Australian Government
Department of Health and Ageing
Office of the Gene Technology Regulator

The Biology of Hybrid Tea Rose (*Rosa* x *hybrida*)

The rose cultivar 'Australian Centenary of Federation' (KORvegata Rebell®) showing the typical Hybrid Tea form of long-stemmed, large, single flowers [Photo credit: Janet Gorst, OGTR]

Version 2: March 2009

This document provides an overview of baseline biological information relevant to risk assessment of genetically modified forms of the species that may be released into the Australian environment.

For information on the Australian Government Office of the Gene Technology Regulator visit
<http://www.ogtr.gov.au>

TABLE OF CONTENTS

PREAMBLE

This document describes the biology of *Rosa* spp. with emphasis on the Hybrid Tea rose (*Rosa* x *hybrida*), and particular reference to the Australian environment, and cultivation for cut-flowers. Information included relates to the taxonomy and origins of cultivated roses, general descriptions of their morphology, reproductive biology, development, biochemistry, biotic and abiotic interactions, toxicity, allergenicity and weediness. This document also addresses the potential for gene transfer to occur to closely related species. The purpose of this document is to inform risk assessments of genetically modified Hybrid Tea roses that may be released into the Australian environment.

In this document, the general term 'rose' is used to describe all members of the genus *Rosa*, subgenus *Rosa*. While roses originated in temperate regions of the northern hemisphere, their widespread domestication now means that they are grown worldwide, primarily for cut-flower production and as garden/landscape specimens. Concomitant with their domestication has been the development of the so-called Modern Roses, a category containing tens of thousands of cultivars derived mainly from the controlled crossing of less than ten wild species. The species *R.* x *hybrida* is an artificial category that encompasses the Modern Roses. Among the Modern Roses, the Hybrid Teas represent the largest class and are characterised by their large, showy blooms.

SECTION 1 TAXONOMY

The *Rosa* genus belongs to the family Rosaceae and is closely related to apple, pear, quince, plum, cherry, blackberry, and strawberry. The genus is divided into 4 subgenera of which subgenus *Rosa* (previously known as *Eurosa*) includes nearly all of the species (see discussion in Gudin 2000; Nybom et al. 2005). In turn, subgenus *Rosa* is divided into sections (Table 1), the actual number of which is still debated (Shaw 1983; Gudin 2000). Roses have a complex nomenclatural history, and taxonomic difficulties of this genus have resulted in reports of anywhere from 100 to 300 *Rosa* species, of which there are innumerable cultivars[1] (Shaw 1983; Phillips & Rix 1988; Ross 1991; Ertter 2001). These taxonomic problems stem from the fact that the morphological characters used to distinguish species are highly variable, and are compounded by the ease with which species naturally hybridize. Classification may also be problematic because of continuous variation of characters, and, for example, in the *Caninae* ('dogroses') section of *Rosa*, the species are identified from species in other sections more by their unique meiotic system rather than by any morphological characters (Nybom et al. 2005; Wissemann & Ritz 2007). This meiotic system in *Caninae* results in a bias towards maternal inheritance and, in its most extreme form, leads to apomixis (see Section 4.1.3) where the progeny plant does not receive any genetic material from the pollen parent (Werlemark & Nybom 2005).

In an effort to better develop a rose taxonomic system, scientists have also turned to less traditional techniques such as chemotaxonomy (especially using the chemicals

---

[1] The word 'cultivar' is a contraction of 'cultivated variety' and describes a group of cultivated plants within a species that are significant in agriculture, forestry or horticulture and have clearly distinguished, heritable, stable and uniform characteristics. 'Cultivar' is synonymous with the term 'variety'. However it is not analogous with the category 'botanical variety' that is used to refer to naturally occurring variants within a species (Hartmann & Kester 1975; Brickell et al. 2004). Cultivars/varieties mentioned in this document are indicated in quotation marks eg. 'La France'.

involved in flower colour and fragrance) and molecular taxonomy (eg DNA fingerprinting, analysis of nucleotide sequences, chromosome painting) but without much success to date (see discussion in Fiasson et al. 2003).

The rose genome is complex, comprising up to five haploid chromosome sets each made up of 7 chromosomes (Yokoya et al. 2000; Nybom et al. 2005). Akasaka et al (2003) and Gudin (2000) discuss the original classification by Hurst (1925) of the diploid species into 5 'septets' (A – E) that were based on morphological, physiological and ecological characteristics, mitotic and meiotic chromosome configurations and genetic tests. Each septet comprised a unit of 7 chromosomes. The polyploid species have more than two identical or different septets. The chromosome number of wild species of *Rosa* varies from 2n=2x=14 to 2n=8x=56 (Table 1), with most species being diploid (2n = 14) or tetraploid (2n = 28) (Nybom et al. 2005). Polyploidy has significant effects on fertility and inheritance of traits. To explain the range of ploidy, it has been hypothesized that *Rosa* spp. descended from a hypothetical arctic decaploid (see discussion in Erlanson 1938). It has been suggested that the section *Cinnamomae* represents the Type of the genus *Rosa* since it shows the widest geographical distribution and the widest crossing ability within the genus (Atienza et al. 2005).

In addition to the wild species of roses there are also tens of thousands of cultivated roses (see eg Phillips & Rix 1988 for descriptions of more than 1400 common garden roses) that comprise categories known as the Old Garden Roses and Modern Roses (see Section 2.1). A number of horticultural classification systems exist for these (Gudin 2000) with the American Rose Society (ARS) Classification Scheme 2000 being the most commonly used (see eg Cairns 2003).

Rosa x *hybrida* is not a species in the botanical sense, but is a complex, artificial species category (Gudin 2003a), that may be used to describe the non-Species Roses and particularly the Modern Rose cultivars (Figure 1). The latter have been derived as a result of centuries of complex crosses involving the limited genepools of a number of mainly diploid species of the genus *Rosa* (see Section 2.1) that are all classified into septet A (see eg Akasaka et al. 2003). The Hybrid Teas and Floribundas (derived from Hybrid Teas) make up the largest and most popular classes of Modern Roses (Phillips & Rix 1988; Cairns 2003; Zlesak 2006). Distinguishing between the many cultivars is problematic because of the low degree of genetic variation. However, Esselink et al (2003), for example, have developed tagged microsatellite site markers that can be used to characterize Hybrid Tea cultivars especially for purposes of registration and cultivar protection. As expected from the derivation of the Modern Roses there is a range of ploidy with the Polyanthas being diploid, the Hybrid Teas and Floribundas tending to be either triploid or tetraploid and the Miniatures ranging through diploid, triploid and tetraploid (Yokoya et al. 2000).

Table 1. Sections that have been proposed for inclusion in the subgenus *Rosa* (taken from Shaw 1983; Phillips & Rix 1988; Gudin 2000; Ertter 2001; Wissemann 2003)

Section	Common description	Predominant chromosome number (2n)	Distribution	Representative species and/or species mentioned in this document
Banksianae		14	Eastern Asia	*R. banksiae; R. cymosa*
Bracteatae		14	Asia	*R. bracteata; R. clinophylla; R. roxburghii*
Caninae	Dogroses	28 - 42	Europe. Eastern Asia, North Africa	*R. canina; R. rubiginosa; R. corymbifera*
Carolinae	Carolina roses	28	North America	*R. carolina; R. foliosa*
Chinensis (Indicae)	China roses	14	Eastern Asia	*R. chinensis (= R. indica); R. gigantea; R. odorata*
Cinnamomeae *(Cassiorhodon)*	Thicket-forming; Cinnamon roses	14 - 56	North America, Asia	*R. rugosa; R. nuktana; R. acicularis; R. blanda*
Gallicanae (Rosa)	French roses	28	Ethiopia, Europe, Western Asia	*R. gallica; R. centifolia; R. damascena; R. alba*
*Gymnocarpae**	Wood and ground; Naked-fruited	14	Western North Amerca; Eastern Asia	*R. gymnocarpa*
Laevigatae	Shiny-leaved	14	Eastern Asia	*R. laevigata*
Pimpinellifoliae	Anise-leaved	14	Asia, Southern Europe	*R. sericea; R. foetida; R. xanthina; R. hugonis; R. spinosissima*
Synstylae	Climbing	14	Western Asia	*R. moschata; R. multiflora; R. sempervivens; R. wichuraiana; R. setigera; R. phoenicia*

* Section *Gymnocarpae* is not commonly listed as a distinct Section and the species within it are usually grouped within *Cinnamomeae*. It is considered by Ertter (2001) to be a separate Section.

SECTION 2 ORIGIN AND CULTIVATION

2.1 Centres of diversity and domestication

The earliest fossil record of rose was found in Alaska and dates back to the Paleocene epoch which ended some 58 million years ago. Roses were widely dispersed by the Oligocene epoch, some 34 million years ago, in the western USA, Europe and Asia (discussed in Becker 1963).

The *Rosa* genus is endemic to temperate regions of the northern hemisphere, including North America, Europe, Asia and the Middle East, with the greatest diversity of species found in western China (Phillips & Rix 1988; Ertter 2001). It is also distributed in warmer areas such as New Mexico, Iraq, Ethiopia, Bengal and southern China (Nybom et al. 2005). There are no endemic *Rosa* species in the southern hemisphere.

There is no single system of classification for roses commonly grown in cultivation, but the ARS Classification Scheme 2000 is widely used (Cairns 2003). Basically the system involves 3 main subdivisions (Figure 1) which also reflect the history of domestication of roses:

Species Roses

These are the wild species roses (see Table 1) and some of their hybrids. Species roses generally have mauve, white, pink or yellow five-petaled (occasionally four-petaled) flowers. There are a few with red flowers and none with blue hues. Growth habit varies from prostrate to climbing with some representatives of the latter being able to grow 7 m in a year. Plants bloom only once each year (seasonal-flowering) (Shaw 1983; Cairns 2003).

Old Garden Roses

The ARS defined this category as those cultivated rose types existing prior to 1867 and further subdivided the category into 21 classifications (see Figure 1). The flower can have one of several forms – quartered, cupped, imbricated or expanded, reflexed, globular or compact - and flowering may only occur once in spring (seasonal-flowering) or can extend through to multiple flowerings (recurrent-flowering – see Section 2.4.2) (Cairns 2003).

Early garden roses were wild species and their natural forms and hybrids, and were cultivated thousands of years ago. They were frequently mentioned in records from the Middle East some 2000 to 3000 years ago and were cultivated extensively during the Roman era (Ross 1991). By the eighteenth century five broad, Old European rose classes (see Figure 1) had emerged, Gallica (eg *R. gallica*), Alba (eg *R. alba*), Damask (eg *R. damascena*), Centifolia (eg *R. centifolia*), and Moss rose (eg *R. centifolia moscosa*) (Marriott 2003). For a description of the roses in these classes see eg Phillips & Rix (1988).

During the later part of the eighteenth century, the Old European roses were crossed with the ‘China Rose’, a complex of species (Section *Chinensis*) and cultivated hybrids that had been grown in China for over 1,000 years (Higson 2007; Wang 2007). In particular four Garden Rose cultivars (known as the China Stud roses) of uncertain origin were used from the China Rose group – ‘Slater’s Crimson China’, Parsons Pink China’, Hume’s Blush Tea-scented China’ and ‘Parks’ Yellow Tea-scented China’. The majority of modern hybrids include genetic material from at least one of these cultivars The China Rose group had distinct features that were lacking in the European roses such as a low branching habit, recurrent-flowering, crimson flower colouring that did not fade with age, new fragrances, distinct flowers with high centres and slender flower buds that unfurled on opening (Higson 2007). The crossing of the China roses with the Old European roses gave rise to a number of new classes (see Figure 1) of roses such as Portland (uncertain origin, maybe Autumn Damask x Slater's Crimson China), Bourbon (Autumn Damask x Parson's Pink China), Noisette (Parson's Pink China x *R. moschata*), Hybrid Perpetual (Portland x Bourbon x Hybrid China [*R. gallica* x *R. gigantea*]) and Tea (China x Bourbon or Noisette) (Marriott 2003; Filiberti 2005b; Higson 2007).

Modern Roses (1867 +)

In broad terms the Modern Roses are considered (see discussion in Gudin 2000) to have originated largely from 10 Species Roses – *R. canina, R. chinenesis, R. foetida, R.gallica, R. gigantea, R. moschata, R. multiflora, R. phoenicia, R. rugosa,* and *R. wichuraiana.*

The first of the Modern Roses were the Hybrid Tea roses, which were derived from crosses between Hybrid Perpetual and Tea roses (Marriott 2003) and thus contained germplasm from *R. damascena, R.moschata, R. chinensis, R.gigantea* and *R. gallica*. This group is also sometimes referred to as the 'large-flowered roses' (Phillips & Rix 1988). The first recognised Hybrid Tea was a cultivar called 'La France' that was 'discovered' in 1867 although there is documentary evidence of earlier deliberate crosses between Hybrid Perpetuals and Teas. 'La France' is thought to be the result of a natural cross between unknown parents but it became the prototype for the new class of roses. The Hybrid Tea class was first recognised in approximately 1880 by the French (*Hybrides de Thé*) but it was not until 1893 that the British National Rose Society officially recognised the class (Filiberti 2005a). In the early 1900's a French breeder, Joseph Pernet-Ducher, made crosses between Hybrid Perpetuals and the Austrian Brier (*R. foetida*) in order to introduce yellow colours (Marriott 2003). Most modern Hybrid Tea cultivars also contain *R. foetida* ancestry (Filiberti 2005a). An American breeder, Brownells, initiated a second important breeding programme by introducing *R. wichuraiana* genetics into Hybrid Teas to try and produce hardier varieties with blackspot resistance (Phillips & Rix 1988).

The most recent Hybrid Tea rose cultivars are mainly upright (1-2 m tall) with mostly single, well-shaped flowers with high spiralling centres at the end of long stems; sturdy, often shiny petals; characteristic pointed buds; large glossy or semi-glossy leaves; and strong stems (Ross 1991; Cox & Pavia 2002). Disease susceptibility and lack of vigour were features of the early Hybrid Tea cultivars and it was not until the development of the cultivar 'Peace' (released in 1945 to mark the end of WWII) that better vigour and health became incorporated into the Hybrid Teas (Marriott 2003). The Hybrid Tea roses have contributed to many of the Modern Rose Classes including Polyantha (*R. multiflora* x Hybrid Tea), Floribunda (Polyantha x Hybrid tea), Grandiflora (Floribunda x Hybrid Tea) and Miniature (Polyantha x *R. chinensis minima*) (Ross 1991; Marriott 2003).

