grouped into locations for the analysis. Grouping of sites in Hawaiian studies was based on altitude, while the grouping of sites in other areas used geographical proximity. Countries were treated as fixed, and cultivar and location within country were treated as random. Data from multiple locations across multiple years enabled the construction of an error term to test the significance of location within country.

The overall mean of kernel recovery across the different studies was 35%. Kernel recovery differed significantly among country and studies but was highly heritable ($H = 0.6$), identical to that found in the previous Australian study. The interaction between cultivar and country or location within country was not significant, again confirming the results from the Australia study that the relative performance of cultivars across environments for kernel recovery is highly stable. This agrees with general observations that the characteristics of Australian selections introduced into Hawaii in the 1950s were similar in both countries (Hamilton and Fukunaga 1962). The significant effect of location within country indicates that cultivar means may be biased if all cultivars are not represented at each location and the analysis does not account for this imbalance.

There is reasonable separation of the predicted cultivar means from this analysis (Table 1.6); however, the precision of the test between the cultivars could be improved by increasing the representation of cultivars across countries. Kernel recoveries for ‘A4’, ‘HAES 849’, ‘HAES 816’, and ‘A16’ are significantly higher than most of the named Hawaiian cultivars (‘Purvis’, ‘Makai’, ‘Dennison’, ‘Kau’, ‘Keauhou’, and ‘Ikaika’). There are no significant differences among the named Hawaiian cultivars, except that the kernel recovery of ‘Pahala’ and ‘Keaau’ are significantly greater than that for ‘Kau’, ‘Keauhou’, and ‘Ikaika’. These results are in general agreement with published standards for these cultivars (Hamilton and Ito 1984), allowing for the difficulty in detecting significant differences in this analysis. Interestingly, ‘A4’, ‘A16’, and ‘Beaumont’, which have relatively high kernel recoveries, grouped in the hybrid clusters in the analysis of genetic diversity (Peace 2005), consistent with the expectation of high kernel recovery for *M. tetraphylla*.

Table 1.6. Predicted cultivar means across six countries for kernel recovery, percentage first grade kernel, kernel mass, and percentage whole kernels.

Cultivar	Kernel recovery (%)	1st grade (%)	Kernel mass (g)	Wholes (%)
A4	41.9	97	3.2	50
849	39.1	91	2.8	62
816	38.9	90	2.9	62
A16	38.1	94	2.9	60
814	37.9	92	1.9	46
Keaau	36.0	92	2.1	48
Pahala	36.0	93	2.3	51
Beaumont	35.9	95	2.3	44
NG18	35.8	92	2.4	63
Own Venture	34.9	92	2.9	58
Mauka	34.5	91	2.3	47
Kakea	34.2	91	2.2	–
Daddow	33.9	92	2.4	48
Purvis	33.7	93	2.6	60
Makai	33.4	95	2.5	57
835	32.1	94	2.2	68
Dennison	31.8	93	2.2	–
856	31.5	93	2.5	45
Kau	31.5	92	2.3	55
Keauhou	31.2	86	2.4	46
Ikaika	30.5	92	2.2	–
lsd (0.95)	4.0	7	0.4	10

Kernel recovery may also be correlated with other important selection traits. A significant correlation was found among phenotypic values reported for kernel recovery and shell thickness ($r = -0.70$) across 93 (mostly *M. tetraphylla*) preliminary selections from seedling orchards in Australia (Leverington 1962a). However, no correlation was found between kernel recovery and percentage insect (and mold) kernel damage ($r = 0.05$), although other studies have demonstrated a strong relationship between shell thickness and damage from *Hypothenemus obscurus* (see earlier discussion). There is also a moderate genetic correlation between kernel recovery and kernel mass.

K. Attributes of Kernel Quality

Kernel quality is considered an important selection objective in macadamia improvement (Cavaletto 1977, 1981; Hamilton and Ito 1984; Nagao and Hirae 1992; Gallagher et al. 1998; Hardner et al. 2006); however, its meaning can be vague and inconsistent. Quality can be

conceptually defined as the value judgment made by the consumer about a product based on available cues within the personal and situational context (Steenkamp 1990). The perception of quality by the consumer is a particularly important factor influencing food choice of luxury goods (Tsai 2005), such as macadamia. This perception may influence immediate purchase decisions, and reinforce product perceptions to support future purchase (Steenkamp 1990; Grunert 2002). In this review, kernel quality is taken to mean the combination of kernel attributes that influence consumer food choice and not a specific kernel attribute, as sometimes used in the literature (e.g., percentage first-grade kernel).

Different sectors of the macadamia supply chain impose quality standards on the product, although, generally, macadamia quality standards are determined by the perceived cues of consumer preference for the roasted snack food product (Cavaletto 1981). A plump, light golden whole kernel, with crisp texture and delicate fresh flavor, and free of visual imperfection, is considered to represent the highest quality of roasted snack product (Cavaletto 1981). However, the importance of different kernel quality attributes may vary with product, market, and consumer. Sensory attributes of odor, appearance, flavor, and texture play important roles in developing and reinforcing quality concepts for the consumer (Moskowitz 1995), although other attributes such as price and health benefits may also be important (Jaeger 2006).

1. Raw Kernel Visual Appearance. The visual appearance of raw kernel has been used as a major criterion of kernel quality in macadamia (Leverington 1962a; Cavaletto 1977; Shimabukuro 1984), presumably based on experience and perceptions that these correlate with the kernel quality of the final product, although there has been little explicit testing of this association. Attributes that give the kernel an appearance inconsistent with the assumed ideal kernel appearance may be regarded as imperfections, and hence of lower quality (Tsai 2005). In addition, the visual appearance of raw kernels may be used as a cue for other undesirable sensory experiences. In this context, a raw kernel that is plump, white to cream colored, and without visual defect is considered to produce roasted kernels with the highest quality (Winterton 1968; Leverington 1971; Hamilton and Ito 1977b; Trochoulias 1995).

A range of visual attributes are considered to impact on kernel quality. The presence of mold or insect-damaged kernel is obviously unacceptable from a food safety perspective (Leverington 1958, 1971). General discoloration of the kernel has been associated with deterioration on the orchard floor due to delayed harvesting (Liang et al. 1996). Other forms

of kernel discoloration, such as dark rings (also called onion rings, Swanepoel and Hobson 1999) and off-color (darkened) tops or bases, are also considered to be unacceptable (Cavaletto 1977, 1981; Hamilton and Ito 1977b; 1977, Simabukuro 1984). Alternatively, others (Leverington 1971) suggested that a light gray base in raw kernel may not be objectionable, if it was subsequently masked by the roasting treatment. However, it is unclear if basal discoloration is defined by the absolute color of the base or relative to the overall color of the kernel, which may also be variable. It has been suggested that the basal discoloration may be the result of absorption of tannins from the shell (Leverington 1971). In some seasons, 'Mauka' may produce some level of discolored kernel (Stephenson 1990a). The occurrence of overall gray discoloration of kernel has been reported and linked with the infection by the bacteria *Enterobacter cloacae* in kernels at field moisture content and the production of off flavor and odors that can spoil entire batches (Nishijima et al. 2007).

The appearance of a yellow, brown, orange, or green strip on the kernel apex following drying is described and attributed to germination (Leverington 1962a, 1971; Guthrie et al. 2004). Nuts exhibiting open cracks in the shell typical of germination generally are removed prior to cracking. It is unknown if, at what level, and when undesirable textures and tastes develop throughout the progress of germination, although cyanogenic glucosides, which impart a bitter taste, are elevated in *M. integrifolia* and *M. tetraphylla* kernels that have commenced germination (Dahler et al. 1995).

Small kernels with a shriveled and deformed appearance have been reported, and this is considered to be due to low oil content of the kernel (immaturity) (Ripperton et al. 1938; Leverington 1962a; Cavaletto 1977; Himsteadt 2002; Guthrie et al. 2004). Shriveled kernel can be a visual cue that the kernel may be susceptible to overroasting and have an objectionably hard texture, conditions commonly associated with low-oil-content kernels. The oil content, mass, and size of kernel classified as shriveled was significantly lower (46%, 1.3 g, 11 mm) compared to kernel classified as sound (76%, 2.4 g, 14 mm), although the oil content of some kernel classified as shriveled was near what would be expected to produce acceptable roasted product (70%) (Ripperton et al. 1938; Mason and Wells 1984). The adherence of the dark lining of the inner shell to the kernel, or of kernel to the inside of the shell, is also considered unacceptable (Leverington 1958, 1962a). Physical damage to raw kernels can be considered to detract from the quality of the product and has been reported to lead to undesirable localized browning of the kernel (Wallace et al. 2001).

Increases in the levels of raw kernel with visual imperfections result in increased sorting costs and increased fixed costs of production per unit mass of acceptable kernel (Hardner et al. 2006). This assumes that all kernels with visual imperfections are rejected; however, kernels with minor degrees of visual imperfections may only be downgraded for use in products that do not demand high visual quality.

There is little information on the genetic architecture of visual kernel disorders. This may be due in part to the problems of applying repeatable and objective assessment methods. Most disorders require visual assessment. Human sensory assessments are prone to bias and can be variable if these are not conducted with a controlled and structured approach (Sidel and Stone 1991; Meilgaard et al. 1999). Often thresholds are used to define reject, unsound, commercial, or sound kernel (e.g. Cavaletto 1981; Liang et al. 1996; Swanepoel and Hobson 1999; Stephenson 2000), but description of these thresholds is generally not given or is simply referenced as ''standard commercial practice'' (e.g., Liang et al. 1996; Swanepoel and Hobson 1999), making comparison among studies difficult. While grades are useful to facilitate the flow of information among different sectors, any classification scheme is dependent on the ability to measure the attribute. Greater accuracy and hence ability to manage is achieved by replacing subjective assessment methods with those that are based on objective measures (Erickson 1994). NIR (near-infrared) technology has successfully been applied to the discrimination of nonreject kernels from kernels that were classified as immature, discolored, insect damaged, and moldy, but was not able to differentiate among other disorder classes (Guthrie et al. 2004) and was not tested against kernels with less severe forms of these disorders. Refinements of instrumental methods eventually may provide an objective means for assessment of kernel visual imperfections. The lack of repeatable assessment methods means that only general observations of differences among cultivars developed by familiarity with the product have been reported. Kernels produced by *M. tetraphylla* genotypes reportedly tend to be darker with a grayish base compared with *M. integrifolia*, which tends to be white (Leverington 1958). Cultivars that have been noted as having discolored base include 'Ikaika' (Winks 1983) and 'HAES 849' (Stephenson and Gallagher 2000). As discussed, genetic variation in germinability under nursery conditions may indicate a genetic basis to the occurrence of visual germination disorders of the kernel (Hardner and McConchie 2006). Differences in the proportion of kernel that were shriveled among samples taken from seedling selections have been attributed to genetic variation (Leverington

1962a); however, the timing of collection of these samples is unknown, as is the relative size of nongenetic effects for these attributes.