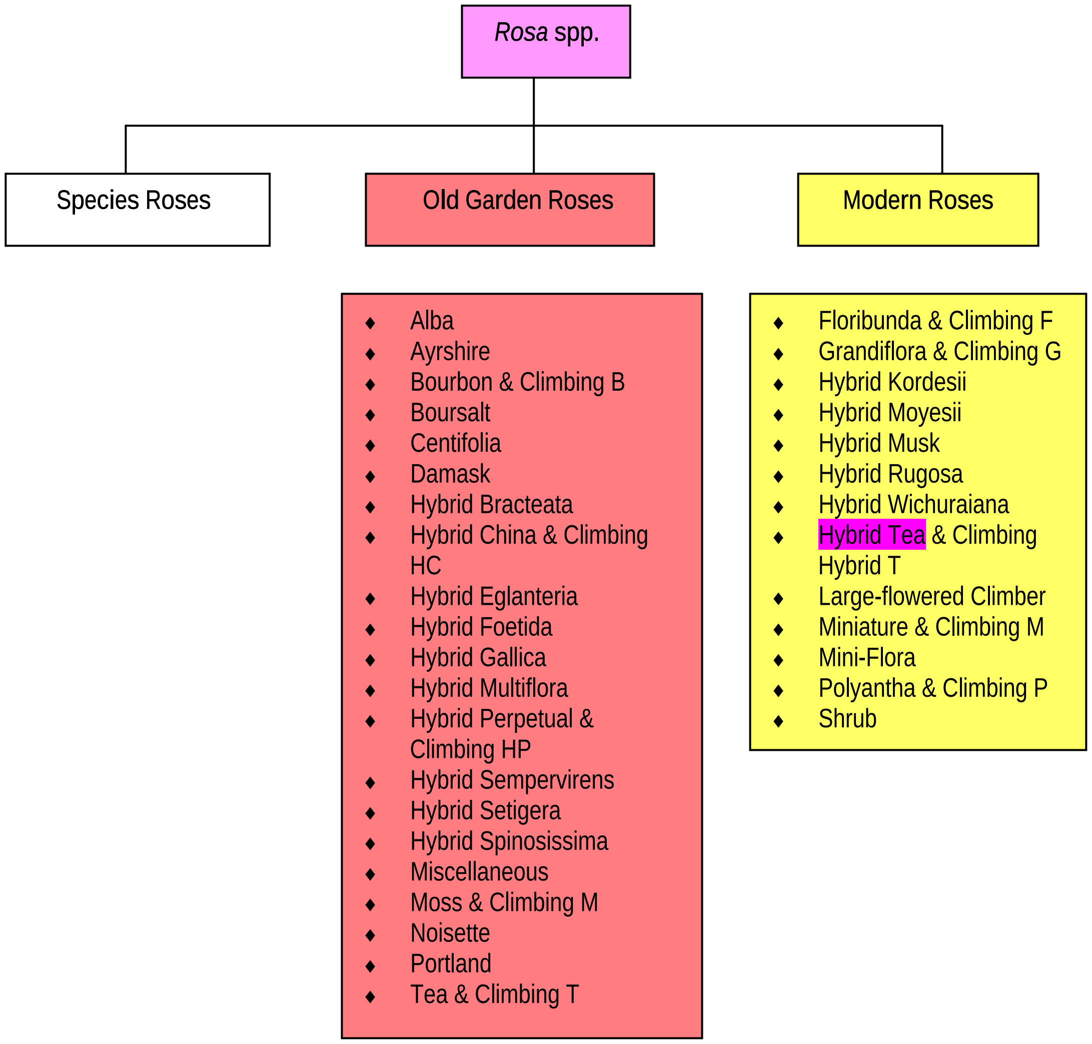

Figure 1. **Classification of cultivated roses according to the American Rose Society Classification Scheme 2000** (taken from Cairns 2003).

2.2 Commercial use

Roses are the world’s most traded cut-flower. Nearly 70% of this trade is with the EU and figures for the top cut flower species sold at the Netherlands auctions (see Table 2) can be used as an indicator for the best sold cut-flower species in the EU).

Table 2. **Top 5 cut flowers from 2001 – 2007 (Netherlands auction turnover € 1,000,000)**[**]

Species	2001	2002	2003	2004	2005	2006	2007
Rosa	653.0	699.8	681.3	705.9	728.6	758.2	795.4
Chrysanthemum (identified as ‘raceme’ from 2003)	289.1	307.1	299.1	285.3	293.1	300.2	296.0
Tulipa	177.3	171.2	185.9	185	191.5	223.0	204.6
Lilium	155.9	168.1	160.0	158.3	164.1	166.7	171.2
Gerbera	103.8	107.7	105.9	115.9	121.2	122.2	126.2

[**] Data compiled from Flower Council of Holland (2007), available at < http://www.flowercouncil.org/int/>

There are basically five main types of roses grown for cut flowers (see Table 3). Figures on the breakdown of the individual classes of *Rosa* that comprise the cut-flower industry are not available. While production used to be centred in Europe and Israel there has been an increasing shift to less developed countries such as India, China and those in South America and Africa (Pertwee 2000). The largest production areas are in Colombia, Ecuador and Kenya (Blom & Tsujita 2003).

Table 3. Characteristics of rose cut-flowers (Pertwee 2000)

Cut-flower type	Class	Feature	Relative production (stems/m^2/year)	Main production areas
Long stemmed	Hybrid Tea	50 – 100 cm stem length; large flowers; 1 fllower/stem	90 -140	USA, Colombia, Ecuador, Mexico, Japan, Zimbabwe, Morocco, France and Italy
Medium stemmed	Floribunda	50 – 70 cm stem length; 1 flower/stem	220	Africa (Kenya, Zimbabwe)
Short stemmed	Floribunda	35 – 55 cm stem length; small flowers; 1 flower/stem	200 - 300	Israel, Africa (Kenya, Zimbabwe), Colombia
Spray roses	Floribunda	approx. 5 blooms/stem		No large-scale production
Miniature roses	Miniature	20 – 40 cm stem length		No large-scale production

While Hybrid Tea roses are grown specifically by commercial flower growers for the cut-flower market they are, to a lesser extent, also used for domestic and industrial landscaping.

Roses have supplied ingredients for use in the perfume and food industries but the Hybrid Tea roses are not the traditional sources of these commercial ingredients, although home growers could possibly utilise them.

- Rose oil is obtained from the petals of rose species such as *R. damascena* and *R. centifolia.* There are two main types of extraction processes (Collin 2003): distillation in which the essential oil (known as rose 'attar') is steam-extracted, and solvent extraction in which purified petroleum ether or benzene are used to dissolve the natural perfume together with some waxes and colour. The latter process eventually yields products known as rose 'concrete' (that contains the natural pigments, waxes and colourings) and rose 'absolute' (that is a highly refined oil representing the most concentrated oil used commercially). Rose oil products are used in perfumes, food flavouring and liqueurs.
- Rose water is also obtained through treatment of rose petals but is much less concentrated than rose oil and can be made using a variety of methods (Cutler 2003). It is used for medicinal, culinary and celebratory purposes.
- Rose hips (the fleshy false fruit of the rose plant – see Section 3.2) particularly those from *R. canina, R. moschata* and *R. rubiginosa* can be utilised to produce a range of products for human consumption such as jams, jellies, marmalades, soup (nyponsoppa is a traditional dessert soup in Sweden), herbal teas, wine, mead (rhodomel is made from rose hips or petals) and rose hip syrup (Widenfelt et al. 1975; Johns & Stevenson 1979; Uggla & Nybom 1999; Cutler 2003; Çinar & Çolakoglu 2005). Hips are high in Vitamin C (see Section 5.3). Chile is a

significant exporter of dried rose hip peel and fruits, and Germany is a major importer (Joublan & Rios 2005).

- Rose fruits (achenes – see Section 3.2) are crushed to produce an oil (called rosehip **seed** oil as the fruit and the seed are essentially a single, inseparable unit – see Section 3.2) that is used in skin products. Commercially, the oil is obtained from the fruits of *Rosa rubiginosa* that grows wild in the south-central Andes. The oil contains the fatty acids oleic and linoleic acid as well as retinoic acid (vitamin A acid) (Rose 1999; Çinar 2005).
- Whole rose flowers may also be eaten (see eg http://www.marketfresh.com.au/flowers/2_flowers_guide/Edible_flowers.asp, accessed 24 November 2008)

In a recent review that summarized the pharmacological and clinical effects of *R. canina* hips and seeds Chrubasik et al. (2008) discussed evidence for a range of health claims associated with hip and seed products. They concluded that certain antioxidative and anti-inflammatory effects have been demonstrated.

2.3 Cultivation in Australia

It is likely that roses were first brought to Australia early in white settlement at the end of the eighteenth century (Cox 1999), and by 1893 the first rose nursery had been established in Melbourne (Brichet 2003). In 1920 the first rose catalogue was produced and growers began to be licenced to grow stock from the northern hemisphere (Brichet 2003). There have been several notable Australian rose breeders who have produced garden roses, including Hybrid Teas for particular Australian conditions (discussed in Cox 1999). As well as *R.* x *hybrida*, many other *Rosa* species have now been introduced into Australia as nursery stock (see eg AQIS 2008). The Hybrid Tea rose is the most commonly grown class in Australia and New Zealand (Ross 1991).

Roses for the garden will grow in most parts of Australia, but are more difficult to manage in hot tropical regions, due to the diseases such as black spot which are more prevalent in hot humid areas. Roses are tolerant of a range of conditions but grow best in full sun, in a temperate climate, in a well-drained sandy or clay loam with a pH of 6-7 (Ross 1991). In 1996 the National Rose Trial Garden of Australia (http://www.nationalrosetrialgarden.net.au/about.htm, accessed 24 November 2008) was initiated. It is a joint venture between the Botanic Gardens of Adelaide, the Rose Introducers of Australia and the National Rose Society of Australia. The trial garden itself is located within the grounds of the Botanic Gardens of Adelaide. The main purpose of the Trial Garden is to provide controlled conditions for assessing the suitability of a wide range of rose cultivars (most of which have been produced in the Northern Hemisphere) for Australian conditions.

Roses for cut-flower production are usually grown under cover (eg glass, acrylic, polyethylene) to prevent rain from getting into the blooms and giving rise to fungal problems (Pertwee 2000). Traditionally, the plants have been grown in soil beds but recent evidence suggests that hydroponic systems[2] for cut-flower rose production are becoming more prevalent in Australia (Hassall & Associates Pty Ltd 2001; Carruthers 2002). Soilless rose production systems have been used in other countries, especially

---

[2] Hydroponics is the production of crops in isolation from the soil, either with or without a medium, with their total water and nutrient requirements supplied by the system (as defined in Hassall & Associates Pty Ltd 2001).

Europe and Israel for about 30 years and increasingly there has been an emphasis on cost-effective, environmentally friendly systems in which substrates and nutrients can be recycled (van Weel et al. 1992; Anderson & Woods 1999; Blom & Tsujita 2003) – see Section 2.3.3. As an example of the scale of production, one major grower in Australia has approximately 30,000 m^2 under glass devoted to hydroponic cut-flower rose growing (Carruthers 2002).

2.3.1 Commercial Propagation

Propagation of roses by seed is used in breeding new cultivars or in the production of rootstock plants of some species such as *R. canina* (for a detailed discussion of seed propagation see Gudin 2003b). Cultivars are not seed propagated because germination is often problematic and because seed derived progeny will segregate widely for traits and therefore have characteristics that differ from the parents (Zlesak 2006).

Traditionally, roses are supplied to the grower as grafted plants in which the cultivar is grafted onto a rootstock. Grafting is a technique in which parts of different plants are physically combined and continue growth as a single plant (Hartmann & Kester 1975). The part of the graft combination which constitutes the upper part of the plant is referred to as the 'scion'. Rootstocks may affect (either directly or indirectly) scion characteristics such as plant architecture, vigour, nutrient status, flower yield and quality, disease resistance and response to environmental conditions (Pertwee 2000; Cabrera 2002; Solís-Pérez & Cabrera 2007)

For roses, the most common method of grafting is referred to as T-budding (or shield budding) so called because of the shape of the cut that is made in the rootstock (Hartmann & Kester 1975). Essentially the technique involves slicing out a shield of bark containing the scion bud and inserting this into the T-cut made in the bark of the rootstock. The bud union is then tightly wrapped and, over a period of time, the vascular systems of the rootstock and the bud will combine and eventually the bud will break dormancy and develop into a shoot.

The Old Garden roses, English roses (hybrids of some of the Old Garden roses as well as of Old Garden roses and Hybrid Teas and Floribundas) and Miniature roses grow vigorously on their own roots and are often not grafted (Costa & Van de Pol 2003). Recent trends in rose cut-flower production (Hybrid Teas and Floribundas) have seen more own-rooted varieties being used for these types (de Vries 2003). However, it is generally held that own-rooted cut-flower plants do not perform as well as grafted plants (Safi 2005). In Australia, with its wide range of climatic conditions and soil types, particular rootstocks are more favoured for particular areas; in Western Australia *R. fortuneana* develops roots that are suited to penetrating light soils, *R. multiflora* is widely used in the cooler climates and neutral- acid soils of south-eastern Australia (New South Wales, Victoria, Tasmania and South Australia), and *R. indica* 'Major' is suitable for the hot, dry alkaline conditions of inland Australia (Brichet 2003).

Rootstock propagation

Rootstock plants for grafting can be propagated from seed ('seedling rootstocks'), but most often are clonally propagated using soft or hardwood cuttings and are referred to as 'clonal rootstocks' (de Vries 2003).

Seedling rootstocks comprise 1 year-old plants grown from seed produced by purpose-grown seedbushes and currently in Europe there are 10 major seedling rootstocks : *R. corymbifera* 'Laxa', *R. multiflora*, *R. rubiginosa* and seven *R. canina* types (collectively known as Edelcaninas). *R. multifora* is popular because it is thornless and not prone to suckering (Hartmann & Kester 1975). Seedling rootstocks are used mainly for budding to make shrubs of Hybrid Tea, Floribunda, English and climbing roses (Akkerman 2003).

In areas of severe cold winters, hardwood cuttings made from mature, quiescent, lignified shoots after the leaves have abscised (Costa & Van de Pol 2003) are taken in late fall or early winter from the previous year's canes (6 to 10mm diameter). Bundles of 15 to 20cm long cuttings are stored in damp peatmoss at about 4°C for the winter and then planted out in the nursery in spring. In milder climates, hardwood cuttings can be taken in the fall and planted directly to the nursery. Hardwood cuttings are ready for T-budding in the first spring after planting in the nursery. Softwood cuttings (made from non-lignified, new-growth stems with a low dry-matter content – (Costa & Van de Pol 2003)) are taken from current season's growth anywhere from early spring to late summer. The timing depends on the new growth becoming partially mature. Rooting of the softwood cuttings occurs in 10 to 14 days under ideal nursery conditions (shading, adequate moisture and good soil contact) and these cuttings can be ready for T-budding in the fall (Hartmann & Kester 1975).

Older clonal rootstocks that have been used include *R. indica* 'Major', 'Manetti' and 'Dr Huey'[3]. A number of vigorous clonal rootstocks have been bred recently including the cultivars 'Moneyway' and 'Marleen' both using *R. multifora adenochaeta* as a progenitor, several *R. canina* 'Inermis' types, and 'Natal Briar', a particularly vigorous rootstock that is used in 80% of rose cut-flower grafted plants in Europe (de Vries 2003).

Grafted plants

Grafted plants are provided to cut-flower growers in one of a number of sizes (information taken from Pertwee 2000 unless otherwise specified):

- Rooted cutting (takes 8 months to bloom): A number of scion buds are grafted onto a rootstock shoot and when they have set the rootstock shoot is cut above and below the graft to make a cutting that is then rooted. A technique known as 'stenting' produces a similar outcome but involves the grafting of a scion stem (with a leaf and a dormant bud) onto the top of a non-rooted rootstock; formation of the graft union and of adventitious roots on the rootstock occur simultaneously (Van de Pol 2003).
- Started Eye (takes 5 – 7 months to bloom): The scion bud is grafted in spring onto a rootstock that has been growing in the field for several months. The bud is prevented from breaking dormancy by the presence of the terminal bud on the rootstock shoot. When the plant is required by the grower, the shoot is cut back to just above the bud and the plant is then lifted.
- One Year Plant (takes 6 months to bloom): This technique is similar to the above except that the rootstock shoot is cut back immediately so that the bud develops into a shoot. The plant is lifted about 6 months later (autumn) and is often then cold stored for a month or so until required.

---

[3] A number of rose rootstocks are referred to just by their cultivar names, presumably because of complex or unknown parentage.

- One and a Half Year Plant (takes 3 months to bloom): This technique is similar to the above except the plant is lifted in the second autumn and is therefore well advanced.

Micropropagation

More recently, micropropagation has been used for propagation and has particular potential to rapidly build up numbers of plants for new releases (see discussion in Roberts & Schum 2003). However, the cost of production, particularly the labour component, is an impediment to the commercial utilization of micropropagation. A feature of micropropagated plants is that they are own-rooted; as discussed above, with advances in growing technology, there has been increasing interest in the use of own-rooted roses especially for pot roses. In the case of Hybrid Tea roses, most growers prefer to graft on to rootstocks to ensure vigour and good flowering.