Significant differences among cultivars for gray kernel discoloration (linked to *Enterobacter cloacae* infection) have been reported (Nishijima et al. 2007) with 'Keauhou' having the lowest incidence of gray kernel discoloration compared to 'Kau' and 'Kakea' in nuts sampled from two Hawaiian orchards and inoculated in the laboratory. This, however, is in contrast to field observations that gray discoloration occurs at a higher frequency in commercial kernels from 'Keauhou' (Nishijima et al. 2007). Further research is require to develop an understanding of the relationship between variability in biological characteristics that may affect susceptibility to infection, such as physical nut structure and phenology, and the inheritance of these characteristics.

General terms have been used to describe raw kernel quality of individual cultivars. Stephenson and Gallagher (2000) describe 'A4' as attractive; 'Daddow', 'A16', and 'HAES 814' as good color; 'Keaau', 'Mauka', and 'HAES 781' as cream to beige in color; 'Keauhou', 'HAES 842', and 'HAES 816' as variable; 'HAES 849' as beige to light brown; and 'Kau' as darker than the other kernels. This is similar to descriptions by Winks (1983) for 'Keaau' (excellent) and 'Daddow' (excellent) and 'Keauhou' (good). Bell and Bell (1987) also describe the appearance of 'A16' and 'A4' as good along with that of 'A268', and they considered 'A199' excellent. However, it is difficult to use these observations for selection, as they depend on the preferences of the observers, which may not be consistent across studies.

Some studies report measures of percentage unsound kernel (e.g., Swanepoel and Hobson 1999; Stephenson 2000; Stephenson and Gallagher 2000). While this is an attempt to quantify the extent of kernel quality, it includes all forms of quality disorders. However, the heritability of an aggregated trait will be low, unless all traits are highly correlated genetically. A low heritability means apparent differences between candidates are due to nongenetic variation that genetic selection cannot exploit. Clearly more work is required to develop objective and repeatable methods to assess of attributes of the visual appearance of raw kernel and determine their genetic basis.

2. Oil Content and Percentage First-Grade Kernel. A relationship between the oil content (as assessed by specific gravity) of raw *M. integrifolia* kernels and the acceptability of oil-roasted kernels has been established (Ripperton et al. 1938; Mason and Wills 1983) and applied as a selection criterion in macadamia improvement (Hamilton and Ito 1984; Stephenson et al. 1999). Initial studies by Ripperton et al.

(1938) demonstrated that raw *M. integrifolia* kernels less than 1.000 g/g specific gravity (SG) (estimated oil content of 72%) were light golden in color, with a mild nutty flavor and crisp texture, and considered the most acceptable when (presumably oil) roasted. These were classified as first-grade kernels. Kernels between 1.000 and 1.025 g/g SG (estimated oil content of 72%–68% oil) were described as having tendency to be somewhat dark in color, with off flavors and a spongy texture, and were considered suitable only for confectionary or bakery products (second-grade kernel). Raw kernels higher than 1.025 g/g SG were small in size, with a shriveled base and hard texture, and on roasting became very dark with an unpleasant burned flavor. These were considered acceptable only for oil products (third grade). First-grade kernel is also referred to as No. 1 kernel (Ito and Hamilton 1980; Allan et al. 1999) or floaters (Ito et al. 1998). These relationships were confirmed by a later study using a hedonic sensory panel with kernels taken from two ground harvests of 'Keauhou' throughout the Australian season (Mason and Wills 1983).

However, a reanalysis of the data for kernel oil content by specific gravity presented in two studies indicates that the relationship between oil content and specific gravity is not consistent across the four different sets of kernels (*M. integrifolia* —Ripperton et al. 1938; *M. tetraphylla*—Ripperton et al. 1938; 'Keauhou' harvest 1—Mason and Wells 1983; 'Keauhou' harvest 2—Mason and Wells 1983). The intercept of the linear regression is significant lower for the 'Keauhou'—harvest 2 (256.8) compared to the *M. tetraphylla* data (304.1), and the 'Keauhou'—harvest 1 (285.7) and the *M. integrifolia* data (285.6) are intermediate and not significantly different from the other intercepts. The slope of the 'Keauhou'—harvest 2 regression (−182.3) is significantly less negative than the other regressions ('Keauhou' harvest 1 = −209.7; *M. integrifolia* = −213.5; *M. tetraphylla* −231.3). The consequence of these results is that predicted oil content of kernels at SG=1.000 differs significantly among the different sets of kernel being 76.0% for the 'Keauhou'—harvest 1 regression, 74.5% for the 'Keauhou'—harvest 2 regression, 72.8% for the *M. tetraphylla* regression, and 72.1% for the *M. integrifolia* regression. This means, for example, that if the *M. integrifolia* regression is applied to the kernels from the first harvest of 'Keauhou' in Australia, kernels with an actual oil content between 72 and 76% would be predicted to have an oil content below 72%.

The most common method used to describe the level of first-grade kernel for selection is the percentage of kernel that are above SG = 1.000 (percentage of first-grade kernel). It is usually determined as the percentage mass of kernels that float in water (Ripperton et al. 1938;

Cavaletto 1981; Mason and Wills 1983). In some studies (e.g., Swanepoel and Hobson 1999), all kernel is included in the sample for assessment of percentage first-grade kernel, while in other studies (e.g., Leverington 1962a), spoiled kernel, such as insect damaged or moldy kernel, are removed prior to evaluation. Timing of sampling may also have important implications for estimation of percentage first-grade kernel. For example, percentage of first-grade kernel has been assessed in some cases using samples taken at peak fruit drop (e.g., Leverington 1962a; Stephenson et al. 1995). However, this may overestimate the percentage of first-grade kernel, if the crop is collected over the entire fruit drop season and includes kernel near the start of the season, where oil content may be more variable (Ito and Hamilton 1983; Ironside 1987). A threshold of 95% percentage of first-grade kernel is used as a standard for cultivar recommendation (Hamilton and Ito 1986; Ito 1995; Stephenson and Gallagher 2000). In addition, cultivars that have a stable production of first-grade kernel across different environments are considered particularly valuable under the highly variable Australian growing conditions (Stephenson et al. 1995).

This review highlights the uncertainties of using percentage of first-grade kernel as a selection criterion. First, the relationships between kernel quality and oil content were established using oil roasting; however, the response of kernels under oil roasting may not be the same as under air roasting. Lighter air roasting can be used to manage some roasting disorders (Cull 1978; Mason 1987), particularly if the target consumers do not have a strong preference for darker-roasted kernels (e.g., O'Riordan et al. 2005). Second, the significant variability in the relationship between specific gravity and oil content among kernel samples discussed suggests the percentage of first-grade kernel may not be accurate at differentiating between the potential of genotypes to produce high-quality roasted product. Finally, a relationship between roasting response and oil content does not confirm variability in oil content as the causal factor, as it may be a surrogate for another correlated compound that is directly involved in the roasting reactions.

There is conflicting evidence for a difference in oil content between *M. tetraphylla* and *M. integrifolia*. No significant difference in percentage of oil content of a range of kernels sampled from open-pollinated progeny of the two species was found when determined directly through extraction (Saleeb et al. 1973), although the SG of the *M. tetraphylla* was lower, in agreement with the regression analysis presented earlier. In contrast, a lower oil content for *M. tetraphylla* is reported by Winterton (1968), although it is unknown if this was

determined by applying the *M. integrifolia* regression to *M. tetraphylla*, which, as demonstrated, would predict a lower percentage of first-grade kernel for *M. tetraphylla*. In addition, Leverington (1971) reports a larger variability in percentage of first-grade kernel among *M. tetraphylla* genotypes, suggesting that the nuts had been collected prior to the completion of oil accumulation (Cameron McConchie pers. comm.). Studies of oil accumulation in macadamia (Jones 1937, 1939; Baigent 1983; McConchie et al. 1996; Trueman et al. 2000) have been undertaken using seed collected from *M. integrifolia* seedlings and cultivars, but little is known of the oil accumulation pattern in *M. tetraphylla*. Differences in oil profile between the two species have also been reported with percentage of the unsaturated oleic (18:1) and eicosenoic (20:1) fatty acids significantly higher in kernels from *M. integrifolia*, while levels of stearic (18:0) and arachidic (20:4) fatty acids were lower (Saleeb et al. 1973).

Percentage of first-grade kernel is under weak genetic control ($H = 0.2$) compared to other nut and kernel traits in a study of 40 cultivars planted at four locations in Australia (Hardner et al. 2001). This is in agreement with the results from a REML analysis undertaken across a range of published cultivar values: Australia (Winks et al. 1987; Stephenson et al. 1999; Stephenson 2001), Hawaii (Ito and Hamilton 1983, 1989; Ito et al. 1983, 1998; Nagao et al. 2003), South Africa (Allan 1989; Swanepoel and Hobson 1999), Brazil (Sacramento et al. 1995) ($H = 0.16$). The average first-grade kernel across all studies was 92%. First-grade kernel differed significantly among countries, studies, and locations. In contrast to the smaller Australian study, the REML analysis indicates the ranking of cultivars for first-grade kernel is sensitive to environmental variation. A stability analysis with an extended data set of the Australian study (two additional sites, Stephenson et al. 1995) also suggested cultivars with low overall percentage of first-grade kernel were more sensitive to environmental variation. Sensitivity of first-grade kernel to environmental variation, particularly to temperature, water deficit, and management practices, has been suggested in other studies (Radspinner 1970;. Stephenson and Gallagher 1986; Allan 1989; Supamatee et al. 1992; Stephenson and Trochoulias 1994; Stephenson et al. 2000; Stephenson 2003).

The limited separation of cultivar means from the REML analysis (Table 1.6) is a consequence of the low heritability of the trait and the presence of a sizable $G \times E$ component of variation. 'A4' is the highest ranked cultivar for percentage first-grade kernel and is significantly different from all named Hawaiian cultivars except 'Makai', which has been described as producing high-quality kernel (Hamilton and Ito 1984).

'Keauhou' is the lowest-ranked cultivar for first-grade kernel, in agreement with previous observations (Hamilton and Ito 1984), although it is only significantly different from 'Makai' and 'A4'. ''Cultivar'' means for percentage of first-grade kernel were only weakly correlated with those for average nut mass ($r_g = 0.40, P > 0.01$), but the correlation with kernel recovery was not significant (Hardner et al. 2001). These results are confirmed by the REML analysis undertaken here ($r_{cv} = 0.17$).

Recovery of first-grade kernel, which is the ratio of first-grade kernel mass to nut mass, is reported by some studies instead of percentage of first-grade kernel (Supamatee et al. 1992; Ito and Iyo 1992; Ito 1995). A cross-study REML analysis undertaken of these values, and values calculated from the previous studies that report both kernel recovery and percentage of first-grade kernel, indicates that the genetic control of this trait was intermediate to these two traits ($H = 0.36$). The presence of interactions of cultivar with country and cultivar with location in this analysis agrees with previous reports of $G \times E$ for this trait (Ito 1995). It appears that variation in kernel recovery is the main driver of differences in first-grade kernel recovery among cultivars as the correlation between these two traits is close to unity ($r_{cv} = 0.98$); the correlation with percentage of first-grade kernel and first-grade kernel recovery is lower ($r_{cv} = 0.48$).

3. Kernel Size. Kernel size is a commonly reported character of cultivars, but the importance of its role in selection is unclear. Sorting costs may be greater with smaller kernel (Leverington 1962a; Winterton 1968; Hardner et al. 2006), and small kernels may be more susceptible to cracker damage (Leverington 1962a, 1971) and overroasting (Storey and Kemper 1960). Kernels less than 1.5 g are considered too small for processing (Supamatee et al. 1992). It has been suggested, however, that large kernels may be prone to underroasting due to incomplete heat penetration to the center (Leverington 1962a; Winterton 1968). Data are not provided to support this hypothesis, and it may be possible to avoid underroasting through modification of the roasting process. It has also been suggested kernels greater than 3.5 g are too large for packaging in cans and bottles (Supamatee et al. 1992).

Kernel size in part defines different raw kernel styles, which differ in value (Hardner et al. 2006) and may be important for marketing; the suggestion is that a few large kernels in a packet are less attractive than a large number of smaller kernels (Leverington 1962a, 1971). Large kernels were favored when consumers were surveyed for their preferences for individual kernels (O'Riordan et al. 2005), but this may not be the same as size preferences when a given mass of kernel is examined (Cameron

McConchie pers. comm.). The ideal size of kernels for commercial use is reportedly 18 to 22 mm in diameter and 2 to 3 g in mass (Leverington 1962a, 1971; Supamatee et al. 1992; Ito 1995).

Saleeb et al. (1973) found no significance difference in size of kernels collected from *M. tetraphylla* and *M. integrifolia* cultivars. However, this result may not represent the natural variability between the two species, as kernel size is highly heritable and was probably included in the selection history for these cultivars.

Average kernel mass is commonly used to describe kernel size. Mass is easier to measure than kernel size, and there is a strong phenotypic correlation between these two traits (Beaumont 1937). Average kernel mass usually is measured by weighing a sample of kernel and dividing this mass by the number of kernels present in the sample. However, as a significant relationship between kernel size and oil content has been established (Mason and Wills 1983), average kernel mass may be biased downward if immature kernels are present in the sample.

Average kernel size has been reported in all the studies listed earlier for kernel and first-grade kernel recovery (except Ito et al. 1983). Again, the results of a REML analysis of the data in these studies are consistent with other studies that report high heritability ($H = 0.6$), limited $G \times E$ (Hardner et al. 2001), and moderate correlation with kernel recovery ($r_{cv} = 0.48$ in Hardner et al. 2001; $r_{cv} = 0.67$ across the 17 studies included in the REML analysis) (Table 1.6). The low $G \times E$ found in these analyses contradicts suggestions by others (Ito 1995) that cultivars should be selected for specific sites with respect to kernel size.

The named Hawaiian cultivars tend to have smaller kernels. There is no significant difference among these cultivars except that 'Keaau' kernels are on average smaller than 'Purvis' (Table 1.6). The cultivars 'A4', 'HAES 816', Own Venture', and 'A16' have significantly larger kernels on average than all the named Hawaiian cultivars except 'Purvis' and 'Makai'.

4. Percentage of Whole Kernels. At cracking, and possibly after, some macadamia kernels split along the line that separates the two cotyledons, producing half kernels. The percentage of whole kernels can influence kernel value as this trait partially defines product styles that vary in price (Wallace et al. 2001; Walton and Wallace 2005; Hardner et al. 2006). In addition, particular market segments may prefer whole kernels (Hardner et al. 2001). In contrast, some earlier authors did not consider the production of halves to be a disadvantage (Leverington 1971).

Percentage of whole kernels is generally assessed by measuring the mass of kernels in a sample that are whole after cracking (Stephenson 2000). A moderate heritability for this trait has been reported ($H = 0.3$, Hardner et al. 2001), while a reduced REML analysis of the limited number of studies that report percentage whole kernel (Barbosa et al. 1991; Swanepoel and Hobson 1999; Stephenson et al. 1999; Stephenson 2001; Nagao et al. 2003; Walton and Wallace 2005) indicates a strong genetic control for this trait ($H = 0.8$). Differences in cuticular structure at the break zone between the two cotyledons were observed between 'HAES 835' and 'Mauka' and related to differences in percentage of whole kernel (Walton and Wallace 2005). Narrow cuticles, denser and more numerous electron-dense objects (possible storage protein bodies), and less cuticle convolutions were associated with a higher percentage of whole kernels. Further work is required to confirm this association over more genotypes.

The percentage of whole kernel may be affected by the use of different crackers (Rodrigues et al. 1998; and to some extent Wallace et al. 2001); however, little is known about the interaction between cultivar and cracker. Small differences in percentage of whole kernels among crackers were reported for a sample of 'A38' nuts, but there were no differences in a sample of 'Keauhou', and differences between cultivars was much larger than differences between crackers (Wallace et al. 2001). While it is suggested that genetic variation for nut size may result in genetic variation for percentage of whole kernels, as differences in nut size may affect cracker efficiency (Liang 1980; Tang et al. 1982), there is no genetic correlation between these two traits (Hardner et al. 2001).

Cultivar means for percentage of whole kernels are not correlated with kernel recovery ($r_{cv} = 0.1$), percentage of first-grade kernel ($r_{cv} = 0.1$), or average kernel mass ($r_{cv} = 0.3$) (Table 1.6), consistent with previous studies (Hardner et al. 2002). Across a range of studies, 'HAES 835', 'NG18', 'HAES 816', 'HAES 849', 'Purvis', 'A16', Own Venture', and 'Makai' produced significantly more wholes than 'Keauhou', 'HAES 814', 'HAES 856', and 'Beaumont' (Table 1.6).

5. Bitter Kernels. Rarely, seedlings arise that produce bitter kernels due to elevated levels of cyanogenic glucosides (Dedolph and Hamilton 1959; Young and Hamilton 1966), which also occur in *M. ternifolia* (Dahler et al. 1995). Production of bitter kernels in grafted scions taken from seedlings known to produce bitter kernels confirms the genetic control of this attribute (Young and Hamilton 1966). Interspecific controlled crossings have indicated that the gene action is recessive (Hardner et al. 2000).

6. Quality Attributes of Roasted Kernel. Roasting improves the odor, appearance, texture, and flavor of macadamias (O'Riordan et al. 2005). Roasting can be undertaken either by immersion in oil (Moltzau and Ripperton 1939; Mason et al. 1995) or using dry air (Winterton 1962; Wesley et al. 2007), although there is little information relating the effect of different treatments under these two methods. It has been suggested that optimum kernel quality is achieved by roasting in oil at 127°C for 15 minutes; lighter roasting produces less desirable kernel (Dela Cruz et al. 1966). Direct testing of Australian consumers found no significant difference in overall liking among four air-roasting treatments (135°C, 12 min; 135°C, 18 min; 155°C, 5 min; 155°C, 8 min). However, consumers preferred the appearance of lighter-roasted kernels over that for medium-roasted kernels, but the odor and flavour of medium-roasted kernels (O'riordan et al. 2005).

Overall kernel color is the most common attribute used to describe the quality of roasted macadamia kernel. In addition, defects such as localized or an extreme darkening of the kernel may become apparent after roasting, commonly referred to as after-roasting darkening (ARD) (Cavaletto 1980; Albertson et al. 2006). Internal browning of kernels also can occur following roasting, if high initial temperatures are used to dry nuts that have a high moisture content, although this defect also may occur simply following particular unfavorable drying conditions (Prichavudhi and Yamamoto 1965). Kernel color usually is assessed as time to reach a desired level of color as judged by an operator (Isaacs et al. 1998) or the color after a defined roasting treatment assessed using color cards, flatbed scanners, or a Minolta color meter (Lemmer et al. 1998; Albertson et al. 2005; McConchie et al. 2007a; Wall and Gentry 2007). Roasted kernels may be allocated to different products, with light-colored kernels used for snack food, darker kernels tending to be used in confectionary and chopped nut products, and very dark kernels rejected (Leverington 1971), although this may depend on market preferences.

A number of authors report observations of a difference in quality of roasted kernel between the two species (Moltzau and Ripperton 1939; Leverington 1958, 1962a, 1971; Cavaletto 1980, 1983). Raw kernels of *M. integrifolia* are described as being light in color that changes to golden brown on roasting, while the roasted color of *M. tetraphylla* is considered more variable with kernels browning faster on roasting. Roasted *M. tetraphylla* kernels are also reportedly firmer and harder in texture, with a sweeter but variable flavor, in contrast to the crisp and delicate texture and mild and uniform flavor reported for roasted *M. integrifolia* kernels

(Leverington 1971). These observations have been used to recommend that the two species should be separated for processing (Winterton 1968; Leverington 1971; Cavaletto 1983) and that *M. tetraphylla* kernels should be oil-roasted at a lower temperature to avoid charring (Moltzau and Ripperton 1939; Leverington 1971). The development of the industry has concentrated on *M. integrifolia* germplasm, partly on the basis of these results, although a preference for *M. tetraphylla* kernels has been reported (Ripperton et al. 1938; Leverington 1963; Gathungu and Likimani 1975).