2.3.2 Cultivation Practices

Roses for the home garden

(information from Phillips & Rix (1988) and Cultural Notes from Treloar Roses website <http://www.treloarroses.com.au/default.asp?contentID=5>)

Rose plants are usually purchased as bare-rooted stock and are planted in autumn, winter or early spring (June & July in Australia) into dry, crumbly soil (eg medium to heavy loam) with some mulch (such as peat, leaf mould, pea straw) on the surface. The hole for each plant should be approximately 30 cm in diameter and 25 cm deep and have a small mound at the bottom over which the roots are spread. Before planting, the roots of the plants should be thoroughly soaked in water and after planting the plants should be watered in thoroughly. The graft union should remain approximately 5 cm above soil level. Fertilizer (especially rotted manure or blood and bone) is best added around the roots once new growth begins. Preventative spraying helps to reduce pest and disease problems (see Section 7.2).

Most roses should be pruned to maintain strong healthy growth and a good shape and this is usually done significantly once a year in late winter/early spring when there is no chance of frost damaging the tender new shoots. Pruning is also carried out to some degree when flowers are harvested or ‘dead-headed’ (removal of spent flowers). With the spring pruning, shoots can be heavily pruned (removal of 50% or more of the length) such that an outward facing bud is left below the excision point. This bud will then develop into the next season’s wood (see Section 4.5 and Figure 6). The more severe the pruning, the fewer but larger the flowers that will be produced.

Cut-flower roses

The ideal conditions for growing cut-flower roses can be supplied by growing them under glass/plastic using varying levels of automation and sophistication, and include (Pertwee 2000):

- a temperature ranging from 28° C daytime mean maximum to 15° C night mean minimum
- a minimum of 10 h/day light
- the ability to raise and maintain humidity if temperatures exceed 25° C
- good air circulation
- clean and abundant water

- well-aerated growing medium
- good nutrition.

Irrespective of the medium in which the plants are grown, a number of factors are involved in production. These are covered in some detail by Pertwee (2000) and Blom & Tsujita (2003) and basically involve striking a balance between leaf area and production of strong stems that will yield high quality blooms. Over 75% of the biomass production for a rose crop is due to light interception and a ratio of leaf surface area : greenhouse area of 4 – 5 is considered optimal (Blom & Tsujita 2003). Numerous models have been devised to estimate and optimise greenhouse performance (see eg Dayan et al. 2001). The factors to be considered in production include (Pertwee 2000; Blom & Tsujita 2003):

- Planting Material: There are a number of size choices for planting material which traditionally consists of a selected rootstock onto which the cultivar has been grafted or budded (see Section 2.3.1). Selection of planting time needs to coincide with market requirements (eg Valentines Day) and/or best prices. The time taken between planting and first bloom depends on the size of the planting material (see Section 2.3.1).
- Early Growth: It is important to build up root energy stores that will be used later to support strong shoot growth. Basal shoots are allowed to develop but flower buds are removed as soon as they appear so that energy is not lost to flowers. New shoots that arise at the top are removed leaving only a few basal shoots. The original main shoot is then also removed leaving the basal shoots to produce approximately 2 strong, flowering shoots. This process is referred to as ‘deshooting’ and may be repeated a number of times.
- Bending: In order to better facilitate light interception the process of ‘bending’ is often carried out (see also Lieth 1998). It involves bending undesirable/non-harvestable stems outwards so that light is accessible to the photosynthesising leaves low down on the stem. The effect of bending is the same as shoot removal in that apical dominance is removed and secondary shoots can develop (see also Section 4.5). Wire supports along the beds assist in holding up stems.
- General Horticultural Practices: These include pruning out weak stems, disbudding flower buds (to remove assimilate competition from the main flower bud in the case where there may be several buds close on the same stem), pinching (removing the upper section of a growing shoot in order to stimulate the development of a new shoot that will flower at a desired date (Lieth 1998)), preventative spraying against pests and diseases, and addition of fertilizer. Annual pruning and resting of plants can be done and would normally occur in winter when light and temperature are not optimal for growth. However, as cut flowers command premium prices over the winter period, many growers supplement lighting and heating over winter in order to maintain flower production and may then prune (and rest plants briefly) in summer. Plants are generally kept for up to 7 years before being replaced.
- Harvesting: This is done by hand and can be hampered in those varieties that require disbudding and/or have prickles. More recently there has been the development of systems to test mechanized harvesting (see eg García Victoria et al. 2007). The stage of development at which a flower bud is harvested is crucial for subsequent opening and depends to some extent on the cultivar and the

anticipated transit time before sale. Buds cut prematurely may fail to open and in a commercial setting this can be as disadvantageous as buds that are cut too late and open too fast. Harvesting may be carried out several times a day if plant development is fast. Cut stems must immediately be placed in clean water before transfer to a packing centre where they are graded and held in cool storage (Çelikel & Reid 2005) before transfer to the distribution chain. Flowers are often wrapped in plastic netting to minimise bruising. Typical yields are given in Table 3. In Australia there are three major flower markets – The National Flower Centre in Melbourne (http://www.melbournemarkets.com.au/); the Sydney Flower Market (http://www.sydneymarkets.com.au/index.html) and the Brisbane Markets (http://www.brisbanemarkets.com.au/cms/) [all 3 websites accessed 24 November 2008].

Basically there are two types of systems in which cut-flower roses are grown:

- Soil Systems (Pertwee 2000; Blom & Tsujita 2003)

  If rose plants are grown in soil, the soil should be a rich (approximately 30% organic matter in the top 40 cm), well-aerated loam with a pH of 5.5 – 6.0. The layout of planting beds depends on the shape and size of the covered area but they are often 1 – 1.5 m in width and 30 – 40 m long. The width is determined by the reach of pickers, and lengths of > 40 m cause inefficiencies in moving flowers to the end of the beds. Commonly 4 rows are planted per bed with plants 34 – 36 cm apart but this varies with the production system. Depending on climate, heating pipes that run along the side of the beds may be required. The irrigation system should be set below the leaves as water damage can affect leaf and flower quality. Irrigation water needs to be drained away and this is often achieved by laying perforated plastic tubing under the beds. Movement of water away from the plants is achieved by having slightly sloping land or a pumping system. In most cases, plants are fertilized through the irrigation lines ('fertigation') with the fertilizer regime depending on the growing conditions.

- Soilless Systems (Hydroponics) (van Weel et al. 1992; Anderson & Woods 1999; Hassall & Associates Pty Ltd 2001; Carruthers 2002; Blom & Tsujita 2003)

  Hydroponic (see Section 2.3 for definition) production for commercial products (lettuce and carnation) was first used in Australia in the early 1970's. There are two categories of hydroponic systems, a) water-based systems used for short-term crops such a lettuce and b) media systems that employ an artificial substrate and are used predominantly for long-term vegetable and flower crops. The use of artificial substrates in rose cut-flower production was first introduced in Europe in the 1980's. The substrates that are used may be inorganic (eg rockwool [a proprietary medium similar to fibreglass insulation – manufactured as Growool in Australia], sand, scoria, perlite, vermiculite, pumice, expanded clay) or organic (eg sawdust, peat, coconut fibre, bark, foam products, processed wood products, gel products).

  Nutrients and water are supplied together through fertigation with monitoring equipment and automation ensuring that the pH and nutrient levels are optimal. Run off is collected and may be sent to waste or can be recycled, depending on the sophistication of the system. Planting densities and therefore yields are higher than in soil.

2.4 Crop improvement

Modern *R.* x *hybrida* cultivars are the result of a long history of rose development through many centuries (see Section 2.1). These roses are highly selected varieties which are vegetatively propagated. They are selected for defined traits such as flower bud and flower qualities (shape, colour, fragrance), stem length, and vase life. Traits that have become important in cut flower roses are often linked to the technological level in which the plants are grown. Thus thornless stems (useful when there is mechanical bunching) and ability to perform well on own roots (this avoids grafting) are beneficial in the high intensity, soilless cultivation systems favoured in northern Europe but are not so relevant to the more traditional production techniques used in a developing country such as Colombia (Gudin 2003a). Over the last 40 years of breeding of cut flower roses, fragrance has been compromised but is now desired by consumers and therefore contributes to commercial value. There has been a long-held view that fragrance is negatively correlated with vase-life (see eg discussion in Zlesak 2006) but recent studies would suggest that this is not the case (Borda et al. 2007). Analysis of fragrance genes (eg Shalit et al. 2003) will provide a basis for generating roses with improved or modified fragrance

Breeding to modify a single characteristic generally results in changes to other characters as well. Thus, current crop improvement strategies incorporate molecular biology techniques to improve *R.* x *hybrida* (see review by Rout et al. 1999). Random amplified polymorphic DNA (RAPD) and restriction fragment length polymorphism (RFLP) markers have been used to determine genetic relatedness of siblings (Vainstein et al. 1995), for cultivar identification (Hubbard et al. 1992), phylogenetic analysis within and among *Rosa* species (Debener & Mattiesch 1999) and mapping rose genes for resistance to powdery mildew or black spot (Linde et al. 2004). Molecular markers have also been used to identify the source of crown gall disease in roses, which was found in many cases to be transmitted via infected rootstock material (Pionnat et al. 1999). The cloning of genes has been undertaken on a limited scale but larger scale cDNA sequencing or a rose genome project would contribute significantly to both traditional and molecular breeding of roses (Tanaka et al. 2003). Compared with many other crop species, the genetic knowledge of roses is still small and, for example the inheritance of only a few horticultural traits is known; this makes it difficult for breeders to be able to combine desired characteristics (Gudin 2003a). Good reviews of rose breeding objectives and technologies have been written by Gudin (2000; 2001)

Manipulation of ploidy levels and embryo rescue have both allowed complex interspecific cross breeding (see Section 9.3) that would not otherwise be possible.

Mutation breeding has also been attempted in rose improvement although adequate diversity can be generated by cross-breeding. It is perceived as a method for modifying and improving, albeit randomly, single traits while conserving the original genome of elite germplasm (Schum 2003). Similarly, genetic modification has also been attempted in order to introduce single traits. To date the only commercial genetically modified rose lines that are available have been altered for flower colour (see Section 2.4.3).

2.4.1 Conventional Crossing

Rose breeders around the world carry out many hundreds of thousands of crosses each year, mainly amongst improved garden/cut-flower roses most of which are tetraploid and therefore represent compatible crosses (Spethmann & Feuerhahn 2003) although seed set may be low (see Section 4.3). The seedlings develop flowers early, often in the first year (Spethmann & Feuerhahn 2003), an important logistical factor in a commercial breeding programme. In broad terms there is no difference between the breeding of garden and cut-flower roses (de Vries & Dubois 1996).

The majority of species in the *Rosa* genus have not contributed to the creation of the Modern Roses and represent a considerable pool of genetic material (eg disease resistance, growth habit) that might usefully be incorporated into Modern Rose cultivars through interspecific breeding (Zlesak 2006). It is estimated that only 5 – 10% of the Species Roses have been included in breeding programmes (Spethmann & Feuerhahn 2003) due to a number of barriers, significant of which are the differences in ploidy, with many species roses being diploid and the Modern Roses being predominantly tetraploid (see Section 1). Other reasons why such crosses may not be horticulturally useful have been discussed by De Vries & Dubois (2001) and include: no guarantee about the mode of inheritance of a desirable trait (eg fungal resistance); germination of the F1 starts in the second year; F1 plants do not flower in the year of seed germination; F1 plants are not recurrent flowering; and horticultural quality of F2s may be dubious. These factors mean that breeding programmes involving species crosses with Modern Roses are time-consuming and expensive.

The fertility of Modern Roses is often low due, in part to meiotic abnormalities and the accumulation of deleterious recessives as a result of the long history of crossing heterozygous, polyploid parents (Zlesak 2006). Inbreeding becomes further compounded when breeders tend to use a limited number of more fertile cultivars and ultimately the genetic base has become eroded (de Vries & Dubois 1996).

In general, it can be said of *R.* x *hybrida* that the gene pool is limited for some traits, distant crosses are limited through incompatibility or differences in ploidy levels among parents, and characters such as uniform growth and synchronous flowering are polygenic (Rout et al. 1999).

Conventional breeding programmes of the rose focus on improvements of various characteristics to enhance ornamental value including colour, size, form and keeping quality of the bloom and plant response to the environment. Spethmann & Feuerhahn (2003) discuss a number of useful traits that could potentially be introduced from Species Roses.

The strategies and procedures for breeding and selecting roses for the cut flower market are detailed in eg Chaanin (2003) and Spethmann & Feuerhahn (2003). It takes at least 5 years from crossing to introduction of a promising line onto the market and this time is basically divided into 3 stages involving 1. Creation of genetic variability by crossing, 2. Selection and testing of elite plants and 3. Propagation of selected plants and market introduction. As an example of the efficiency of the breeding strategy Chaanin (2003) cites one example where 1000 initial crosses provide 4 – 6 marketable lines. Rose breeding is mainly carried out by amateurs or commercially by highly competitive companies, thus the genetic knowledge is often proprietary and unpublished (Gudin 2000). Professional and amature hybridists have bred many roses specific for Australian conditions (Cox 1999).

2.4.2 Mutation Breeding

Mutations, commonly known as ‘sports’, can arise by chance during routine rose cultivation and have resulted in new commercial cultivars. One of the most well known Hybrid Tea cultivars 'Peace' has given rise to 21 sports (Roberts & Lewis 2003). Alterations to flower colour or form are particularly sought after in the Hybrid Teas.

At least two features in the Modern Roses have been incorporated through crossing with sports that have arisen in a Species Rose:

- Recurrent-flowering (see Section 4.1.2) first occurred in *R. chinensis* and was first used in breeding in China 1000 years ago (Roberts & Blake 2003). The mutant gene (everblooming = *evb*) is recessive and both reduces the length of the juvenile stage and eliminates the requirement for vernalization between flowering flushes (see discussion in Hess et al. 2007). Little is known about the gene apart from its classical genetics but development of a BAC library of *R. chinensis* 'Old Blush' will allow molecular cloning and analysis of the gene (Hess et al. 2007).
- Recently, it has been found that the 'tea' scent for which the Tea roses were named is accounted for by a volatile molecule (3,5-dimethoxytoluene), the production of which is due to a natural mutation (single amino acid polymorphism) in a key enzyme in *R. chinensis* (Scalliet et al. 2008).

Induced mutations have been used to create a number of new rose cultivars, especially with unique flower characteristics. Both γ-rays (eg Gupta & Shukla 1971) and X-rays (eg Walther & Sauer 1986) and, more recently, ion beam irradiation (Yamaguchi et al. 2003) have been used to irradiate *in vitro*-derived shoot meristems. Roberts & Lewis (2003) list several examples of rose cultivars with altered flower colour derived through mutagenesis. According to Schum (2003) there were 64 commercial rose induced-mutants in total produced up to the year 2000, with the mutations ranging through characteristics such as flower colour, petal number, leaf size, leaflet number, plant growth habit and pathogen resistance. A comprehensive discussion of mutation breeding in rose is included in reviews by Broertjes (1988) and Schum & Preil (1998).

2.4.3 Genetic modification

Early experiments with rose established plant tissue culture regeneration systems, a necessary precursor to successful transformation. Rose explants are able to regenerate from a variety of explants via two main pathways – shoot organogenesis (either direct or indirect from callus) and somatic embryogenesis via callus (see discussion in Schum & Dohm 2003). However, protocols often require refining for individual genotypes and regeneration frequencies can be low.

All genetic modification systems to date have involved gene transfer to callus tissue and then regeneration of somatic embryos. The first report of genetic modification of *R.* x *hybrida* was by Firoozabady et al. (1994), who developed an *Agrobacterium*-mediated system for 'Royalty' and recovered somatic embryos (containing various marker genes) from callus derived from stamen filaments (Noriega & Söndahl 1991). This system was, however, strongly cultivar dependent. A biolistic-mediated modification system was developed by Marchant et al. (1998) for the Floribunda rose *R.* x *hybrida* 'Glad Tidings' and somatic embryos (containing the marker gene *nptII)* were obtained from callus derived from petioles. A three-step regeneration procedure for *R.* x *hybrida* involving callus induction on excised adventitious roots formed on stem slices, induction of somatic embryos, and outgrowth of shoots, was developed by van der Salm et al. (1996). This system was then used to obtain genetically modified plants (expressing the *ROL* genes from *Agrobacterium rhizogenes*) via *Agrobacterium*-mediated transformation (van der Salm et al. 1997). The protocol is considered to be a robust one for genetic modification of *R.* x *hybrida* but there has been further refining of the technique (see eg Condliffe et al. 2003).