The difference in roasting performance between the two species has been attributed to a higher sugar content of *M. tetraphylla* (6–8%) compared to *M. integrifolia* (4%) (Winterton 1968; Cavaletto 1980, 1983) Amino acids have been implicated in the roasting process in macadamia (Albertson et al. 2006), and a significantly higher absolute content for *M. integrifolia* has been reported, although there is virtually no difference in amino acid profile (Saleeb et al. 1973).

A recent study, however, has suggested that more detailed reconsideration of the *M. tetraphylla* germplasm is warranted (McConchie et al. 2007c). Although these authors found significant differences for change in color with roasting among three *M. integrifolia* cultivars, a hybrid cultivar, and five accessions *M. tetraphylla* from the wild, differences could not be grouped on the basis of species status, except at extreme roast conditions that would not be commercially acceptable. In addition, the authors report no significant difference in sucrose content between the different germplasm types and very low overall levels of reducing sugars. A more thorough analysis using germplasm sampled from the wild is warranted to fully characterize species differences.

Several other studies report differences among cultivars in the appearance of roasted kernels (Isaacs et al. 1998; Lemmer et al. 1998; McDonagh 2003; McConchie et al. 2007d; Wall and Gentry 2007) and further demonstrate the difficulty of determining roasting quality from species status. A generalized linear model analysis was undertaken of the means presented in Isaacs et al. (1998) for percentage of roasting rejects and roasting time for eight cultivars ('A16', 'A4', 'Mauka', 'Makai', 'Hinde', 'Heilscher', 'Keauhou', and 'Kau') stored under five conditions and oil roasted to a standard color. Percentage roasting rejects were significantly greater for 'A16' (7.3%—hybrid) and 'Keauhou' (5.9%—*M. integrifolia*) compared to 'A4' (3.5%—hybrid) and 'Heilscher' (0.6%—*M. integrifolia*), with 'Mauka' (5.6%—*M. integrifolia*), 'Makai' (4.7%—*M. integrifolia*), 'Hinde' (4.5%—*M. integrifolia*), and 'Kau' (4.1%—*M. integrifolia*) intermediate. However, results for roasting time from this study appear to be biased

as there is a significant correlation with appearance (as judged by a hedonic sensory panel) and roasting, which would be not expected if the treatment of roasting to a standard color was applied without bias. The correlation among cultivar means for roasting rejects and appearance preference was not significant.

The sensitivity of 'Keauhou' to roasting has been noted in other studies. Using a color chart to assess differences in color, the cultivars 'Keauhou', 'Pahala', and 'Kakea' were reported as being more variable in color and darker than 'Mauka' and 'Fuji' when oil or dry roasted to a common time (Lemmer et al. 1998). The visual response of cultivars considered hybrids ('Nelmak 1', 'Nelmak 2', 'Nelmak 26', and 'Beaumont') was similar to that of 'Keauhou', and 'Kakea'. In a separate study (McDonagh 2003), 'Keauhou' was consistently darker (as assessed using color density calculated from a scanned image) than 'A38' and 'A16' when roasted under a range of times and temperatures. This is supported in a more recent and comprehensive study (McConchie 2006b) that found roasted 'Kau' and 'Keauhou' kernels were significantly darker (as assessed using color meter) than kernels from 'HEAS 849' and 'A16'. This study also found significant differences among cultivars for preroast (raw) color and the change in color with roasting, although it is difficult to determine if this is correlated with preroast color. Further work is required to determine if post-roast color can be managed through sorting based on raw kernel color. Significant cultivar differences in darkening after extreme roasting conditions have been reported (Albertson et al. 2005), with 'Own Venture' exhibiting less extreme reaction than the other cultivars examined ('A16' and 'HAES 814'). No significant differences in reducing sugar content and internal color of kernels after were found among 'Kakea', 'Keauhou', 'Kau', and 'Keaau' (Wall and Gentry 2007).

There is conflicting evidence on the significance of genetic variation for other sensory attributes in macadamia. Although a thorough descriptive sensory analysis of macadamia using a trained sensory panel found significant differences in odor, flavor, aftertaste, and texture of roasted kernels between air roasting and aging treatments, no significant effect of source, which encompassed a range of cultivar, geographic, and management variability in Australia, was found (O'Riordan et al. 2005). This supports suggestions that only minor flavor differences among cultivars exist (Cavaletto 1983). Significant differences in texture preference were also not found among eight cultivars assessed by a hedonic sensory panel (Isaacs et al. 1998), following an analysis of the published means. In contrast, a REML analysis of means for texture

preference assessed by a hedonic panel presented in Gallagher et al. (1998) for a larger study of kernels from 18 cultivars stored at different conditions both prior to and post roasting (assumed to oil roasting to specific color), indicated significant differences among cultivars. Significant differences among cultivars for flavor preference were also apparent following a REML analysis of means presented in both studies (Gallagher et al. 1998; Isaacs et al. 1998). The analysis of the larger study data also indicated that raw cultivar means for texture and flavor preferences were significantly correlated with preferences for roasted kernels (texture: $r_{cv} = 0.85$; flavor: $r_{cv} = 0.87$).

The texture of 'HAES 816', 'HAES 849', and 'Own Venture' were significantly preferred in the larger study over kernels from 'Keauhou', 'A4', 'HAES 842', 'Daddow', 'HEAS 814', 'A16', 'Kau', 'Mauka', and 'Keaau', which produced the least preferred kernel, although there were no significant differences in texture among eight cultivars (which included 'A4', 'A16', 'Kau' 'Keauhou', and Mauka') in the smaller roasting study (Isaacs et al. 1998). Flavor of roasted kernels from 'Mauka', 'Keaau', 'HAES 849', 'HAES 816', 'HAES 781', 'Keauhou', and 'NG13' were significantly preferred over the flavor of 'NG18', 'HAES 842', 'Daddow', 'A16', and 'A4' in Gallagher et al. (1998). The ranking of 'Keauhou', 'Kau', 'A16', and 'A4' was similar in the smaller study (Isaacs et al. 1998), although the preference for 'Mauka' was inconsistent, as it was the least favored in the smaller study. While not tested in the larger study, kernel from 'Makai' was the most preferred for flavor in Isaacs et al. (1998). There was no correlation among cultivar means for texture and flavor preferences in Gallagher et al. (1998) ($r_{cv} = 0.2$). However, it is difficult to compare results from across hedonic studies and relate these to consumer preferences (Mialon and Murray 2001).

Attempts have been made to use a single measure to describe differences in kernel quality among cultivars (Hamilton and Ito 1984; Gallagher et al. 1998; Nagao et al. 2003). There were significant differences among cultivars in overall quality preference from a hedonic sensory assessment when cultivar means presented in Gallagher et al. (1998) were analyzed using the REML approach. Cultivar means were not correlated with preferences for flavor preferences ($r_{cv} = 0.34$), and the correlation with texture preferences was only slightly significant ($r_{cv} = 0.50$). Preference for the quality of 'HAES 849' and 'HAES 816' kernels was significantly higher than for 'Kau', 'A16', 'Keaau', and 'A4'. However, these measures suffer from the deficiencies of the hedonic sensory approach discussed earlier in that they may not predict well the preferences of target markets or consumers in general.

The quality of roasted kernel have been described using general terms from ''fair'' to ''excellent'' (Hamilton and Fukunaga 1970, 1973; Hamilton and Ito 1976, 1986; Hamilton 1984) or using kernel rating system (1 = fair to 4 = excellent) (Hamilton and et al. 1981; Hamilton and Ito 1986; Nagao et al. 2003). The quality of 'Pahala' is described as 3.6 or ''excellent'' in comparison with 'Purvis' (3.4) and 'Keauhou' (2.9) (Hamilton et al. 1981). In a separate study (Nagao et al. 2003), the kernel quality rating of 'Makai' was also high (3.5 compared to 3.3 for 'Pahala'). 'HAES 849' had the lowest quality of cooked kernels (3.1), but this does include 'Keauhou'. The cooked quality of 'Makai' has also been described as ''excellent'' in other studies (Hamilton and Fukunaga 1973; Hamilton and Ito 1984, 1986). Other cultivars considered to produce kernels with ''excellent'' cooked quality include 'Keaau', 'Mauka', 'Dennison' (Hamilton and Fukunaga 1970, 1973; Hamilton and Ito 1976, 1984, 1986). The kernel quality of 'Kau' was considered ''excellent'' by some (Hamilton and Fukunaga 1973; Hamilton and Ito 1976) but dropped to ''very good'' in Hamilton and Ito (1984 and 1986). 'Purvis' was also considered ''very good'' by Hamilton (1984) but ''excellent'' two years later by Hamilton and Ito (1986). The reported quality of 'Kakea' was variable from ''fair'' in Hamilton and Fukunaga (1970), to ''good'' (Hamilton and Fukunaga 1973), ''very good'' (Hamilton and Ito 1976), and ''excellent'' (Hamilton and Ito 1984, 1986). Cooked kernel from 'Ikaika' was consistently considered ''fair.'' Again, these terms are subjective and difficult to compare across studies and use for selection, particularly if trade-offs are required among several traits.

7. Shelf Life. The quality of roasted kernels may be compromised by the development of unpleasant flavors due to changes in chemical composition of the kernel with age (rancidity) (Himsteadt 2002; O'Riordan et al. 2005), despite the fact that the extracted oil of macadamia being highly resistant to rancidity (Saleeb et al. 1973). The storage life of roasted *M. integrifolia* kernels is considered to be longer than for *M. tetraphylla* (Leverington 1958, 1962a). It is suggested that the poorer shelf life of *M. tetraphylla* kernels is a consequence of undercooking, as kernels from this species may be roasted using lighter conditions in an attempt to manage their perceived sensitivity to roasting. However, this hypothesis has not been confirmed in later trials (Mason et al. 1995).

Free-fatty acids and peroxide values have been used as measures of the level of rancidity in macadamia kernels, although these measures may not correlate well with sensory perceptions of rancidity or

staleness (Frankel 1998; Himsteadt 2002; Mason et al. 2004). Maximum values in industry guidelines are 0.5% and 3 to 5 meq/kg respectively (Mason et al. 2004). Season, kernel size, and processing method were found to have greater influences on peroxide values compared to the species type of a cultivar (pure *M. integrifolia* versus hybrid) (Luttig and Kruger 1999). In contrast, the effect of cultivar was highly significant effect (free-fatty acid $Pr(F) < 0.001$; peroxide values $Pr(F) = 0.009$) when the means of the storage-roasting trial of eight cultivars (Isaacs et al. 1998) were reanalyzed. However, the lack of significant interaction with cultivar and storage treatment suggests that differences among the cultivar samples prior to storage were maintained throughout the trial.

Although scant, published evidence does not support a genetic basis in macadamia of susceptibility to rancidity. No significant effect of source (representing different cultivars from different farms), or a interaction between source and aging treatment, was detected on sensory perception of rancidity (O'Riordan et al. 2005). In addition, no significant difference was detected among the flavor preference of three cultivars ('Ikaika', 'Keauhou', and 'Kakea') following storage (Dela Cruz et al. 1966). Further, the REML analysis of the hedonic studies already outlined (Gallagher et al. 1998; Isaacs et al. 1998) found no significant interaction between cultivar and storage treatment for hedonic preference, indicating that all cultivars respond the same way to aging. It has been suggested that genetic variability in the profile of antioxidants could be used to select for cultivars less susceptible to flavor deterioration with aging (Mason 2000). However, levels of antioxidants are low in macadamia and probably not effective for the stability of kernel flavor (Cavaletto 1980; Rosenthal et al. 1984; Kaijser et al. 2000; Himsteadt 2002; Wu et al. 2004).

L. Performance in Extreme Environments

There has been interest in development of cultivars that perform well in cold environments (Xiao et al. 2002b). Many consider *M. tetraphylla* germplasm better suited to cooler environments (Cavaletto 1983; McCubbin and Lee 1996; Wiid and Hobson 1996; Allan et al. 1999; Xiao et al. 2002a). 'Beaumont', 'Own Choice', and 'Hinde' reportedly perform well in cooler environments of inland China (Xiao et al. 2002a, 2002b; Zheng and Zhang 2002), New Zealand (Gordon 1987; Richardson and Dawson 1991; Warren 2003), and South Africa (Allan 1993). In a trial of 10 cultivars across a range of environments in Thailand from latitudes 7.5° to 19.8°N, altitude 100 to 1300 m, average annual rainfall from 1,050

to 3,200 mm, and maximum temperature from 23° to 33°C, 'Kakea' was identified as the most susceptible cultivar to high temperatures (Supamatee et al. 1992). There are a range of physiological processes affected by high and low temperatures and interactions with other environmental variables (Stephenson and Trochoulias 1994; Huett 2003). Further work is required to develop a quantitative understanding of how these processes impact productivity and nut and kernel characteristics, so that they can be manipulated through breeding and selection.

V. PROPAGATION AND ROOTSTOCK TRAITS

Elite cultivars of macadamia are commonly propagated by grafting onto seedling rootstocks, and less commonly using clonal rootstocks or own rooted cuttings (Stephenson 1990a; Nagao and Hirae 1992; Trochoulias 1992; Bell 1996; Hardner and McConchie 2006). Clonal propagation of rootstock provides greater control of genetic variation and can lead to more uniform orchards (Howard 1987).

A. Germination and Seedling Growth

Horticultural experience with macadamia is that germination of nuts is usually spread over several months with germination occurring from four weeks (Storey and Kemper 1960) to five (Wills 1939; Hamilton 1957) or eight months (Ojima et al. 1976) after sowing. Genetic variation in germinability (percentage germination) and rate of germination has been reported (Hamilton 1957; Ojima et al. 1976; Kadman and Joffe 1981; Hardner 2004; Hardner and McConchie 2006).

In a nursery study on rootstock propagation of 15 genotypes (Hardner 2004; Hardner and McConchie 2006), germinability after six months was highest for 'HAES 849', 'D4' (also known as 'Renown'), 'Mauka', and 'Beaumont' and lowest for 'A268', 'A38', and 'Keauhou'. High germinability of 'Beaumont' nuts has also been reported by others (Allan 1989). Germinability for 'Hinde' (currently the favored seedling rootstock in Australia), 'Kau', 'HAES 781', 'HAES 814', 'HAES 816', 'HAES 842', 'A16', and 'NG8' was intermediate (Hardner 2004; Hardner and McConchie 2006). No general difference between *M. integrifolia* and hybrid cultivars was observed. It has been suggested that nuts from *M. tetraphylla* germinate faster than those from *M. integrifolia* (Phiri 1985; Nagao and Hirae 1992) or that thin-shelled nuts germinate faster (Wills 1939; Leverington 1962a; Nagao et al. 2003). It is possible that alternative nursery condition may produce different results.

M. tetraphylla seedlings reportedly grow faster and are more uniform (Phiri 1985; Hamilton 1988; Nagao and Hirae 1992; Trochoulias 1992), enabling grafting to occur six months earlier than expected with *M. integrifolia* rootstocks (Hamilton 1988). Significant genetic variation in nursery growth rate among seedlings from 15 cultivars has been reported (Hardner 2004; Hardner and McConchie 2006). One year after potting up, seedlings from 'Beaumont' were the most vigorous. The least-vigorous seedlings were progeny from 'HAES 849', 'Keauhou', 'HAES 842', 'HAES 781', and 'Kau', with the height of 'HAES 814', 'NG8', 'HAES 816', Mauka', 'A38', 'A16', 'Hinde', 'A268', and 'Renown' intermediate. Growth of progeny was not correlated with the germinability of the nuts of the cultivar.

B. Rooting and Growth of Cuttings

Several studies report significant differences in rooting success among cuttings collected from different cultivars (Cormack and Bate 1977b; Hardner 2004; Hardner and McConchie 2006). Cuttings taken from 'Beaumont' consistently demonstrate high rooting success (Cormack and Bate 1977b; Cruz-Castillo et al. 2000; Hardner 2004; Hardner and McConchie 2006). In a survey of 12 cultivars propagated as cuttings (Hardner 2004; Hardner and McConchie 2006), strike was superior for 'Beaumont' (80%), 'A268' (76%) and 'NG8' (70%), and 'HAES 814' (68%). Rooting success of cuttings from 'Ikaika' was also comparable to 'Beaumont' (Cormack and Bate 1977b). These authors also considered 'Keauhou' and 'Elimbah' moderately easy to root (Cormack and Bate 1977b). This is in agreement in part with Hardner and McConchie (2006), who report rooting success for 'Keauhou' (59%) to be similar to 'Mauka' (61%), 'A16' (61%), 'Kau' (54%), and 'HAES 781' (55%). These studies also identified 'Kakea' and 'Keaau' (Cormack and Bate 1977b) and 'HAES 842' (40%), 'HAES 816' (34%), and 'HAES 849' (23%) (Hardner and McConchie 2006) as recalcitrant germplasm. The relationship between rooting response of cultivars and stem carbohydrate levels of the mother plant is variable (Cormack and Bate 1977b), and no correlation has been demonstrated between the average strike success of cuttings from a cultivar and the germinability of seeds (Hardner and McConchie 2006). In general, it is difficult to find support in these results for the hypothesis that Hawaiian-derived cultivars are more difficult to root than Australian selections, as suggested by others (Bell 1996).

Although some work has been undertaken to develop tissue culture methods for clonal propagation macadamia (Mulwa and Bhalla 2000,

2007), there is no information on genetic differences in tissue propagation success. These authors report identical correspondence between the marker profile of stock plants and tissue-cultured plantlets, and compare this with RAPD polymorphisms detected in similar studies in other species, to suggest that clonal identify is maintained with propagation using auxiliary bud proliferation from single nodes. However, while promising, these results do not suggest that other nonsampled loci are unaffected.

Variation in nursery growth due to genetic differences has been reported in several studies (Cormack and Bate 1977a; Hardner 2004; Hardner and McConchie 2006). These studies indicate that cuttings from cultivars that have a high strike success also tend be vigorous in the nursery ($r_{cv} = 0.6$, Hardner and McConchie 2006), and less vigorous cuttings tend to be have a lower root mass and are more variable in vigor (Cormack and Bate 1977a).

C. Graft Compatibility

Grafting of rootstock and scions of *M. tetraphylla*, *M. ternifolia* and *M. integrifolia* has been reported to be successful in any combination (Storey and Frolich 1964). Significant genetic variation for budding success of scion and rootstock has been reported across a range of genotypes (Hardner 2004; Hardner and McConchie 2006). The effect of scion genotype was larger than the effect of rootstock genotype; however, this is likely to be confounded with nongenetic effects as generally all scions from the same cultivar were budded on the same day in this study. Budding success was superior for 'A268' (51%) 'NG8' (29%), and 'HAES 814' (23%) compared to 'Kau', 'Mauka', 'HAES 816' (all 6%), and 'HAES 842' (2%). No effect of rootstock type (clonal or seedling) on scion budding success was found. Rootstocks with low ($<10\%$) average take across several scions were 'Mauka', 'HAES 842', and 'A16', compared to 'Beaumont' (34%), which was the superior rootstock for budding success. Although this study also reports no effect of rootstock vigor on budding success, some selection for this trait was undertaken prior to propagation.

D. Rootstock Effects on Scion Performance

Despite the impact of rootstocks in other crops, particularly in apple (Rom and Carlson 1987), there is little quantitative evidence of strong rootstock effects in macadamia. Reviews of industry publications (Phiri 1985; Nagao and Hirae 1992) suggest *M. tetraphylla* rootstocks are

less susceptible to disease and have a better root system compared to *M. integrifolia* rootstocks; however, there are little data to support these hypotheses, and certainly rigorous field experiments with genetic material representative of the two species are lacking. Scions on *M. tetraphylla* stocks reportedly produce higher yields (Hamilton 1988; Nagao and Hirae 1992), although no significant difference in yield was observed in a field trial of five Hawaiian *M. integrifolia* cultivars propagated as cuttings (own-roots) or on *M. tetraphylla* seedling rootstocks (Phiri 1985).

Overgrowth of *M. integrifolia* scions on *M. tetraphylla* rootstocks, or ''later-age incompatibility,'' has been observed (Hamilton 1988). Cracks in the trunk at the graft union may also be present and provide an entry point for disease (Hamilton 1988). However, there are no data available on the extent of this syndrome or the effect on production or other traits (Hamilton 1988).