Initially, genetic modification involved the expression of marker genes but as procedures have become more refined the emphasis has shifted to modification involving traits such as flower colour and disease resistance. As examples:

- Souq et al. (1996) modified 'Madame G Delbard deladel' using a gene encoding chalcone synthase (the first committed enzyme in flavonoid biosynthesis - see Section 5.3) to alter the anthocyanin biosynthetic pathway in an attempt to obtain white flowers.
- A range of colour modified *R.* x *hybrida* lines have been obtained by inserting other genes in the anthocyanin biosynthetic pathway (flavonoid 3',5'-hydroxylase, anthocyanin 5-acyltransferase, dihydroflavanol-4-reductase) in order to incorporate the 'blue' delphinidin pigment into flowers (OGTR 2006; Katsumoto et al. 2007; JBCH 2008a; JBCH 2008b).
- Enhanced resistance to powdery mildew was observed in GM *R.* x *hybrida* 'Carefree Beauty' modified with an antimicrobial protein gene (Li et al. 2003).
- Genetically modified *R.* x *hybrida* rootstock 'Moneyway' containing *rol* genes from *A. rhizogenes* showed a threefold improvement in adventitious rooting of cuttings (van der Salm et al. 1997).

Approval for the commercial release of two GM *R.* x *hybrida* lines modified for flower colour was made in Japan in 2008 (JBCH 2008a; JBCH 2008b). Field trials of GM *R.* x *hybrida* lines modified for flower colour have been approved in Australia (OGTR 2006), California (see information in APHIS 2008) and Colombia (public documentation not available). Field trials of GM fungal resistant *R.* x *hybrida* have been approved in New York state (see information in APHIS 2008).

SECTION 3 MORPHOLOGY

3.1 Plant morphology

Across the *Rosa* genus, stems can be erect, trailing or climbing (Walsh & Entwisle 1996; Harden 2000). Hybrid Teas have erect stems and usually form plants that are 1 – 2 m tall.

Recurrent flowering roses such as the Hybrid Teas are perennial woody shrubs that continuously produce new shoots. Basically, a shoot comprises a succession of 8 – 15 repeating units, each one consisting of a leaf, an axillary bud a node and an internode (Blom & Tsujita 2003). The Modern Rose cultivars are largely sold as grafted plants or cuttings and growth consists of the development of a number of branches on the initial propagule as a result of the activity of axillary buds after release from inhibition/apical dominance (see Section 4.5). These branches then produce a further succession of axillary shoots (André 2003). Whether plants are grown commercially for their blooms or are in managed gardens, it is common horticultural practice for annual pruning to be done (see Section 4.5). This pruning plays an important part in determining the nature of subsequent growth.

Stems of rose plants characteristically bear prickles (Figure 2), often mistakenly referred to as 'thorns', that originate from the epidermal layer and are usually more densely distributed at the proximal (basal) end of the stem (André 2003). Many cultivars of Modern Roses have been bred to have no or few prickles.

Figure 2. **Prickles on the base of a rose stem.** [Photo credit: Janet Gorst, OGTR]

Roses have compound leaves (a number of leaflets borne on an axis called a rachis) and the arrangement of the leaflets is odd-pinnate (see Figure 3). The middle leaves of Hybrid Tea roses usually have 5 - 7 leaflets, while some Asiatic species may have up to 19 leaflets (Torre 2003). At the base of each rachis there are structures called ‘stipules’ (leaflike appendages) that are adnate (closely attached) to the rachis (Figure 4).

Figure 3. **Odd-pinnate (5-leaflet) leaf of a Hybrid Tea rose. The leaf is termed pinnate because the leaflets arise on both sides of the rachis; the leaf is odd-pinnate because the leaflets are in pairs except for the solitary leaflet at the tip.** [Photo credit: Janet Gorst, OGTR]

Figure 4. Young leaf (just below a flower) showing adnate stipules (arrowed) at the base. [Photo credit: Janet Gorst, OGTR]

Leaves differ in morphology depending on where they are produced on the stem (Figure 5). Leaves at the base of new shoots tend to be scale or bract-like leaves consisting of fused stipules, middle leaves have the maximum number of leaflets and more recently produced leaves may have less than the maximum number of leaflets (Torre 2003). Except for a few species in southeast Asia, which are evergreen or nearly so, the vast majority of roses are deciduous (L.H.Bailey Hortorium 1976).

Figure 5. Variation in leaves on a hybrid tea rose stem. [Photo credit: Janet Gorst, OGTR]

There are two main types of shoots produced by rose stems (Zamski et al. 1985):

- shoots produced by buds in the axils of lower leaves and bract-like leaves are 'proleptic' ie undergo a period of inhibition (due to apical dominance) at a very early stage;
- shoots produced by buds in the axils of the uppermost leaves beneath the flower are 'sylleptic' ie grow continuously from their initiation without a period of inhibition.

This occurrence of the two shoot types is because apical dominance ceases when the vegetative apical bud is converted to an inflorescence and therefore vegetative buds close to the flower bud are not affected by apical dominance (Bredmose 2003). Both types of shoots initially make an angle of approximately 45° with the stem but the long proleptic shoots, which form the bulk of the plant structure (Figure 6), tend to straighten while the shorter sylleptic shoots maintain the angle (André 2003).

The morphology of the root system on a rose plant differs according to whether the root system develops on a seed-propagated plant, a rooted cutting (own-rooted plant), or a rootstock (grafted plant) – see Section 2.3.1. In addition, factors such as nutrition and pruning have a strong influence on root morphology (Skytt Andersen & Fuchs 2003).

Figure 6. New season proleptic shoots (arrowed) developing below the pruning cut (circled) done in early spring. [Photo credit: Janet Gorst, OGTR]

3.2 Reproductive morphology

The flowers of the wild species in *Rosa* can be solitary, corymbose, or panicled and have 5 petals (except for *R. sericea* which often has only four petals (Wissemann 2003)), many stamens (50 – 250 depending on species) and many pistils (L.H.Bailey Hortorium 1976) (Figure 7). *R. setigera* is the only member of the genus in which male and female flowers are present on different plants (dioecious); the flowers also appear to be macroscopically similar and the plants are therefore referred to as 'cryptically' dioecious (Kemp et al. 1993).

Figure 7. **Flowers of the *R. chinensis* cultivar 'Mutabilis' showing 5 petals.** Note too, in this cultivar, the different petal colours of different flowers. [Photo credit: Janet Gorst, OGTR]

A stylized diagram of a typical flower is given in Figure 8. The flowers are said to be homogamous (the male stamens [anther + filament] and female pistils [stigma + style + ovary] mature at approximately the same time) and perigynous (the sepals, petals and stamens of each flower are attached to the margin of a cup-shaped receptacle/hypanthium – referred to as the 'hip'- which, in turn, surrounds many ovaries). Flowers generally have no nectar but produce copious quantities of pollen (Kevan 2003).

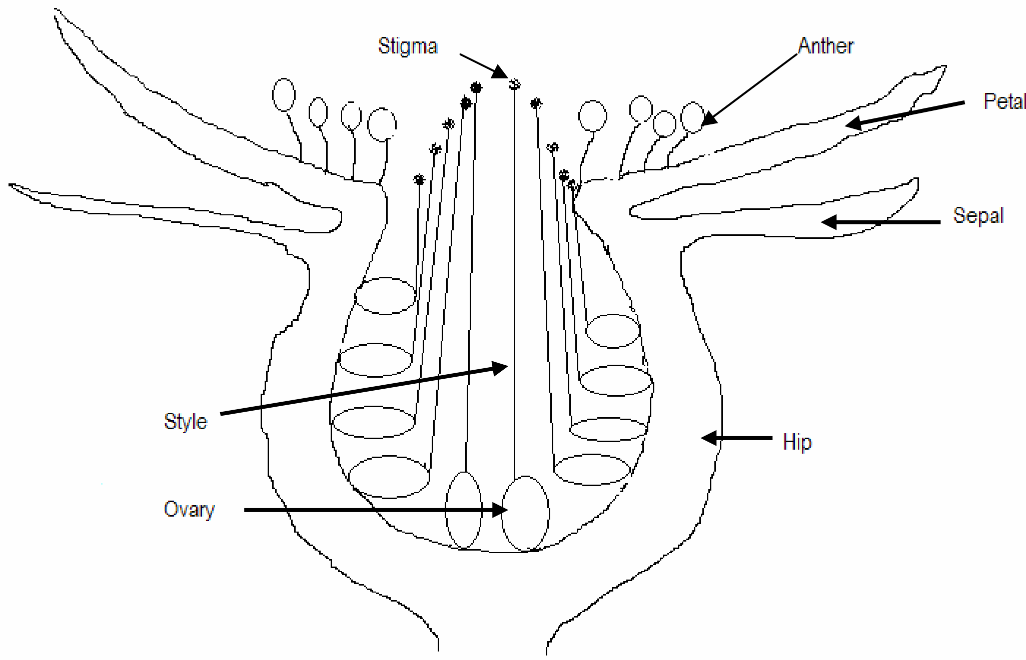

Figure 8. **Drawing of a typical flower of *Rosa* spp. showing the main parts**

The flowers of the Hybrid Tea cultivars (Figure 9) have many more petals than the flowers of wild species and show wide variability in the number of reproductive organs (see Table 4).

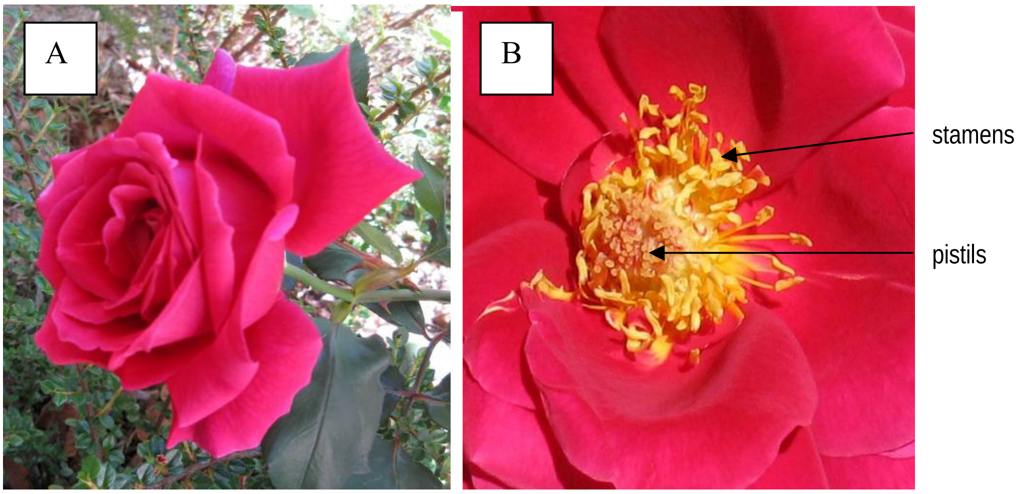

Figure 9. A) Flower of the Hybrid Tea cultivar 'Mr Lincoln' showing the arrangement of petals and B) the reproductive parts in the centre of the flower. [Photo credit: Janet Gorst, OGTR]

Plant Name	Flower Diameter (cm)	Petal Number	Pistil Number	Stamen Number
Febesa	9	23	146	106
Moerigna	8 – 9.3	30 - 35	80	50
Dr Bob Harvey	11.5	38 - 40	150	100
WEKvoosun	9 – 12.8	29 - 41	140	185
Meimarkize	8	97	172	57
KORtiglo	10 - 12	100 - 120	50 - 60	120 - 140
Meifacul	11 - 13	38 - 40	90	110
Hadque	11 - 12	34 - 36	146 - 156	165 - 175

Table 4. Flower descriptions of a range of Hybrid Tea roses that have been patented (information taken from entries in freepatentsonline http://www.freepatentsonline.com/)

Rose pollen is elliptical in shape with a constant ratio (2:1) length : width (Jacob & Ferrero 2003). Within the genus *Rosa* the size of pollen grains ranges from approximately 32 – 65 µm and there is a correlation between pollen size and ploidy level, particularly for diploid and tetraploid plants (Jacob & Pierret 2000).

The fruit (that develops from a fertilized ovary) of the rose plant is an achene (Figure 10) and is often mistakenly called a seed because of its small size and hard texture. In fact, each achene is really a single seed/fruit unit consisting of an embryo enclosed in a thin testa (seed coat) that is fused to the fruit by a thick pericarp (mature ovary wall) comprising an inner fibrous layer and an outer woody layer (Jackson & Blundell 1963). The achenes are contained within the hip. Mature rose hips are usually red, but a few (eg *R. spinosissima*) have dark purple to black hips (L.H.Bailey Hortorium 1976). The shape and size of the hip varies with species (Figure 11).

Figure 10. Achenes of *R. chinensis.* [Photo credit: Tracey Slotta. Provided by ARS Systematic Botany and Mycology Laboratory. Italy, La Mortola.. (http://plants.usda.gov/java/profile?symbol=ROCH)]

Figure 11. Section through a rose hip (unknown species) showing the achenes inside. The leaflike structures at the top are the remains of the sepals. [Photo credit: Éducation à l'Environnement http://environnement.ecoles.free.fr/index.htm]

SECTION 4 DEVELOPMENT

4.1 Reproduction

Across members of the genus *Rosa* there are multiple reproductive strategies that range from apomixis to outcrossing. In addition, vegetative propagation occurs naturally in some Species Roses and is widely used for commercial production of all cultivated roses for cut-flower and gardens/landscaping because seedlings derived from crosses show high heterozygosity and tend to segregate widely for traits.

4.1.1 Asexual reproduction

Many roses destined for use as cut-flowers or in the garden or landscaping are commonly propagated by stem cuttings (see Section 2.3.1). Undifferentiated cell divisions (callus formation) at the basal end of a cutting is a prerequisite for optimal development of adventitious roots (Costa & Van de Pol 2003). In a commercial setting a number of factors (eg the status of the mother plant from which the cuttings are taken, position of the cutting on the mother plants, carbohydrate status of the cutting, water status of the cutting, application of rooting hormones) effect how well cuttings strike and establish (Costa & Van de Pol 2003).

A lack of information to the contrary in the literature would suggest that Modern Roses do not reproduce vegetatively outside of a managed horticultural environment. Stem pieces that have been left on the ground after pruning have been observed to produce a few adventitious roots but only rarely (Graham Evans[4], personal communication); such pieces would normally be removed as part of cultivation practices.

Species Roses can show a variety of natural vegetative propagation mechanisms eg:

- The noxious weed, *R. canina,* that occurs in Australia (see Section 8.2) is able to reproduce vegetatively by suckering from the crown and by layering (development of adventitious roots on a stem that is still attached to the parent plant) and this leads to the formation of dense clumps (Parsons & Cuthbertson 2001). Suckering from the crown also occurs in the other Australian noxious weed, *R. rubiginosa*.
- *R. multiflora* canes root at the tip when canes touch the ground. New stems can also arise from root sprouts and rhizomes (Eastman 2003).
- It has been reported that mowing of the weed *R. bracteata* (Macartney Rose) in Texas (USA) pastures actually resulted in the cut canes being dispersed and forming adventitious roots if they were dropped in moist soil (Haas et al. 1970).
- *R. rugosa* is an invasive weed in many European countries and produces rhizomes that produce suckers as well as being able to break off and establish in new areas (Bruun 2005; Weidema 2006).

4.1.2 Sexual reproduction

Horridge and Cockshull (1974) identified 10 successive but distinct stages in the development of a flower and Maas et al. (1995) detailed these in scanning electron micrographs. These latter authors concluded that once a flower bud reaches a height: width ratio greater than 1.5 and also shows signs of pistil and stamen

---

[4] Graham Evans is the Head Gardner at the Old Parliament House & National Rose Gardens, Canberra

development then it has passed the critical stage in which adverse conditions may initiate flower abortion (see Section 6).