It has been suggested that rootstock genotype may affect nutrient accumulation, and variability in macadamia orchards has been attributed to genetic variation among seedling rootstocks (Nagao and Hirae 1992). Again, there are little data available to enable these hypotheses to be examined. In a limited field trial with two macadamia cultivars (Trochoulias 1992a), differences in yield between rootstock genotypes propagated as seedlings or cuttings were not consistent across years, and no differences in kernel traits were observed. No significant effect of rootstock on early field growth height (at two years after planting) was found in a trial of 12 cultivars propagated as own-rooted cuttings or grafted onto clonal and seedling rootstocks of the same 12 cultivars (plus three additional seedling rootstock cultivars), although significant scion effects were detected (Hardner and McConchie 2006). Further quantitative information is required on the effects of rootstock on production, nut characteristics, and kernel quality attributes (Hamilton 1988; Hardner and McConchie 2006).

VI. CULTIVAR UTILIZATION

Cultivar utilization must consider a range of important criteria (Hamilton and Fukunaga 1959; Hardner and McConchie 1999; Stephenson and Gallagher 2000). However, as discussed, much of this information for the various selection criteria is descriptive, making comparison among cultivars, and hence accurate selection, difficult. This uncertainty in the performance of cultivars is likely to be a major issue limiting the potential of macadamia production.

A. Scion Cultivars

1. Hawaii. Cultivar recommendations in Hawaii were developed using a culling approach to selection and the standard described above for yield, tree structure, number of nuts per cluster, nut size, kernel recovery, percentage of first-grade kernel, and kernel size (Hamilton and Fukunaga 1973; Hamilton and Ito 1976, 1984, 1986). However, there is little detail on rationale for the recommendation of specific cultivars.

Following the release of the first five cultivars from the Hawaiian selection program in 1948, three of the five recommended cultivars in 1948 ('Pahau', 'Nuuanu', and 'Kohala') were no longer on the recommended list by 1953 (Wagner-Wright 1995). There is no record of the reasons for the rejection of these cultivars. 'Kakea' is considered to be reasonably hardy and consistent with upright and rounded (but not spreading) canopy, producing exceptional yields and kernels of high quality, but can produce stick-tights and has a long harvest period (Hamilton and Fukunaga 1970; Hamilton and Ito 1976, 1984).

Recommended cultivars in 1956 were 'Keauhou', 'Wailua', 'Kakea', and 'Ikaika' (Hamilton and Storey 1956), although 'Wailua' (released in 1952) was dropped by 1959 (Hamilton and Fukunaga 1959), again for unknown reasons. 'Ikaika' is described as hardy and precocious, but later age yields tend not to be as great as other cultivars (Hamilton and Ito 1984).

By 1970, 'Keaau' had been added to the list of standard cultivars for Hawaii, which also included 'Keauhou', 'Kakea', and 'Ikaika' (Hamilton and Fukunaga 1970). 'Keaau' is described as being favored for an upright growth habit, outstanding nut and kernel characteristics, and short harvest period, but has a problem with germination of nuts in wet conditions (Hamilton and Ito 1984).

After the release of new cultivars in the 1970s, 'Keauhou' was dropped from recommended cultivars in Hawaii because of variable kernel quality (Hamilton and Ito 1984; Nagao and Hirae 1992), presumably percentage of first-grade kernel. Certainly, as discussed, 'Keauhou' has a lower percentage of first-grade kernels and may produce a high frequency of roast rejects under certain roast conditions, but the flavor and texture of the kernel is similar to that of other Hawaiian cultivars. 'Keauhou' may require different processing conditions from some other common cultivars, and this may be unsuitable for commercial operations. The cultivar is considered to produce good yields but has a broadly spreading tree structure and is susceptible to wind damage (Hamilton and Ito 1984).

By 1984, 'Ikaika' had also been dropped from the list of recommended cultivars, which at this stage included 'Purvis', 'Kau', 'Kakea', 'Keaau', 'Mauka', 'Pahala', and 'Makai' (Hamilton and Ito 1984). 'Purvis' is described as good cropping, with high percentage of first-grade kernel and kernels of exceptionally good quality and flavor (Hamilton and Ito 1984). 'Kau' is considered more upright, hardier, and more wind resistant than 'Keauhou', but with better kernel quality (Hamilton and Ito 1984; Stephenson 1990a). 'Mauka' is regarded as hardy, with upright growth and higher kernel recovery and percentage of first-grade kernel compared to 'Kau' (Hamilton and Ito 1984). 'Pahala' is also considered to be narrow and upright, with high kernel recovery and good kernel quality (Hamilton and Ito 1984). 'Makai' reportedly resembles 'Keauhou' in tree form, yield, and nut characteristics but is considered to produce kernels of outstanding quality. Of the newer selections, 'HAES 816' was rejected in Hawaii due to high incidence of stick-tights and 'HAES 849' due to thinner shells and low yields (Nagao et al. 2003).

Cultivar recommendation in Hawaii also considered site suitability (Nagao and Hirae 1992). 'Ikaika' was particularly favored for poorer-quality sites, where soil fertility was low or suffered exposure to the wind (Hamilton and Fukunaga 1959; Hamilton and Ito 1984). The altitude range present in the Hawaiian islands stimulated an interest in the suitability of cultivars to 600 m elevation and above (Ito et al. 1990; Nagao and Hirae 1992). In Hawaii, cultivars reported as having a wide range of suitability to elevations up to 610 m include 'Kau', 'Keaau' 'Pahala', 'Makai', and 'HAES 816'. 'Dennison' is considered better than other cultivars below 150m, and 'Purvis' and 'HAES 835' are less suitable at elevations above 450 m. 'Mauka' is reportedly more suited to elevations above 200 m and '856' to high elevations up to 670 m. There is however, no information on what data were used in for these recommendations.

It has been suggested that the main drivers of grower adoption of recommended cultivars in Hawaii were suitability to location, grower preference (Hamilton and Fukunaga 1973), and availability of budwood (Hamilton and Ito 1984). It has also been suggested that the popularity of 'Kau' may be due in part to the attractive and distinctive tree form of this cultivar (Ito and Hamilton 1989). Similar to other horticultural crops, it was reported that exaggerated and misleading claims were commonly encountered (Hamilton and Fukunaga 1973).

The impact of insect damage on crop loss, and the apparent presence of genetic variability for susceptibility, has led some to strongly suggest that resistance to insect damage should be included in selection

decisions (Jones 2002). However, an increase pest resistance needs to be balanced against variability in other key selection traits.

The majority of orchards in Hawaii are planted with HAES-released cultivars, with limited areas planted with cultivars selected outside this group (e.g., 'Chong 6' and 'Honokaa Special') (Hamilton and Fukunaga 1970; Hamilton and Ito 1977b; Yamaguchi 2006). 'Keauhou', 'Ikaika', and 'Kakea' were reportedly the major cultivars planted in older orchards in 1989 (Ito and Hamilton 1989), no doubt due to their popularity during the expansion phase of the industry prior to 1980 (Yamaguchi 2006). However, 'Kau', 'Keaau', and 'Mauka' were preferred for establishment of new orchards after 1980 (Ito and Hamilton 1989; Yamaguchi 2006). By 2003, 'Pahala', 'Makai', and 'Purvis' were the most common cultivars in the younger orchards (Nagao et al. 2003), although the majority of the orchard estate remained planted with 'Keauhou', 'Ikaika', 'Kau', 'Kakea', and 'Keaau' (Yamaguchi 2006).

2. Australia. Cultivar utilization in Australia prior to the 1980s was hampered by lack of reliable data, particular for Australian conditions (Winks 1983; Stephenson 1990a). The development of the Australian industry has largely been based on Hawaiian cultivars, mainly because information on their performance, albeit in Hawaii, was available (Winks 1983; Stephenson 1990a). The early Hawaiian cultivars 'Keauhou' and 'Kakea' were available in Australia by the early 1960s (McConachie 1980). By the early 1980s, the cultivars 'Keaau', 'Kau', 'Mauka', 'Makai', 'Purvis', and 'Pahala', and three other HAES selections ('HAES 781', 'HAES 794', and 'Dennison') had been introduced (Winks 1983). Other HAES selections (705, 762, 772, 783, 789, 'Fuji', 795, 804, 807, 814, 815, 816, 828, 835, 836, 837, 842, and 849) became available in Australia in the late 1980s (Winks et al. 1987).

Several authors suggest the performance of Hawaiian cultivars in Australia is poorer than their performance in Hawaii, particularly for yield and kernel quality (Cull 1978; Winks 1983; Hamilton and Ito 1986; Trochoulias and Burnside 1987; Stephenson 1990a), implying these cultivars are less suited to Australian growing conditions. For example, 'Kakea' is considered intolerant of the hot and dry conditions in Australia, although this cultivar is considered hardy in Hawaii (see earlier discussion, Stephenson 1990a). While 'Kau' was highly regarded in Hawaii, it reportedly has not performed as well in Australia (Stephenson 1990a; Gallagher et al. 1998), particularly due to low kernel recovery, erratic yields in some environments (Stephenson and Gallagher 2000), and susceptibility to ''abnormal vertical growth'' (O'Farrell and Searle 2003, see earlier discussion).

Australian experience appears to confirm the Hawaiian experience with 'Ikaika', of poor later-age productivity (Stephenson 1990a). 'Makai' produces high-quality kernel under Australian conditions similar to its performance in Hawaii (Stephenson 1990a). 'Keauhou' is reported as having similar variable kernel quality to that found in Hawaii, and produces nuts with high incidence of open micropyles under some Australian conditions (Stephenson 1990a). However, it is one of the most widely planted cultivars in Australia and is considered an industry standard, in contrast to its status in Hawaii (Stephenson et al. 1997; Stephenson 1990a). The proposition that relative performance of cultivars is different between Hawaii and Australia is challenged by the similarity in relative ranking for yield of the limited number of cultivars planted in both locations. Whether the difference in performance between Australia and Hawaii demonstrates the potential of selection for local suitability, or simply reveals the limits of the Australian environment, requires further investigation.

There is little information on the utilization of Australian selections prior to 1990 (Winks 1983; Winks et al. 1987; Stephenson et al. 1995), with only 'Own Choice' and 'Hinde' having been recorded as being of commercial significance (Stephenson 1990a). 'Own Choice' is described as an upright tree, although slightly spreading, that crops heavily and produces high-quality kernel but can suffer a high incidence of stick-tights (Stephenson 1990a). 'Hinde' was considered more suitable to cooler environments and was popular prior to 1990 (Stephenson 1990a; Hardner et al. 2006). A series of cultivars trials established over six sites in 1984–1985 greatly expanded the knowledge of cultivar performance in Australia (Winks et al. 1987; Stephenson et al. 1995, 1999; Stephenson and Gallagher 2000; Hardner et al. 2001, 2002; Mayer et al. 2006). Further cultivar trials were established in 1992, 1995, and 1996 (Stephenson 2001). By 2000, the most widely planted cultivars in Australia were reportedly 'Keauhou', 'Kakea', 'Ikaika', 'Makai', 'Keaau', 'HAES 849', 'Hinde', A4', 'A16', and 'A38' (Peace et al. 2000).