The Species Roses generally produce flowers only during a short (2 – 4 weeks) flowering season (seasonal-flowering), whereas the Modern Roses possess a recessive mutant gene (see Section 2.4.2) that permits flowering throughout the year (recurrent-flowering) if the plants are grown under glass or throughout the season if plants are grown outside (Roberts et al. 1999). In the first growing season, seasonal-flowering rose plants do not flower whereas the recurrent-flowering plants are able to produce flowers soon after germination (Roberts & Blake 2003).

Recurrent-flowering roses such as the Hybrid Teas have no specific environmental requirements for flowering (such as long days or vernalization) and are described as self-inductive (Horridge & Cockshull 1974; Chimonidou-Pavlidou 2000; Roberts & Blake 2003). There is a close relationship between the stages of vegetative and reproductive development (see Section 4.5). Soon after bud-break in spring, the apical meristem on a shoot changes from vegetative to reproductive providing that a certain number of leaves have been initiated. There is a suggestion that endogenous levels of gibberellins may be implicated in floral initiation (Roberts et al. 1999).

The recurrent-flowering roses are said to produce flowers in 'flushes'. In commercial cut-flower roses, the stem of a shoot bearing a bloom is cut so as to leave a few nodes. The axillary buds thus released from apical dominance (see Section 4.5) then produce new shoots from which another round of blooms (a flush) is produced. On stems in which the subtending shoot has been removed, both stem elongation and floral initiation in the axillary buds occur at approximately the same time; buds are not competent to initiate a flower as long as stem elongation is being inhibited by apical dominance (Horridge & Cockshull 1974).

Roses show a high degree of outcrossing and therefore have high levels of heterozygosity. However, the fertility of the Modern Roses is considered to be low since hip set and seed germination are often both less than 50% (Gudin 2003b).

4.1.3 Apomixis

Apomixis occurs generally across the Rosaceae family and within the genus *Rosa* is particularly associated with species in the section *Caninae* (Carneiro et al. 2006) where there is evidence that a small percentage of the offspring obtained from interspecific crosses within the section are the result of apomixis (see eg Werlemark & Nybom 2001). It has also been noted to occur in *R.* x *hybrida* (Crespel et al. 2001), albeit under artificial crossing conditions. Apomixis adds further taxonomic confusion to the *Rosa* genus because it helps to perpetuate inter-specific and intra-specific hybrids (Carneiro et al. 2006).

4.2 Pollen dispersal and pollination

The stigma is ready for pollination when it shows a shiny secretion; in most species this occurs shortly before the pollen in the same flower becomes viable (Spethmann & Feuerhahn 2003). The stage at which pollen is released (anther dehiscence) may vary across the genus, from when the flower bud is still closed to when it has opened, and is also affected by ambient factors such as humidity, temperature and solar radiation (Jacob & Ferrero 2003).

A wide range of insects may be attracted to rose flowers, not all of which may function as pollinators (Kevan 2003; Bruun 2005; Jesse et al. 2006; MacPhail &

Kevan 2007). Bumble bees (*Bombus* spp.) and honey bees (*Apis mellifera* – Figure 12) in particular collect pollen and are considered to be the main pollinators globally. Hover flies (Syrphidae) are also considered to be important pollinators. Invertebrates from several orders (eg Diptera, Coleoptera, Hymenoptera) are known to feed on pollen and could serve as pollinators of *Rosa* spp. (Jesse et al. 2006). Since flowers of most species are nectarless, the attraction of pollinators is to the pollen itself and it is likely that pollen odour may play an important role (Dobson et al. 1999). Other stimuli such as visual (appearance of the anthers; flower colour) and fragrance also influence the selection of flowers that will reward the pollinator. Bees perceive colour in the wavelength range 300 – 550 nm with maximum spectral sensitivities at 340 nm (UV), 430 nm (blue) and 540 nm (green) (see discussion in Gumbert et al. 1999) and it is widely held that blue flower colour is preferred by bee pollinators (Harborne & Williams 2000). However, others contend that colour *per se* is not significant in attracting bees (see discussion in Gumbert et al. 1999) and the example of Species Roses, which lack blue hues (see Section 2.1), would support this.

In the Australian context, *Apis mellifera* is widespread in all states of Australia; it is native to Eurasia and Africa and was introduced into Australia in the 1800s (Cunningham et al. 2002). There has been no work reported on the pollinator activities of native Australian bees but they represent potential pollinators. *Megachile* species (leafcutter bees) occur in all states of Australia and other members of the Megachilidae family, *Chalicodoma* spp. (resin bees), *Coelioxys* spp. (cuckoo bees) and *Afranthidium repetitum* (carder bees) occur in Queensland (CSIRO Entomology 2004). Halictine bees (Family Halictidae) commonly called sweat bees, are a group of ground nesting bees and have been implicated in the pollination of *Rosa* spp. in various parts of the world (Bruun 2005). Australian genera include *Homalictus, Lasioglossum, Lipotriches* and *Nomioides*. Hover flies are widespread in Australia and genera include *Ischiodon, Simosyrphus, Episyrphus* and *Eristalinus.*

Figure 12 ***Apis mellifera* pollinating Hybrid Tea flower** [Photo credit: Janet Gorst, OGTR]

Natural pollination across the genus *Rosa* has not been widely studied. It would appear, however, that there is a range between self-pollination (autogamy) and cross-pollination (xenogamy), that while a species may be self-pollinating it may require cross- pollination in order to set fruit and that most diploid but not polyploid species are self-incompatible (Ueda & Akimoto 2001; Kevan 2003). Following pollination it takes 12 – 24 h for the pollen tube to reach an ovary and fertilize an egg cell (Jacob & Ferrero 2003).

Within the horticultural cultivars of the Modern Roses, there are many that may lack pollen, may have missing or incomplete sexual organs or may not set fruit (Kevan 2003). While there is significant use of controlled cross-pollination by rose breeders, Hybrid Tea roses left to breed naturally are generally self-pollinated, a trait which has been enhanced through several centuries of controlled breeding. The close proximity of the anthers and stigmas, coupled with the fact that modern hybrid roses have been selected both to contain more petals (generally 25 to 35) and for slow opening of the petals, has resulted in greatly reduced access by insects and a tendency for pollen to be shed in the un-opened bloom (Bell 1988).

In wild *Rosa* species, flowers produce pollen with generally high viability. However viability can vary with ploidy (eg see discussion in Visser et al. 1977; Spethmann & Feuerhahn 2003) and may even vary significantly in the same plant over time depending, for example, on what time of year the pollen is produced (Gudin et al. 1991). Ueda & Akimoto (2001) analysed pollen viability (as measured by acetocarmine staining) in 48 *Rosa* spp. with varying ploidy levels and found that it ranged from 4.3% to 99.6% although only seven species (three of which were pentaploids from section *Caninae*) had pollen with less than 50% viability. Spethmann & Feuerhahn (2003) in their collation of pollen germination results from a number of different sources similarly showed a range from 0 – 100%. Some authorities contend that the most appropriate test of pollen viability is *in vitro* pollen germination (Spethmann & Feuerhahn 2003). Still others have suggested that the measurement of the length of pollen tubes from pollen germinated *in vitro* is a more accurate method for establishing viability as it appears to be correlated with fertilizing capacity (Gudin et al. 1991).

The Modern Rose cultivars often have low pollen viability (eg see discussion in Visser et al. 1977) that results from a variety of male meiotic or post-meiotic aberrations (Jacob & Ferrero 2003). This poor viability leads to poor seed set and, for example, even under optimal conditions of artificial crosses, a Hybrid Tea flower may produce only 5 – 15 seeds (de Vries & Dubois 1983); multiple successive pollinations can significantly increase the number of achenes obtained.

Pollen viability is quickly lost over several days if grains are left unprotected at ambient temperature (Khosh-Khui et al. 1976). Rose breeders often need to overcome temporal or spatial differences in flowering by storing pollen of a male parent until pollination can be done. If stored correctly, particularly with regard to temperature and humidity, pollen can retain viability for extended durations (Khosh-Khui et al. 1976). Many breeders now use cryostorage (in liquid nitrogen) as a method for long term (eg 12 months) storage (Rajasekharan & Ganeshan 1994).

Even if pollination could result in significant fertilisation, rose plants grown for commercial cut-flowers have little opportunity to be pollinated since pollinator access is limited at a number of points (see relevant concepts discussed in Section 2.3.3) – plants are often grown inside, flower stems for sale are harvested before the buds have opened, any flower stems not required for sale are also harvested before buds have opened to prevent unnecessary diversion of assimilates, and stems are then kept in storage (usually chilled) prior to sale. In the event of pollination occurring while the flowers are on display after sale, success is unlikely because of the limited vase life of the flowers. This can vary depending on the cultivar as well as the use of preservation techniques/chemicals but a general approximation quoted by florists is 7 – 10 days (see eg < http://www.discoverprotea.com/tips_top10_vaselife.htm>). During this time, flowers are senescing and physiological processes are adversely affected (Zieslin 1988).

4.3 Fruit/Seed development and seed dispersal

Achenes (see Figures 10 & 11) begin to develop rapidly 3 – 4 weeks following fertilisation, are morphologically complete in a further 8 weeks and fully mature in a further 2 – 4 weeks (Ueda 2003; Drewes-Alvarez 2003b). Potentially, the number of achenes that develop in a hip is the same as the number of pistils that the flower has (which may be over 170 – see Table 4). In reality, in the Modern Roses, the achene content of a hip varies between 1 – 30 but is usually low (Gudin 2003b) (see also Section 4.2).

A prolific Species Rose such as *R. multiflora* may produce as many as 500,000 seeds per year (Munger 2002). Species such as *R. rugosa* that produce many hips (Figure 13) may, if the hips are allowed to fall to the ground, also show a proliferation of seedlings.

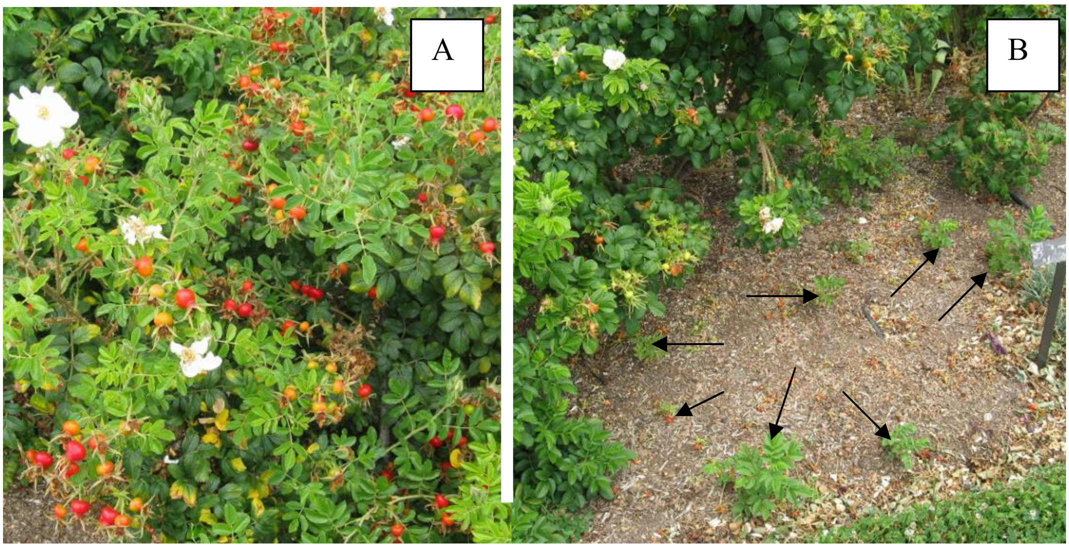

Figure 13. Plant of *R. rugosa* in mid-summer showing A) extensive hip production and B) seedling proliferation (arrowed) around the base of the plant. [Phot credit: Janet Gorst, OGTR]

In the native environment of roses, seed dispersal is mainly by birds and mammals that eat the hips (endozoochory) (Eastman 2003; Gudin 2003b) and this is also considered to be the case with *R. canina* and *R. rubiginosa* both of which are regarded as weedy species in Australia and New Zealand (see Section 8). The hips of both species are brightly coloured and are eaten by birds (eg pied currawongs – *Strepera graculina;* eastern rosellas - *Platycerus eximus,* crimson rosellas- *Platycerus graculina* and emus – *Dromaius novaehollandiae*) and other animals such as foxes, cattle, horses and possums that then excrete the seed in a viable condition (Hatton 1989; Parsons & Cuthbertson 2001; SAMDBNRMB 2008; Massey University 2008).

Both species also have the potential to be spread long distances in waterways, in runoff from slopes and in mud that becomes stuck in the fur or hooves of animals (SAMDBNRMB 2008).

As an example of specialised dispersal mechanisms within the genus, the Japanese Rose (*R. rugosa*) is particularly adapted for dispersal in water since, unlike other rose species, the hips and achenes are very buoyant and can float for many weeks in both fresh and salt water (Bruun 2005; Weidema 2006).

4.4 Seed dormancy and germination

Rose species show both physiological dormancy (endogenous chemical inhibitors) and physical dormancy (physical restraints to germination) (Zlesak 2006).

The rose hip is produced in autumn under cool, short-day conditions that do not favour germination and therefore the seeds undergo a period of dormancy. This is controlled by a balance between the plant hormones abscisic acid (ABA) localised in the pericarp of the achene (Yambe et al. 1992) and gibberellic acid or cytokinin (Ueda 2003).

Stratification (or moist chilling) is a period of exposure to low temperatures and is often used to bring about prompt and uniform seed germination (Hartmann & Kester 1975). Rose seeds generally require a period of stratification before they will germinate. *Rosa multiflora* requires about 6 weeks of moist chilling at 3°C for optimum germination, but other species such as *R. rugosa* and *R. hugonis* require 4 to 6 months, and *R. blanda* 10 months of stratification prior to germination. *Rosa canina* germinates best if the seeds are kept moist at room temperature for two months followed by an additional 2 months at 0°C (Hartmann & Kester 1975). However, in Australia seeds of *R. canina* and *R. rubiginosa* may germinate at anytime of the year provided moisture is available (Parsons & Cuthbertson 2001).

In addition, a number of Species Roses appear to be ‘two year species’ (Jackson & Blundell 1963) in which there is a requirement for the seed to have a warm period in the soil (perhaps to initiate disintegration of the pericarp) followed by a period of low temperature to after-ripen the embryo. Germination percentages in these seeds may therefore be much higher in the second year they are in the soil compared to the first year.

It has been shown that, at least in *R. multiflora*, seeds will germinate after a short exposure to red light and that this is reversed by exposure to far-red light, thus suggesting the involvement of phytochrome and the benefit of germinating seeds in the light (Yambe et al. 1995).

During germination, the rose achene pericap splits along a suture and then separates as germination proceeds (Yambe & Takeno 1992). Poor germination (less than 20%) is one of the major problems encountered in rose breeding programmes (see eg Anderson & Byrne 2007) and has been attributed to both an inability of the embryo to expand because of the thick pericarp of the achene, and growth inhibitors produced by the achene (Jackson & Blundell 1963). Embryo rescue, where the embryo is physically removed from the achene and cultured on an artificial medium, has been found to overcome this poor germination (Marchant et al. 1994). This technique, is, however, labour intensive and not suitable for large batches of seed. Other methods used to improve germination include treatment with: gibberellic acid (GA3) (Hosafci et al. 2005), macerating enzymes (Yambe & Takeno 1992), sulphuric acid (Younis et al. 2007) and activated charcoal (Yambe et al. 1992).

In nature, germination may be aided by partial breakdown of the pericarp following ingestion of the hip and fruits and then excretion of the seeds by frugivores. Soil microorganisms may also play a part in pericarp permeabilization of any seeds that may fall to the ground (Gudin 2003b).

An allelopathic substance (α – pyrone derivative) contained within the seed of *R. canina* aids in the establishment of its own seedlings by inhibiting the germination of other species (Lohaus et al. 1985).

Reports on seed longevity of Species Roses vary. For example, seeds of *R. rubiginosa* may remain viable in the soil for 3 or 4 years (Parsons & Cuthbertson 2001), while seeds of *R. multiflora* may remain viable in the soil for 10 – 20 years (Munger 2002).

4.5 Vegetative Growth

As emphasised in Section 3.1, the development of rose shoots and the shape of each plant is a continuous cycle of axillary bud outgrowth. Development of axillary buds into shoots is controlled by apical dominance (also referred to as correlative inhibition) a phenomenon in which the apex of each shoot controls the outgrowth of the buds. When it is present, the apex inhibits axillary bud outgrowth but within a few hours of apex removal (eg after pruning or floral initiation), elongation and development of the buds begins (Cline 1997). This response is mediated predominantly via the phytohormone auxin although the exact mechanism is still debated and is further influenced by factors such as the location of buds, plant developmental stage and environmental factors (Dun et al. 2006).

In seasonal flowering roses (see Section 4.1.2) the secondary shoots remain vegetative whereas in recurrent-flowering plants, the secondary shoots can produce flowers. When the flowering stem is harvested the lower (proleptic) buds are released from inhibition and, in turn will develop into flowering shoots (Chimonidou 2003). The number of secondary shoots that develop is dependent on both genotype and environmental conditions (Roberts & Blake 2003).

From the above considerations, it can be seen that there are two distinct stages in the development of an axillary bud (Blom & Tsujita 2003):

1. formation of the bud meristem but inhibition of its outgrowth. During this stage the meristem forms leaves, secondary buds and stem tissue. Therefore the longer a bud remains in this stage, the more leaf primordia it develops and the longer it will take for the bud to break once it is released from the influence of apical dominance.
2. bud break following release of apical dominance.

Eight stages of development have been recognised in the development of a shoot from bud break to flowering in a typical Hybrid Tea rose (Chimonidou-Pavlidou 2000):

1. bud expansion but not elongation
2. bud elongation to > 20 mm; first 3-leaflet leaf not visible; considered as the transition stage from vegetative to reproductive
3. appearance of first 3-leaflet leaf
4. appearance of second 3-leaflet leaf
5. appearance of first 5-leaflet leaf
6. appearance of second 5-leaflet leaf

7 all leaves expanded; flower bud visible

8 flower bud 5 – 7 mm in diameter.

The changeover from vegetative to reproductive apex occurs during Stage 2 and vegetative apices are not observed (ie microscopically) on shoots that are longer than approximately 50 mm, except if there has been a prolonged period of low temperature (Horridge & Cockshull 1974).

Leaf area affects photosynthesis and plant growth and is also an important consideration in growth and survival of cuttings. It is affected by a range of environmental considerations including temperature, light, water, salinity, CO_2 and humidity (Torre 2003). In temperate climates, rose plants growing outside tend to shed leaves in autumn and enter a dormant phase until bud break in spring (Roberts & Blake 2003).

SECTION 5 BIOCHEMISTRY

5.1 Toxicity

There have been no reports in the literature of toxicity as such of rose plant parts including pollen or rose products (eg rose oil, rose hips, or other rose derived foods). *Rosa gallica* is listed as containing pyrogallol tannins in levels that may cause symptoms such as gastroenteritis if ingested (Spoerke & Smolinske 1990).

5.2 Allergenicity

Studies have suggested the possibility of occupational rose allergy developing in people working in rose cultivation (Ünlü et al. 2001; Demir et al. 2002), rose oil extracting plants (Akkaya et al. 2004), and processing powdered rose hips (Kwaselow et al. 1990). However, there is not conclusive evidence that rose plant parts and/or products cause allergic reactions.

The study by Kwaselow et al. (1990) examined only 13 workers at a processing plant which made vitamin C tablets from ground rose hips in Detroit, Michigan. Eight of the 13 were positive for rose hip skin test and 6 of these (6/8 or 75%) had asthma symptoms. Five of the 13 workers were negative for the rose hip skin test and 3 of these (3/5 or 60%) had asthma symptoms. The number of workers examined was low and there was no statistical analysis presented for interpretation of the data. Only three workers had skin tests done with other potential causal agents (eg ascorbic acid, vitamin C tablets). At least one of the workers had asthma prior to working in the rose hip processing plant and data on the other workers was not presented. At best this study suggests a possible link between the allergy to powdered rose hip and occupational asthma.

The study by Akkaya et al. (2004) examined 52 workers from 4 different rose oil extracting plants in Turkey, as well as 30 control subjects. The study demonstrated a statistically significant 8-fold increase, in a positive response to a specifically prepared skin prick test using a *R. damascena* allergen, in workers compared to the control group. However, there was no significant difference in the pulmonary function measured, suggesting no link between hypersensitivity and occupational asthma.

The study by Ünlü et al. (2001) surveyed 600 workers employed in rose cultivation in Turkey. Of the 600, twenty (3.3%) were found to suffer from allergenic disorders such as rhinitis, rhinoconjunctivitis or both. There was no control population for comparative purposes, thus it is not known if this is significantly different from the general population. Fourteen of the twenty workers examined had increased IgE levels but seven of these workers were also positive to other allergens in the skin prick test, suggesting other allergens may have caused their increased IgE levels. These results suggest that an IgE mediated reaction to *R. damascena* may be responsible for the respiratory symptoms of the some of the 20 workers examined and indicates the need for further investigation using proper controls.

A study by Demir et al. (2002) suggested that villagers in Turkey who worked in the rose industry may develop allergy to roses, but did not rule out a number of other agricultural causes of their allergy-like symptoms. Their study lacked a control population which did not have a history of exposure through working in the rose cultivation. Interestingly, their study seemed to suggest that villagers' complaints about allergy symptoms were reduced 3-fold during the rose season as compared to the rest of the year. This may indicate some beneficial effect of working with the roses during the flowering season.

In a study of 680 patients Eriksson et al. (1987) reported that 11% of atopic and 22% of non-atopic patients reported asthma and rhinitis symptoms related to flowers of *Rosa* spp. The study did not distinguish whether the symptoms were elicited via reagin-mediated pollen allergy or odorants or irritants originating from the flowers. The American Academy of Allergy Asthma and Immunology (AAAAI) website (www.aaaai.org) suggests that respiratory reactions to rose pollen are rare, probably because of the fact that rose pollen is heavy and sticky, and designed for insect pollination rather than wind dispersal. However, Karakaya & Kalyoncu (2003) documented the case of 47 year old Turkish man with multipollen sensitivity who experienced anaphylaxis after drinking dew that had collected in the flowers of *R. damascena*. The authors concluded that it was the pollen in the dew that had led to the reaction since the man did not have any problems with ingesting juice extracted from the flowers.

5.3 Other Phytochemicals

Interest in sequencing projects in *Rosa* has focussed particularly on those genes concerned with fragrance biosynthesis and flavonoid biosynthesis as these are commercially important characters (Winkel-Shirley 2001; Vainstein et al. 2001; Tanaka et al. 2003).

Fragrance Chemicals

The fragrance profile of *R.* x *hybrida* is characterized by 41 compounds including alcohols (eg geraniol, nerol and citronellol, phenethyl alcohol); aldehydes (eg geranial, nonanal, and decanal); sesquiterpenes (eg β-caryophyllene); esters (eg 2-phenylethyl acetate, *cis*-3-hexenylacetate, geranyl acetate and citronellyl acetate); and aromatic ethers (3,5 dimethoxytoluene, benzyl methyl ether, orcinol dimethyl ether, estragole and methyl-eugenol) (Kim et al. 2000; Lavid et al. 2002; Shalit et al. 2003).

Guterman et al. (2002) identified genes associated with fragrance in *R.* x *hybrida* using a genomic approach that included cDNA sequencing, microarray gene expression analysis, chemical analysis of the volatile composition of rose petals, and biochemical analysis of candidate proteins. They created a rose petal Expressed Sequence Tag (EST) database containing some 2,873 high-quality sequences. Another rose petal database was created for *R. chinensis* by Channeliére et al. (2002). *R. chinensis* is one of the progenitors of *R.* x *hybrida* and contributed recurrent flowering and the 'tea' scent (see Section 2.4.2) to many of the Modern Roses.

Flavonoids

Rose flower colour is primarily due to the presence of anthocyanins in petal epidermal cells. Anthocyanins are part of a diverse family of aromatic molecules called flavonoids, derived from phenylalanine and malonyl-coenzyme A (Winkel-Shirley 2001). Flavonoids are water-soluble and accumulate in the vacuoles (Rosati & Simoneau 2006). Anthocyanins are the biggest subclass of plant flavonoids and in most cases are responsible for the orange to blue colours of flowers and other plant organs. There are three major types of anthocyanins that contribute to flower colour (Jay et al. 2003):

- delphinidins that produce blue or purple flower colour
- cyanidins that produce red or magenta flower colour and
- pelargonidins that produce orange, pink or brick red flower colour.

Anthocyanin biosynthesis in roses is unlike the pathway used in other flowers because roses possess a unique glucosyltransferase enzyme in the biosynthetic pathway (Ogata et al. 2005). Biolley & Jay (1993) made a comprehensive study of the anthocyanins involved in the perceived colours of *R.* x *hybrida* cultivars and concluded that the main contributors were cyanidin 3,5-diglucoside and pelargonidin 3,5-diglucoside, in combination with the co-pigments quercetin and kaempferol glycosides. Rose flowers do not normally have blue pigments because they lack that part of the anthocyanin biosynthetic pathway that produces delphinidins; however some rose cultivars produce delphinidin in their leaves (Tanaka et al. 2003). A few cultivars are marketed as having ‘blue’ flowers although the colour tonalities at best are lavender or mauve (Gonnet 2008). The Floribunda cultivar ‘Rhapsody in Blue’ contains cyanidin as the only anthocyanin but the cyanidin is stored in anthocyanic vacuolar inclusions (AVIs) in the petal epidermal cells. The high concentration of the pigment molecules in the AVIs causes a bonding that favours the quinonoidal base form of the pigment which, in turn, imparts a bluer tonality to the petals (Gonnet 2008).

Flavonols are another class of flavonoids occurring in roses with quercetin and kaempferol being the two types. The Hybrid Teas show a strong positive correlation between kaempferol and pelargonidin (Jay et al. 2003). While the anthocyanins contribute directly to petal colour, the flavonols act as co-pigments and, together with factors such as vacuolar pH, anthocyanin concentration, and anthocyanin ratios, serve to stabilize and enhance colour (Jay et al. 2003; Rosati & Simoneau 2006).

Beneficial Phytochemicals

As discussed in Section 2.2, rose hips are regarded as a good source of vitamin C and *R. canina* hips grown in Australia contain 468 mg/100 g, considerably higher than orange flesh (53 mg/100 g) and capsicum (152 mg/100 g) (FSANZ 2006). One study in Chile showed that vitamin C content of raw frozen hips could be as high as 6,694 mg/100 g (Joublan & Rios 2005). A number of other beneficial chemicals are also found in rose hips including carotenoids, and flavonoids that act as anti-oxidants, lycopene, and minerals such as calcium and potassium (Çinar & Çolakoglu 2005).

SECTION 6 ABIOTIC INTERACTIONS

6.1 Abiotic Stresses

Members of the *Rosa* genus show a wide genetic base for abiotic stress tolerance that is mirrored by the ability to grow in a variety of environments. They are found in the majority of northern hemisphere climates, ranging from the arctic to the tropics. Nearly all species are able to tolerate hot summers, and are hardy down to around -15° (Phillips & Rix 1988). Some of the species found in China are not hardy at cold temperatures (-10°C), including *R. gigantea*. This species was used in the development of Hybrid Tea roses, and consequently Hybrid Teas are also susceptible to low temperatures (Phillips & Rix 1988). In general roses are resistant or tolerant to salinity, drought, low relative humidity + high air temperature, and high irradiance (Urban 2003). Species such as *R. rugosa* are renowned for general hardiness and tolerance of a range of extreme conditions such as frost, heat, drought and salt (Bruun 2005).

In the commercial setting, rose production is limited by factors such as light, temperature, humidity, mineral nutrition and salinity (Lorenzo et al. 2000). In particular there is an interaction between temperature, light and CO_2 levels as these are related to photosynthetic ability; temperature management should aim to balance productivity with flower quality under a given set of light conditions (Blom & Tsujita 2003).

6.1.1 Nutrients

Under commercial cut flower conditions, especially in greenhouse and hydroponic systems, roses are well supplied with nutrients and are arguably oversupplied particularly with nitrogen (Evans 1998; Cabrera 2003). Roses growing in the garden are adaptable to a range of nutrient conditions but deficiencies may occur (eg nitrogen, iron, manganese, magnesium) especially under conditions of extreme pH that reduce nutrient availability (Roxburgh 2008).

6.1.2 Temperature

Temperatures of less than 15° C may cause Hybrid Tea cultivars (particularly ‘Baccara’) to produce malformed flowers, ‘blind’ shoots and poor flower colours (Moe 1988). Floral malformations include ‘bullheads’ (Lindenbaum et al. 1975) where flower buds have a flat-topped appearance instead of the pointed tip normally preferred and are larger in size and weight than normal, have many short petals and petaloids, and have a profusion of secondary florets bearing carpels near the base of the flower. Blind shoots are formed when the floral axis fails to develop a complete set of floral organs and the partially formed flower then abscises (Chimonidou 2003). The colour of flowers grown under low temperature may be very dark (Moe & Kristofferson 1969).

Increasing temperatures above 12° C increases plant growth and development as well as the yield of flowers and number of flushes. However at temperatures of greater than 21° C flower stems may become weak and shortened, flowers may be small in size (reduced number and size of petals) and flower colour may be pale (Moe & Kristofferson 1969; Moe 1988).

6.1.3 Light

In a commercial setting roses are considered to have a high light requirement and optimal production is achieved with a light sum of 12 – 15 mol $m^{-2}day^{-1}$ that, in plants grown undercover, necessitates the use of supplemental lighting (Blom & Tsujita 2003). Low light intensity (together with low temperature) exacerbates the formation of blind shoots (Moe & Kristofferson 1969; Moe 1988). Leaves developing in winter under low light accumulate less nitrogen and therefore have a lower photosynthetic capacity than leaves developing in summer (Urban 2003).

6.1.4 Water

Rose plants respond to water stress via three adaptive mechanisms common to many plants: osmoregulation, turgor adjustment and changes in water partitioning between the apoplasm and symplasm. Over a short time, these mechanisms allow rose cells to maintain a high water content in adverse conditions (Urban 2003).

In experiments designed to ascertain the effect of water stress, Chimonidou-Pavlidou (1996) found that the stage after petal initiation but prior to stamen initiation (Stages 4 & 5 – see Section 4.5) was the most damaging to the development of roses in terms of quantity and quality for cut-flower production with production losses as high as 70% occurring and being accompanied by a reduction in floral stem features such as length, fresh weight, and petal numbers. Water stress applied at Stages 1 or from Stage 6 onwards does not have negative effects on flower quantity and quality.

Roses have an abscission zone (an area at the base of a plant part containing tissues that play a role in the separation of the part from the plant body) at the junction of the flower stalk (peduncle) and the stem. The flower can lose significant amounts of water and during water stress may be sacrificed by the plant in order to protect the main axis (Chimonidou 2003).

6.1.5 Other considerations

Salinity

Under intensively managed systems, especially where poor quality water or recycled nutrient solution is used there may be reductions in flower yield and quality associated with high electrical conductivity (salinity). This may be exacerbated by even low concentrations of Na and Cl in irrigation water (see discussion in Cabrera 2003). Shoot elongation and uptake of ions such as nitrate, potassium and phosphate can be negatively affected by high sodium concentration (Lorenzo et al. 2000). Roses have typically been classed as sensitive to salinity but at least one study has suggested this may not be so (Cabrera 2001). It appears that cultivar plays an important role in tolerance and that evaporative demand and water supply both impact on response to salinity (Urban 2003). In addition, the rootstock of grafted plants also influences the response to salt (Solís-Pérez & Cabrera 2007).