All cultivars that were utilized in the 1980s in the Australian industry were considered to have at least one major defect including (in order of importance): yield, quality, poor tree habit, stick-tights, excessive length of fruit drop period, low yield at a young age, susceptibility to insect and disease, susceptibility to early germination, susceptibility to heat stress, excessive premature nut drop 5 to 8 weeks after anthesis, and incidence of open micropyles (Stephenson 1990a). More recently, other selection criteria were identified, including attributes affecting kernel quality such as flavor, texture appearance, shelf life, percentage of whole kernels, and kernel size (Hardner and McConchie 1999), although the extent of

genetic control, and thus the potential for changing these through genetic selection, is unknown.

Recommendations for cultivars in Australia have been made by initially rejecting cultivars with serious defects and then considering yield per tree of first-grade kernel (Stephenson and Gallagher 2000). Thresholds for 22 desirable characteristics have been described: robust, compact and open habit; resistant to wind damage; tolerance of suboptimal conditions but responsive to good management; absence of stick-tight nuts; absence of pregermination in nuts or kernel; tolerance of major pest or diseases; short-harvest season, with 80% to 90% of the harvest completed within six months of mature nut fall; precocious, with bearing by three or four years after planting; at least 1 kg/year increase in NIS yield per tree from age of first crop to reach at least 6.5 kg per tree by 10 years; NIS remains in husk after it falls from the tree; easy separation of nuts from husk and no husk adhering to nut after dehusking; nuts regular and round; no nuts smaller than 18 mm in diameter; sound kernel recovery greater than 36%; high and stable first-grade kernel (over 95%); high percentage of whole kernels; regular round kernels; kernel color uniform and free from discoloration; even color after roasting; and acceptable sensory quality to processors, marketers, and consumers. However, as some of these selection criteria are not well defined or quantified, accuracy of predicting cultivar performance is likely to be low. In addition, application of thresholds over such a large number of selection criteria is likely to lead to reduce gain compared to a selection index (Cotterill and Dean 1990). Based on evaluation of cultivars across six sites, combined with expert knowledge from growers, 'Mauka', 'HAES 783', ' HAES 814', 'HAES 842', 'HAES 849', 'Daddow', and 'A16' were recommended as acceptable across the Australian industry in 2000 (Stephenson 2000). Recommendations of specific cultivars for particular regions in Australia were also made based on trial results (Stephenson et al. 1995; Stephenson and Gallagher 2000), although the data for these recommendations are limited as each region was represented only by a single site, and there was only a maximum of four replications for each cultivar at each site.

The selection index developed to identify elite selections in the Australian Macadamia Breeding Program (see discussed earlier) has been applied to the evaluation of 20 cultivars over two of the trial sites in Stephenson et al. (1995) (Hardner et al. 2006). Economic weights for eight traits (canopy width at 10 years—m; age of first crop—year; average rate of yield increase during the accumulation phase of production—kg/year; percentage of reject NIS—kg NIS/100 kg NIS; total kernel recovery—kg kernels/100 kg NIS; percentage reject

kernel—kg kernels/100 kg kernels; percentage if marketable kernels—kg kernels/100 kg kernels; average grade of marketable whole kernel—mm) were calculated as the change in relative profitability (profit/total costs) of an economic model of production and processing costs, and the value of raw kernel. The model indicates that to offset the reduction in value of a 1% point lower total kernal recovery, a cultivar would require a canopy width of 0.1 m less, a rate of yield increase more than 0.1 kg/year higher, 1.3% less reject NIS, 2.1% less reject kernel, 10% more wholes or an average kernel size of 10 mm smaller.

Applying the economic weights to 20 cultivars tested over two sites in subtropical Australia (southeast Queensland and northern NSWs) suggested that the top five cultivars for this region based on these traits are 'HAES 849', 'Own Venture', 'HAES 814', 'A4', and 'HAES 804' (Hardner et al. 2006) This study illustrates the importance of the selection based on overall performance. 'HAES 849' was ranked only tenth for average rate of yield increase and tree size but had the third lowest age to first yield, the second highest kernel recovery, and the third highest percentage of whole kernels. The cultivar with the highest yield was 'HAES 344', but this cultivar was the sixth largest cultivar and had poor kernel recovery and percentage of whole kernels. Cultivar rankings were reportedly robust to a 20% change in land costs, other production costs, processing costs, and kernel prices (Hardner et al. 2006).

The importance of different criteria for selection is determined not only by the value of the economic weight but also on the ability to change the trait through selection (i.e., heritability). Average rate of yield increase, canopy width, and total kernel recovery were the largest contributors to the variation in the index value. In contrast, the index was only marginally affected by differences in proportion of whole kernel, kernel size, and age to first yield. These results could be used to prioritize the assessment of traits for selection. Other selection criteria, which may or may not be important, were not included in this analysis (e.g., tree structure, nut size and shape, pest and disease resistance, flower and nut drop phenology, visual appearance of raw kernel, quality of roasted kernels, or shelf life). However, cultivars that produce high-quality nuts and kernel may not be suitable if production characteristics are unfavorable (Cull 1978).

3. South Africa. Graft-wood of the older Hawaiian cultivars became available in South Africa by 1969 following earlier introductions of these cultivars (Allan 1995). More recent cultivars and selections were introduced in the 1970s. The cultivar 'Beaumont' was introduced into South Africa from California in 1968 (Wiid and Hobson 1996).

Similar to experiences in Australia, early Hawaiian cultivars ('Keauhou', Kakea', and Ikaika') reportedly did not perform well in South Africa, although 'Kau' and 'Keaau' are considered better (Allan 1993). It is suggested that *M. integrifolia* cultivar types are less productive under cooler subtropical conditions of South Africa than cultivars of hybrid origin (Wiid and Hobson 1996; McCubbin and Lee 1996; Allan et al. 1999). The high quality of raw kernel from some *M. tetraphylla* and hybrid selections has also been used to suggest that these may be more suited to cooler areas, although further testing of roasted kernel product is required (Allan 1993).

Cultivar recommendations in South Africa are based on Hawaiian kernel quality standards (i.e., average kernel mass between 2–3 grams, greater than 34% kernel recovery, and 95% first-grade kernel), resistance to anthracnose, fairly uniform shell thickness with no open micropyle, even round shape of the nut, limited variation in nut size, round kernel, absence of basal discoloration or discolored rings, roasting ability, shelf life, yield per tree of greater than 45 kg NIS at 10 years of age, resistance to stink bug, lack of soft kernel, time of flowering, harvest season, and tree shape and branching habit (Allan 1989; Oosthuizen et al. 1989). However, it is not clear how some of these standards are defined, assessed, and prioritized.

In 1989, 'Keaau', 'Kau', 'Kakea', 'Keauhou', and 'Ikaika' were recommended for both the southern Lowveld and Soutpansberg growing areas (Oosthuizen et al. 1989) based on standards of nut size, kernel recovery greater than 33%, kernel mass between 2 and 3 grams, greater than 75% oil content of kernels, and productivity determined from four trees of each cultivar at two locations. 'Nelmak 2' was also only recommended for the southern Lowveld and 'Selection 26' only for Soutpansberg.

By the 1990s, 'Mauka', 'Pahala', and 'Makai' were considered to be superior in South Africa to 'Keauhou', Ikaika', 'Kakea', 'Purvis', and 'Cate', based on superior kernel quality and reasonable yield (Allan et al. 1999). Others cultivars considered superior were 'Keaau' and 'Beaumont' in particular, and 'Kau', 'HAES 781', 'HAES 814', 'HAES 816', and 'Nelmak 2' (Allan et al. 1999). In contrast, others (McCubbin and Lee 1996) consider 'A4', 'A16', and 'Beaumont' superior to 'Kau', 'Mauka', 'HAES 816', and 'Makai', primarily because of precocity. Some concerns have been expressed about a high proportion of stick-tights, germination, and the vigorous growth of 'Beaumont' (Allan 1989; McCubbin and Lee 1996). It was suggested that this cultivar may be more suitable to particular production systems of hand harvesting or as a temporary tree in high-density plantings (McCubbin and Lee

1996), although other work has suggested this cultivar is productive at later ages in high-density plantings (Wiid and Hobson 1996). The limited availability of reliable yield data for South Africa makes recommendations difficult to evaluate.

A profitability index was calculated to assess cultivars based on average NIS price, yield at six or eight years after planting, sound kernel recovery, percentage of first-grade kernel, and tree spacing (Swanepoel and Hobson 1999). This is the value of NIS production per hectare with the assumption that all unsound kernels are rejected, all kernels greater than 1.000 specific gravity will produce kernel with no value, and there are no differences in costs associated with the variability in these traits. A REML analysis (to account for unbalance of cultivars across sites) of the profitability values published in this study indicates that the value of production from 'HAES 814', 'Nelmak 2', 'A4', and 'Beaumont' was significantly superior to the other cultivars examined ('Fuji', 'A16', ' Kau', 'Pahala', Mauka', Keaau', 'HAES 816', 'Purvis', 'HAES 789', 'HAES 862', and 'Makai'). However, these recommendations are made with limited data and may not accurately reflect cultivar performance.

The main cultivars in commercial orchards in South Africa by 1999 were 'Keauhou', 'Fuji', Nelmak 2', 'Keaau', and 'Kau' (Swanepoel and Hobson 1999). The cultivar 'Beaumont' has also been planted widely throughout the country and is also popular as clonal rootstock (Bell 1996; Wiid and Hobson 1996; Hardner and McConchie 2006).

4. China. A range of Hawaiian (all major releases) and Australian ('Hinde', 'Own Choice', 'A4', and 'A16') cultivars were introduced into China in the 1970s (Xiao et al. 2002b). During the 1980s, these cultivars were used to establish orchards in coastal areas (Guanxi, Ueng Nang, Shichuan, Hainan, and Fujien provinces); however, these orchards suffered extensive cyclone damage (Lu et al. 1998b; Xiao et al. 2002a, 2002b). Since 1997, new plantings have been undertaken in the inland areas (Uengnang and Shichuan provinces), although the cooler temperatures and high rainfall in these areas may limit macadamia productivity (Xiao et al. 2002a). 'Hinde', 'Own Choice', and 'Beaumont' were observed to be tolerant of cold and wind and to produce good yields in the Panxi region of the Shichuan province (Zheng and Zhang 2002; Xiao et al. 2002a, 2002b). 'Hinde' is reportedly vigorous with yields of 8 to 10 kg per tree at nine years in experimental trials, and is considered very hardy to cold wind and drought but susceptible to poor soil. 'Beaumont' is considered precocious and suitable for inland and mountainous areas in China. 'Own Choice' is favored as it is more

resistant to wind (Lu et al. 1998b, 2004) and is reported to be resistant to drought (Xiao et al. 2002a). Most of the main Hawaiian cultivars except 'Pahala' were not favored due to poor flowering at age four (Xiao et al. 2002a). 'Makai' exhibits poor growth in China. Similar to conclusions developed in South Africa, experience in China suggests that *M. tetraphylla* genotypes are more suitable for these cooler environments and *M. integrifolia* cultivars should be ignored (Xiao et al. 2002b).

5. Other Countries. There is limited information about the utilization of genetic material in other macadamia-producing countries. Hawaiian cultivars reportedly dominated the orchard estate in Brazil in the 1990s, with the five most common cultivars being 'Kau', 'Kakea', 'Keaau', 'Mauka', and 'Makai' (Sacramento et al. 1995). *M. tetraphylla* cultivars ('Elimbah' and 'Cate') were preferred in California because the species is considered more suitable to the cooler climate (Cavaletto 1983). Several elite *M. tetraphylla* and hybrid selections have been identified for Kenya (Gathungu and Likimani 1975). Hybrid cultivars also appear popular in New Zealand, with 75% planted to 'Beaumont' and smaller plantings of 'Renown' in 1991, although orchards with 'Own Choice' and some Hawaiian cultivars have also been established (Gordon 1987; Richardson and Dawson 1991; Warren 2003). Cultivar utilization appears to be hampered by limited evaluation trials. In addition, kernels produced by *M. tetraphylla* selections may not be as commercially acceptable as kernel from the *M. integrifolia* cultivars that dominate the market (Hamilton 1988).

B. Rootstocks

M. tetraphylla was favored for seedling rootstocks in Hawaii from the 1960s (Storey 1976; Hamilton 1988; Nagao and Hirae 1992; Trochoulias 1992), probably due to perceived superior nursery performance (Hamilton 1988; Stephenson 1990a; Trochoulias 1992) and stronger root system (Wagner-Wright 1995). However, observations of ''later age incompatibility symptoms'' prompted a conversion to *M. integrifolia* (Hamilton 1988; Nagao and Hirae 1992).

M. tetraphylla seedling rootstocks were also used in Australian in the 1970s, apparently because of faster and more even germination and growth (Stephenson 1990a). 'Eggshell' was reportedly used as a source of seedling rootstocks for the expansion of the Australian industry by the CSR company in the mid-1960s (Trochoulias et al. 1989), although the relationship with the early Australian seed parent of the same name (Petrie 1935) is not known. Seedling progeny from

'Renown', a hybrid cultivar, became popular in the 1980s (Trochoulias 1992), but since the early 1990s, the majority of Australian orchards have been established with seedling rootstocks from 'Hinde' (Stephenson 1990a; Trochoulias 1992; Hardner and McConchie 2006). This cultivar is reportedly favored because it has a broad stem that is considered advantageous for grafting at an early age (Stephenson 1990a).

A hybrid cultivar 'Beaumont' has been used as a clonal rootstock in South Africa due to its high strike success and vigorous nursery growth (Wiid and Hobson 1996 and earlier discussion). Orchards in California have been reportedly established with *M. tetraphylla* rootstocks, primarily because this species is considered more suitable to cooler environments (Hamilton 1988). There may also be the potential to use *M. ternifolia*, which is generally smaller than *M. tetraphylla* and *M. integrifolia*, as a dwarfing rootstock (Hardner et al. 2000; Peace 2005), although work is required to test for the transmission of cyanogenic properties from the rootstock to the scion, which has been reported for other seedling material (Hamilton and Young 1966).

Currently there is insufficient information to support selection for rootstocks based on effects on scion performance (Storey 1957; Hobson 1971; Hamilton 1988; cf. Huett 2003; Hardner and McConchie 2006). As such, performance of rootstocks in the nursery will continue to be the dominant rationale for choice among rootstock genotypes.

VII. SUMMARY

Macadamia is an iconic Australian plant. Most species are endemic, the genus is one of the few current rain forest representatives of the ancient Gondwanan family Proteaceae, the plant has important cultural meanings for the indigenous peoples of Australia, it is the only member of the Australian flora that has become an international commercial food crop, and Australia is the world leader in the production of this highly valued nut.

Genetic improvement has supported the development of the industry in Hawaii and its expansion worldwide, and has delivered substantial gains across a range of traits. This is particularly true for traits that are highly heritable and easy to measure, such as nut size, kernel recovery, and kernel size. In some cases, although no quantitative method has been used to measure traits, high heritability has enabled identification of cultivars that are easy to propagate, have an upright structure, and are free of bitter kernels.

Breeding generally has been undertaken following the conventional method of intense selection among seedling progeny followed by clonal replication of a reduced number of candidates. However, selection among the seedlings has commonly used phenotypic performance without controlling environmental variation; hence selection accuracy for genetic effects is likely to be low, particularly for traits with low heritability. While selection accuracy is expected to be high in the clonal trials, selection intensity is generally low, as generally only a few candidates are evaluated. It may be possible that greater gains could be achieved with a different balance between selection intensity and accuracy in the different testing phases.

Although there is a general understanding in macadamia of selection traits and their interaction with the production system, much of this information is imprecise and based on anecdotal knowledge or limited data. This lack of detailed understanding is likely to have restricted the opportunities of improving key selection criteria. For example, this review has highlighted uncertainties associated with traits such as stick-tights and some attributes of kernel quality. Methods of assessment of traits may also vary among studies, making results difficult to compare for selection decisions. Selection response may also be compromised by the limited information on genetic architecture of many traits, particularly when mass selection strategies are implemented for traits with low heritability. These traits are improved more efficiently through quantitative approaches. Further, it is often difficult to deduce the relative importance of different traits in selection programs. This can lead to a waste of selection pressure on traits with little importance, compromising gain in traits that actually can impact on the production system, and has the potential to introduce personal biases in selection decisions that are difficult to evaluate. This is particularly so for kernel quality attributes, where there are very little data on appearance attributes that can be used for selection.

This chapter has underlined the limited genetic diversity of the Hawaiian germplasm that is the basis of much of the world industry. Given the short selection history of this germplasm and the relatively weak selection pressure (due to low accuracy), it is highly unlikely this material represents the only source of elite germplasm available in *Macadamia*. Opportunity to make significant advances may exist by increasing the genetic base of breeding programs by introduction of novel germplasm unrepresented in the Hawaiian gene pool. Gene pool diversity and avoidance of inbreeding could be managed using information from the neutral genetic marker studies on the genetic structure of the domesticated and wild germplasm. This study

could be extended to examine if there is an association between variation in selection traits and marker variation, particularly species composition.

There is a need to better understand the performance of many selection criteria across a wider germplasm pool for management of current genetic resources and future genetic improvement. Selection origin does not offer an adequate description of the relatedness of germplasm or genetic performance. In addition, species status is not a consistent indicator of genotype performance. In particular, major gaps in the knowledge of the behavior of commercially important traits in the *M. tetraphylla* germplasm is likely to hamper the utilization of this resource in current improvement programs. Similarly, systematic evaluation is required to determine whether there are useful traits in other two species of the macadamia southern clade, *M. ternifolia* and *M. jansenii*, that can be introduced through hybridization with the cultivated species.

A better understanding of the relative performance of germplasm in diverse environments may provide opportunities for more efficient utilization of the genetic resources of macadamia. Experience suggests that *M. tetraphylla* germplasm is suited to cooler climates. However, work is required to confirm that this is general and that the use of this germplasm does not compromise the benefits that could be gained from the use of alternative genetic material. In addition, data on the performance of common cultivars across different environments are needed to evaluate the hypothesis that Hawaiian cultivars are less suited to environments foreign to their selection origin. In this review, data from several studies were integrated to demonstrate that the relative performance of cultivars across countries was very stable for kernel recovery, but cultivar ranking for first-grade kernel was inconsistent across these environments. This approach could be extended to other key selection traits, particularly yield.

The limited development of the genetic resources of macadamia means the existing wild populations of the species are an extremely valuable resource for future genetic improvement. However, these populations currently are highly fragmented. An ex situ collection of samples from many of the known populations has already been established. The most up-to-date knowledge of the distribution of the three main species of the southern clade has been published in this review. The next important step in conservation of the wild populations is to develop more comprehensive knowledge of this distribution. Detailed knowledge of the genetic structure and dynamics of these populations, combined with ecological and demographic studies, is

required to underpin the management of these populations for national and international benefit.

VIII. ACKNOWLEDGMENTS

This review is dedicated to the memory of Henry Bell (1927–2008), a pioneer of the modern Australian macadamia industry. Henry was passionate about improving macadamia horticulture and made major contributions to conservation of wild germplasm, propagation technology, selection methods, high-density planting, and genetic improvement through the development of a private breeding program that produced the A varieties that are have now been widely adopted thoughout Austrlia and overseas. Henry was always happy to share his time and wealth of knowledge with any similar passionate soul, and the success of macadamia is in no small part a consequence of his enthusiasm and foresight for the crop.

Many people have contributed to the production of this review. Foremost we wish to thank Kaye Guidetti of CSIRO Information Technology Services who, along Patrick Ledwith and Robyn Mills (also CSIRO ITS), provided enormous assistance in gathering the obscure and difficult-to-access publications cited in this review. Carl Davies of CSIRO Plant Industry prepared Fig. 1.3 and assisted with the final version of Fig. 1.1a and 1.1b. Anfernee Tseng and Sharon de Wit assisted with translation of several non-English articles. We also wish to thank Russ Stephenson, David Mayer, Andre Drenth, Andrew Miles, Olufemi Akinsanmi, Ruth Huwer, Craig Maddox, and Lisa McFadyen, who made contributions to an initially planned larger review of macadamia natural history, utilization, and horticulture. We hope this second phase of the review of macadamia will be published in the near future. Last, we wish to thank our families for their continued support throughout the long days of thought and synthesis.

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