SECTION 7 BIOTIC INTERACTIONS

7.1 Weeds

Commercial greenhouse production of roses as cut or potted flowers generally involves culture in sterile soil, sterile soil-less media, or by hydroponics, thus reducing the opportunity for weeds to be present.

In gardens or small-area landscapes, practices such as mulching, use of weed mats and hand weeding usually provide adequate weed control. As roses are shallow rooted, mechanical cultivation (eg with a hoe) should be done with caution. In more extensive plantings, herbicides are used and include (Karlik 2008):

- pre-emergent (ie before weeds emerge) eg oryzalin and pendimethalin. These will control grasses and some broadleaf plants
- post-emergent (ie after weeds have established) eg fluazifop-p-butyl, sethoxydim, and clethodim. However, roses are sensitive to some postemergent, broadleaf herbicides such as 2,4-D, triclopyr dicamba and glyphosate and care should be taken to avoid drift if using these.

7.2 Pests and Diseases

7.2.1 Invertebrate Pests

Roses in Australia are attacked by a number of invertebrate pests (Table 5) including those that chew (Lightbrown apple moth, Painted apple moth), suck (Cottonycushion scale, California red scale, Rose aphid, Rose scale, Twospotted mite, White fly) and rasp (Plague thrips, Western flower thrips). In addition, nematodes (microscopic worms) can damage root systems and may cause severe losses. Control of invertebrate pests is mainly by chemical spraying, although there are a number of specific biological controls that can be used. Detailed information on a number of pests that are significant worldwide is given in Roberts et al. (2003).

7.2.2 Vertebrate Pests

Anecdotal evidence on a number of websites indicates that, in Australian gardens, new growth on roses, rose buds and flowers are attractive to several vertebrates including possums (the Brushtail possum - *Trichosurus vulpecula* and the Common Ringtail possum - *Pseudocheirus peregrinus*), rabbits, rosellas (*Platycercus* spp.) and cockatoos (*Cacatua galerita*). As indicated in Section 4.3, a number of vertebrates also consume the hips. These pests will probably not destroy the plants but will inflict damage. All native animals, are protected under the Wildlife Act 1975, and cannot be trapped (unless under licence) or harmed in any way.

In unmanaged or minimally managed environments, it is likely that parts of rose plants are consumed by a variety of vertebrates (see also Section 4.3). Specific information on this is lacking in the Australian literature but, as an overseas example, one review of the weed species *R. multiflora* in the USA lists rose plant parts being consumed by chipmunks, white-tailed deer, opossums, coyotes, black bears, beavers, snowshoe hares, skunks, mice and cottontail rabbits (Munger 2002). Grazing livestock may also find plant parts palatable (see Section 8.3).

7.2.3 Diseases

Diseases affecting roses in Australia are largely the same as those affecting plants in the northern hemisphere (Brichet 2003). These have been summarised in Table 6. The disease known as stem canker is caused by a variety of fungi and results in dieback of the stem as a result of entry of spores through pruning or wounding of the crown (Botanic Gardens Trust 2008a). Some visual characteristics of more prevalent diseases are shown in Figures 14 & 15.

7.3 Other interactions

Roots of roses are associated with mycorrhizal fungi (*Glomus* spp. and *Gigaspora* spp.) that enlarge the surface area for absorption of nutrients and water (Skytt Andersen & Fuchs 2003). Mycorrhizae allow rose plants to maintain leaf turgor and conductance at greater tissue water deficits and lower leaf and soil water potentials when compared with nonmycorrhizal plants (Auge et al. 1986). This symbiotic relationship is of less importance for commercially grown plants where water and nutrients are likely to be at optimal levels.

Fungal endophytes [an endophyte is a microoganism able to reside inside the host without causing disease symptoms] have been reported to occur in the vascular bundles of *R.* x *hybrida* leaves (Salgado et al. 2007).

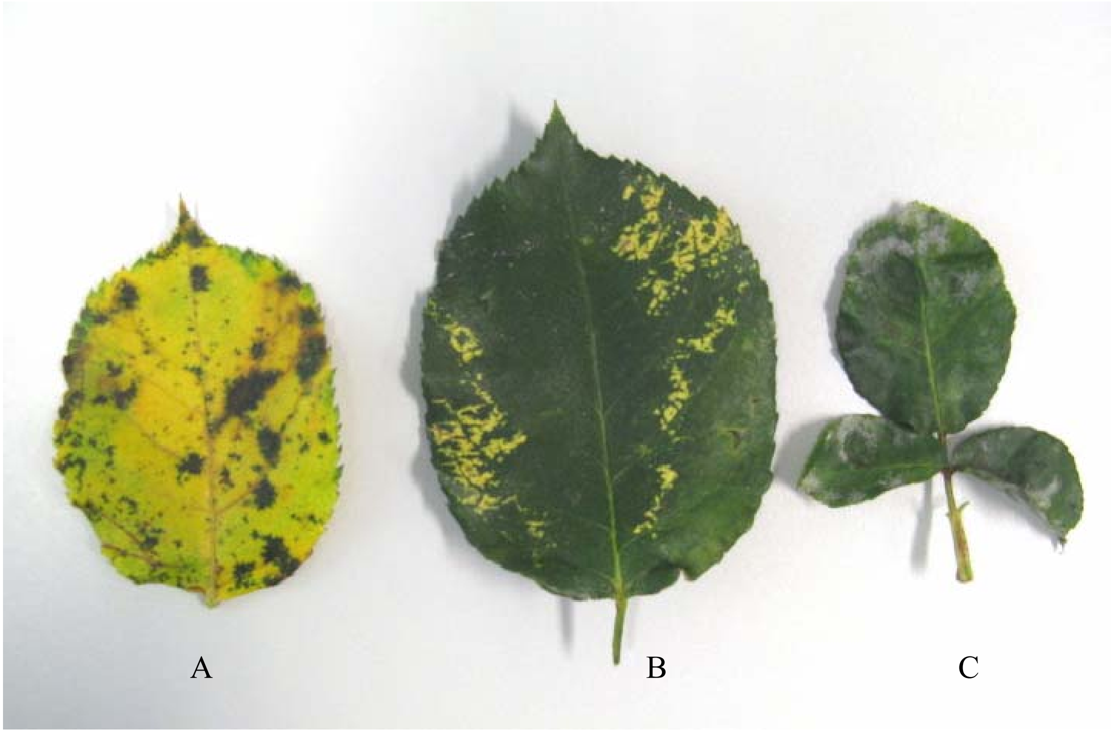

Figure 14. Leaves taken from plants suffering from A) black spot, B) rose mosaic virus and C) powdery mildew. [Photo credit: Janet Gorst, OGTR]

Figure 15. Stem canker in a particularly susceptible variety of *R. chinensis.* [Photo credit: Janet Gorst, OGTR]

Table 5. Invertebrate pests of roses

Classification	Taxonomic name	Common name	Impact and control other than spraying
Arachnid			
Acarina:			
Tetranychidae	*Tetranychus urticae*	Two-spotted spider mite	Nymphs and adults suck leaves which may then become bronzed and shrivelled and fall off. Flowers and growing points are also attacked and may become distorted. This insect pest can be controlled biologically by *Phytoseiulus persimilis or Typhlodromus* (predatory mites that have been imported into Australia).
Insect			
Coleoptera:			
Curculionidae	*Asynonychus cervinus*	Fuller's rose weevil	Generally feeds on leaves, young shoots and buds. Several biological controls (parasitic wasps, praying mantises) and cultural controls are available.
Hemiptera:			
Aleyrodidae	*Trialeurodes vaporariorum*	White fly	A sap sucker that is found on a number of specis. Can be controlled biologically by the parasitic wasp *Encarsia formosa.*
Aphididae	*Macrosiphum rosae*	Rose aphid	Aphids, also called greenfly or blackfly, are the most common rose pests. They attack young shoots, particularly in dry weather, leading to the distortion of shoots and stunting. Ladybird beetles (*Hippodamia parenthesis*) and the parasitic wasp *Aphideous rosae* can be used as a biological control.
Diaspididae	*Aonidiella aurantii*	California red scale	This and other scale insects can infest rose plants causing weakening of the plant, increased susceptibility to other diseases, and possible death. The honeydew attracts ants that can then spread scale to other plants. Pruning can eliminate infected branches and shoots. The parasitic wasps *Aphytis melinus*, *Aphytis lignanensis*, and *Comperiella* spp. are used in Australia in many Integrated Pest Management (IPM) programs to control scale insects.
	Aulacaspis rosae	Rose scale	Heavy infestations may reduce bloom production and new shoot growth. Neglected plants may die.
Margarodidae	*Icerya purchasi*	Cottony cushion scale	A native insect infesting many plant species. Nymphs gather along the midveins on the underside of leaves and eventually migrate to the stem.

Classification	Taxonomic name	Common name	Impact and control other than spraying
Lepidoptera:			
Lymantriidae	*Teia anartoides*	Painted apple moth	Caterpillars eat or skeletonise a variety of plant species
Tortricidae	*Epiphyas postvittana*	Lightbrown apple moth	A native insect that attacks a variety of plant species. Caterpillars graze on leaves and young shoots. Rarely a major problem in Australia, as numbers tend to be low and can easily be controlled manually.
Thysanoptera:			
Thripidae	*Frankliniella occidentalis*	Western flower thrip	Found in all Australian states except the Northern Territory and is a pest of a variety of ornamental, fruit and vegetable crops. Lives and feeds on flowers and new plant growth and causes distortion of growing parts.
	Thrips imaginis	Plague thrip	Feeds on soft, new growth by scraping surface cells and then sucking the cell contents. Generally causes aesthetic damage due to infestations in the flowers which turn brown and shrivel. Can be controlled biologically using predatory mites, lady beetles, and soil-dwelling mites.
Nematode			
	Meloidogyne spp.		Damaged roots develop root knots which may cause slow growth, wilting and yellowing of leaves. Nematodes are spread via garden tools and introduction of infected plants. Some rootstocks eg *R. fortuneana* confer some resistance to nematodes.

Sources: (Williams & Pullman 2000; Reid 2005; Botanic Gardens Trust 2008a; Botanic Gardens Trust 2008c)

Table 6. Common diseases of roses

Pathogen classification	Pathogen name	Disease	Impact of disease	Management
Bacterium				
Rhizobiales	*Agrobacterium tumefaciens*	Crown gall	Formation of galls on the stem, particularly at ground level but sometimes on aerial parts. Plants are stunted. The pathogen can be transmitted through rootstocks (Pionnat et al. 1999)	Cultural practices: eg use of certified plants/rootstocks, avoidance of wounding, planting in disease-free soil, hygiene when pruning, removal of infected plants. Biological control: preplant root dip of *Agrobacterium radiobacter* strain K84 which is antagonistic to *A. tumefaciens*.
Fungus				
Agaricales	*Armillaria mellea*	Armillaria root rot	Soil borne fungi which can destroy the roots of roses. Rare in Australia.	General management practices for control of fungal diseases include a mixture of: Cultural practices, eg use of resistant cultivars, removal of all dropped plant parts, removal and destruction of infected parts, good air movement, watering plants at the base, avoidance of wounding, sanitation of tools/equipment, good nutrition (especially potassium) of plants. Fungicide sprays.
Erisyphales	*Podosphaera pannosa (Sphaerotheca pannosa)*	Powdery mildew	First appears as tiny blisters followed by a fine powdery deposit on the surface of leaves and shoots, and is usually favoured by warm humid weather. It is not very damaging to the rose plant, and is more an aesthetic problem. There is variable resistance (from none to high) among the rose varieties including the hybrid tea roses.	
Helotiales	*Botrytis cinerea*	Grey mould/Botrytis rot	Flecks on petals that develop into brown, necrotic spots. Finally causes petal abscission and collapse of the flower. Major problem in the cut-flower industry.	
	Diplocarpon rosae	Black spot	The disease appears as more or less circular black spots on the leaves (generally one spot per leaflet), which can then turn yellow and fall prematurely. Is not too serious for modern roses, but some species	

Pathogen classification	Pathogen name	Disease	Impact of disease	Management
			(especially the yellow-flowered rose species) can be completely defoliated by this disease in wet summers.	
Myriangiales	*Elsinoe rosarum*	Anthracnose	Occasionally affects roses in Australia, and appears as black spots on the leaves (generally several spots per leaflet). Anthracnose is often misdiagnosed as black spot.	
Peronosporales	*Peronospora sparsa*	Downy mildew	Usually infects young shoots but can also infect other plant parts. Leaves show dark, irregular spots (can be confused with Black spot) and will drop off. Flowers and flower buds may be malformed	
Pythiales	*Phytophthora cinnamomi*	Dieback	Soil-borne fungus that can destroy roots. Roses are not overly susceptible to the fungus	
Uredinales	*Phragmidium* spp.	Rust	Appears as bright orange powdery spots on the underside of leaves with the upper leaf surface becoming speckled with yellow.	
Virus				
		Rose wilt virus	Most noticeable in spring is young leaflets which recurve so that the leaf is balled up with a thick and brittle texture.	Cultural practices: eg use of virus-indexed plants, destruction of infected plants, cleaning tools. There are no chemical controls.
		Rose mosaic (Prunus necrotic ringspot virus)	This gives various line patterns on the leaves according to the PNRV strain, the rose cultivar and environmental conditions. It may also cause flower delay; deformed flowers, and early leaf fall in autumn.	It is transmitted by grafting so use of virus-indexed plants is important; hygienic practices. There are no chemical controls.

Sources: (Curtis & Moran 1986; Hert & Jones 2003; Gleason & Helland 2003; Xu & Pettit 2003; Linde & Shishkoff 2003; Shattock 2003; Drewes-Alvarez 2003a; Oregon State University 2008; Botanic Gardens Trust 2008a; Botanic Gardens Trust 2008b)

SECTION 8 WEEDINESS

Roses are long-lived plants and may be found in isolation in situations where deliberately planted roses have been left unattended (eg abandoned properties or cemeteries). There are examples of *R. banksiae* and *R. giganteum* plants that are over 500 years old and a *R. praelucens* plant estimated to be approximately 1,000 years old, all still vigorously growing in China (Wang 2007). A *R.* x *indica* rootstock thought to have arrived in Australia as part of a grafted plant in the early 19th century is still surviving (see also Section 8.1).

In general, it is the Species Roses that are most likely to become weed problems while the Hybrid Tea cultivars are not associated with weediness. The reasons for this have been discussed in various Sections of this document and are summarised below.

Species Roses

- Many have features that allow establishment through natural vegetative reproduction (eg suckering, layering, adventitious root formation on stem pieces) without the use of horticultural practices (eg use of rooting hormone, bottom heat).
- Exhibit robust sexual reproduction through
    - production of large amounts of viable pollen
    - simple flower shape that allows easy access by pollinators
    - utilization of common, generalist insect pollinators; therefore potential spread is not dependent on co-evolved mutualistic relationships
    - production of large numbers of seed that can also be widely dispersed by vectors especially birds
    - natural interspecific hybridization, especially where ploidy levels of the parents are the same.
- Roses, even those considered to be weedy, are generally poor competitors at the seedling stage and are also susceptible to grazing. However, once mature and with prickles, plants show more resilience in the landscape and many are also tolerant of adverse conditions. Information on rose websites (see eg Shaw 1983) invariably describes Species Roses in terms of their being vigorous bushes that thrive on neglect and tend to be exceptionally hardy, especially with regard to insect and disease attack.

Modern (Hybrid Tea) Roses

- While normally propagated through vegetative means for commercial sale, the Modern Rose cultivars do not routinely exhibit vegetative reproduction outside a managed horticultural environment.
- Exhibit poor sexual reproduction because
    - they have been developed through traditional breeding among thousands of existing cultivars and present a number of barriers (eg low fruit set, few seeds per hip and low seed germination rates) to the successful establishment of natural crosses (see eg discussion in Gudin 1995).
    - interspecific hybridization between *R.* x *hybrida* cultivars and Species Roses is problematic (see Section 9) and even within the *R.* x *hybrida* grouping,

controlled crossing between cultivars may not be able to yield progeny (Gudin 1994). Discussion in Section 2.4.1 also provides more detail of problems associated with crossing.

- Information on rose websites (see eg Shaw 1983) describes Hybrid Tea roses as being less hardy as a class, especially if left without care (pruning and spraying) and especially if own-rooted. As discussed in Section 2.3.1, cultivars grafted onto rootstocks may show more vigour, and therefore would have the potential to survive for longer if left unattended. Nonetheless there is no report of Hybrid Tea roses achieving weed status in any part of the world.

8.1 Weediness status on a global scale

Randall (2002) lists some 55 *Rosa* species, botanical varieties or hybrids that are regarded as weeds around the world; *R.* x *hybrida* is not listed. It is probably fair to say that *Rosa* spp. do not become weeds in their native habitats where there are natural controls and seed predators, except in rare instances, and that it is only when species are introduced to new locations that they may become a weed problem. Thus, for example, native North American species do not have weed status but some introduced species have escaped cultivation and become problematic. In particular *R. multiflora*, a prolific seed producer (see Section 4.3) and native of East Asia, has been declared a noxious weed in a number of states of the USA and causes both economic damage through lost pasturage and ecological damage to a large number of habitats (Bryan & Mills 1988; Amrine Jr. 2002; Munger 2002). *Rosa bracteata* imported into Texas from eastern Asia infested more than 500,000 acres of productive grasslands in 40 southeastern Texas counties and *R. laevigata* from China became a severe weed in the Black Belt region in central Alabama. On the other hand the introduced species *R. rubiginosa, R. canina* and *R. rugosa* have also escaped cultivation but are not significant weed problems in the USA (Amrine Jr. 2002). However, hybridization between escaped and native species may represent a pathway for the formation of invasive hybrid genotypes and, for example, this is a concern where *R. rugosa* and the native *R. blanda* grow in sympatry (share the same geographical range) in the USA (Mercure & Bruneau 2008).

Some introduced species are more likely to become weeds in a particular environment. As indicated above, *R. rugosa* is not a significant problem in the USA. However it is considered an invasive species in the British Isles, Denmark and other European countries, especially in coastal dune communities (Bruun 2005; Weidema 2006). *R. canina* and *R. rubiginosa* are not significant problems in the USA but are considered problems in Australia (see Section 8.2).

It is possible for rootstocks to persist and sucker in grafted plants where the scion has died out. In many instances this does not result in the rootstock becoming weedy, as seen, for example, with *R.* x *indica* 'Major' occurring in Camden Park garden (originally owned by John and Elizabeth Macarthur, prominent early settlers in Sydney, Australia) (Cox 1999). However, *R. canina* is now established in most of the temperate world, including Australia, and its spread is associated with the fact that it is widely used as a rootstock (Parsons & Cuthbertson 2001).

8.2 Weediness status in Australia

No Modern Rose cultivars have become naturalised in Australia, despite a long history of cultivation. It is pertinent to note that, while Carr et al. (1992) listed *R.* x *hybrida* cultivars as a 'potential threat' to one or more vegetation formations in the Australian state of Victoria, in the 17 years since the publication of their book the species has not been listed in any subsequent publications as a weed. The potential has therefore not been realized.

Six Species Roses are regarded as minor weeds in Australia (Walsh & Entwisle 1996; Lazarides et al. 1997; Harden 2000; Groves et al. 2003) and have been classified as follows (Groves et al. 2003):

- *R. chinensis* and *R. wichuraiana* – naturalised and may be a minor problem in natural ecosystems but not considered important enough to warrant control at any location. Walsh & Entwisle (1996) note that plants collected near Aberfeldy, Bunyip and Mitcham (all localities east of Melbourne in Victoria) 'appear referable to *R. chinensis* or a hybrid or cultivar derived from that species'.
- *R. laevigata* and *R. roxburghii* – naturalised and known to be a minor problem in natural ecosystems warranting control at 3 or fewer locations within a State or Territory. Both species occur on the North Coast of New South Wales.
- *R. bracteata* - naturalised and known to be a minor problem in natural ecosystems warranting control at 4 or more locations within a State or Territory. It has a wide distribution in New South Wales, occurring on the North Coast, Central Coast, Northern Tablelands and South West Slopes as well as being found in Queensland.
- *R. gallica* – categorised as a weed species by Lazarides et al. (1997) and Randall (2007) but not by Groves et al. (2003).

In addition to the above, Randall (2007) also lists *R. odorata* as being 'naturalised somewhere in Australia'.

Two Species Roses, *R. rubiginosa* (Sweet Briar Rose) and *R. canina* (Dog Rose) are fully naturalised and have become noxious weeds in temperate Australia (Parsons & Cuthbertson 2001; SAMDBNRMB 2008). Both species are considered a problem because they are unpalatable to stock, will outcompete desirable pasture species, have the potential to invade native bushland, and represent a potential biosecurity risk in that they can host fruit fly (SAMDBNRMB 2008). The following detailed information on the two species is largely taken from Parsons & Cuthbertson (2001):

- *R. rubiginosa* is a common noxious weed, and occurs in all Australian states, except the Northern Territory. The species has probably been in Australia since early settlement. By 1919 it was declared one of the 20 worst weeds of NSW (Hatton 1989). It is considered to be an important weed in the cooler, high rainfall areas of NSW, Victoria and South Australia, and also extends to more arid areas (Figure 16). It is widespread in Tasmania, mainly on roadsides. It is also found in Western Australia and the cooler areas of Queensland, but is not considered an important weed in these areas. It invades disturbed bushlands and open unimproved grasslands in Australia, and grows on a wide range of soil types. It reproduces from perennial roots and seeds, and seeds can germinate at any time of the year. Seedlings lack early vigour, and are often out-competed by other plants. However, seedling survival is enhanced in disturbed habitat (eg eroded areas, rabbit scratches). The species was originally spread through deliberate plantings, but this has long since stopped. Seed dispersal by animals and birds is now the only method of spread for this plant. Some fruit and seed movement may occur along streams and in flowing water. Seeds remain viable in the soil for 3 to 4 years. *R. rubiginosa* plants once established may survive for hundreds of years.

Figure 16. Areas of Australia in which *R. rubiginosa* is considered a major weed problem (taken from Weeds Australia http://www.weeds.org.au/, accessed 4 December 2008)

- *R. canina* is a strongly growing prickly perennial shrub that, in Australia, often occurs along river flats, irrigation channels, roadsides and waste places, and occasionally extends into pastures. The species disperses locally due to seedling development around the base of clumps, as well as growth from root stocks and layering (see Section 4.1.1). Animals and birds are also responsible for seed dispersal. Seeds germinate in autumn and spring, but can germinate at any time of the year, provided there is enough moisture in the soil. Seedlings are slow growing and easily damaged, but are hardy and long-living once established. Areas in which it is found include the central western slopes and south western plains of NSW, in the Grampians of Victoria, in the Adelaide plains, Mount Lofty Ranges, mid-Murray district and lower south east of South Australia, and in settled areas in Tasmania. Ross (1991) notes that in 1840, self-sown seedlings of *R. canina* were collected along creeks in the hills near Adelaide to be planted as hedges. *R. canina* is not as common or widespread in Australia as *R. rubiginosa*.

New Zealand is a near neighbour of Australia and has a similar history of colonization and climate to the south eastern regions of Australia. *R. rubiginosa* and *R. canina* are both introduced species that have become serious weeds there. *R. rubiginosa* is particularly prevalent in the drier areas of the South Island where it causes a loss of available pasture and impedes the passage of stock (Syrett 1990). Conditions such as rabbit infestations that reduce pasture vigour further encourage the spread of the weed (Massey University 2008).

Both *R. rubiginosa* and *R. canina* are in the section *Caninae* and are pentaploids (Wissemann 2003) that therefore tend to be better seed parents than pollen parents (Spethmann & Feuerhahn 2003). Although natural fertile hybrids (designated *R.* x *nitidula*) between these two species have occurred in the British Isles where both species are native (The British Database of World Flora and Fauna - http://www.nature.british-towns.net/, accessed 24 November 2008) there have been no reported incidences of these hybrids in Australia or New Zealand. There have also not been reports of hybridization between either of these species and any Modern Rose cultivars. It has been noted (Nybom et al. 2005) that hybrids produced between species from section *Caninae* and other wild species have low (or non-existent) pollen viability thought to be due to the breaking up of the strict bivalent formation between homologous genomes (see discussion in Section 9.3).

8.3 Control Measures

As noted in Section 7.1, roses are sensitive to some postemergent, broadleaf herbicides such as 2,4-D, triclopyr, dicamba, and glyphosate and these can therefore be used to control plants where they are not wanted. In South Australia, 2,4-D and picloram are registered for the control of *R. canina* and metsulfuron methyl is registered for control of *R. rubiginosa* (SAMDBNRMB 2008). Parsons & Cuthbertson (2001) further list imazapyr spray and hexazinone placed on the soil near the crown as effective chemicals for control of both species.

Other types of control that can be used for *R. canina* and *R. rubiginosa* include (Parsons & Cuthbertson 2001) mowing and deep ploughing/ripping to bring the roots of plants to the surface, use of domestic stock such as goats and sheep to destroy seedlings, and hand grubbing of smaller clumps. As both species are poor competitors in the seedling stage, the development of other, more favourable species (eg pasture) will reduce the likelihood of *Rosa* establishment (Massey University 2008).

Some *Rosa* species may show considerable resilience to non-herbicide control methods. For example:

- established plants of *R. multiflora* took 2 years to kill under a regime of clipping to a height of 7.5 cm every 2 weeks during the growing season (Bryan & Mills 1988)
- *R. rugosa* is tolerant to both mowing and burning and may even require follow-up digging of resprouts from rhizomes after the extensive application of excavator and riddles to dig up and remove plants (Bruun 2005).

SECTION 9 POTENTIAL FOR VERTICAL GENE TRANSFER

Interspecific hybridization is an important source of variation in ornamental breeding but while natural hybrids can exist, pre- and post-fertilization barriers often mean that laboratory techniques such as *in vitro* pollination, ovule culture and embryo rescue need to be employed (Van Tuyl & Lim 2003). In this document consideration of controlled crosses that do not occur naturally is of significance only in the context of broadening an understanding of unaided gene transfer (OECD 2006).

9.1 Intraspecific Crossing

Rosa x *hybrida* cultivars in managed mass plantings (eg the Rose Gardens at Parliament House, Canberra) do not show a proliferation of seedlings. A number of factors may contribute to this including inherent low fertility, a tendency for the Hybrid Teas to drop hips before seeds have matured, and cultivation practices that see the roses regularly dead-headed and winter pruned (Graham Evans, personal communication).

It is likely that Hybrid Tea cultivars in unmanaged environments, where hips have more opportunity to remain on plants, may produce seedlings but Gudin (2000) has suggested that hybridization among modern cut rose or garden cultivars can result in hip set as low as 25%, with only 4 seeds per hip, and only 18% seed germination. Within *R.* x *hybrida* there appears to be little opportunity for successful crosses to occur naturally because of low sexual reproduction status (Gudin 2001), and a tendency for self-pollination (Bell 1988). Even between cultivars of *R.* x *hybrida*, it may be impossible to obtain progeny by conventional means (Gudin 1994).

9.2 Natural Interspecific Crossing

While opportunity exists for natural interspecific hybridization, the probability of its success is higher between species with the same ploidy level (Spethmann & Feuerhahn 2003). Most Species Roses are diploid (see Table 1) and the concept of biological species is largely inapplicable to this grouping since nearly all the species are interfertile with each other and produce viable, fertile offspring (Wissemann & Ritz 2007). On the other hand, crosses between plants of different ploidy levels are associated with developmental disorders between embryo and endosperm (Spethmann & Feuerhahn 2003). Triploid progeny are common in crosses between diploids and tetraploids and are usually sterile (see discussion in Gudin 2000). This problem is the main reason why there has been little success in attempts to introduce germplasm from the Species Roses into the largely tetraploid Modern Roses (Nybom et al. 2005). Evidence from experts, presented in JCBH (2008a), suggests it is unlikely that *Rosa* x *hybrida* cultivars could cross with wild species under natural conditions.

Another reason for lack of hybridization between Species Roses and *R.* x *hybrida* may be limited opportunity. The Species Roses are mainly seasonal flowering (see Section 4.1.2) and therefore flower only once a year for a few weeks. There is only a limited time in which both categories of roses would flower simultaneously.

It is possible that some so-called species are actually the result of spontaneous hybridization. As examples of this, Gudin (2003a) lists *R. damascena* (thought to have arisen from *R. gallica* x *R. moschata* [Autumn Damask] or *R. gallica* x *R. phoenicia* [Summer Damask]), *R. alba* (*R. canina* x *R. gallica*) and *R. centifolia* (*R. rubra* x *R. moschata*). Ellstrand et al. (1996) in a survey of the flora of the British Isles noted that 36 spontaneous hybrids occur in the genus *Rosa* (see also Stace & Thompson 1997). They listed a number of plant features that are associated with spontaneous hybridization and occur in Species Roses: typically outcrossing (which provides opportunity for hybridization); perennial habit (which allows the hybrids to be found and identified); mechanisms for clonal reproduction that stabilize hybridity. It has been postulated that the origin of the section *Caninae*, one of the largest within the genus *Rosa*, lies in multiple hybridization across the genus *Rosa* (Ritz et al. 2005). However, because of the unbalanced heterogamy and predominant pentaploidy that is now a feature of the species within *Caninae*, hybridization with species of different ploidy is difficult (see Section 9.3).

Spethmann & Feuerhahn (2003) provide an extensive summary table of naturally occurring interspecific hybrids. This table indicates that such crosses are possible even if there are differences in ploidy between the parents.

9.3 Crossing under experimental conditions

There are numerous examples of controlled pollinations between Species Roses, especially within the Section *Caninae,* in order to introduce germplasm that may be useful commercially or to observe characteristics of the crosses (eg Uggla & Nybom 1999; Ueda & Akimoto 2001; Werlemark & Nybom 2001; and see particularly, the summary tabulations in Spethmann & Feuerhahn 2003). However, there may be symptoms of hybrid breakdown such as embryo abortion, poor seed germination, albinism, production of more than two cotyledons, weak growth, chlorosis, dwarfism and distortion of leaves/blooms (Zlesak 2006). Discussion in Section 2.4.1 indicates that, while potentially useful for introducing valuable genetic material into Modern

Roses, crosses between Modern Roses and Species Roses have even less chance of being successful.

Van Huylenbroeck et al. (2007) made a number of hand-pollinated reciprocal crosses between tetraploid *R.* x *hybrida* (predominantly Floribunda) cultivars and 13 different wild species (although insufficient flower numbers allowed only 9 crosses using the wild species as the female parent). The wild species were largely from the section *Caninae* with varying chromosome numbers [as noted in Section 1, species in the section *Caninae* are characterised by their unbalanced meiosis where the male parent contributes one genome whereas the female parent contributes 3 – 5 genomes, a phenomenon described as matroclinal inheritance, depending on the ploidy level (Werlemark & Nybom 2001; Wissemann & Ritz 2007)]. Their results showed the general poor success of such crosses (Table 7) especially with regard to the number of seeds produced per hip. If a *R.* x *hybrida* cultivar was used as the female parent, all the progeny were largely triploid, whereas ploidy of the F1 varied if *R.*x *hybrida* was the male parent. De Vries & Dubois (2001) obtained some unexpected ploidy levels in F1s obtained from crosses between *R.* x *hybrida* (female parent) and Species Roses with ploidy ranging from 4x – 8x. Both studies (de Vries & Dubois 2001; Van Huylenbroek et al. 2007) also noted that the pollen of triploid F1 progeny can be either haploid (and usually sterile) or diploid (and usually fertile).

	Tetraploid as female parent (9 combinations)	Tetraploid as male parent (13 combinations)
% hip set	9.1% - 35.9% (av = 24%)	3.4% - 62.8% (av = 18.6%)
Fruits/hip	1 – 3.1 (av = 1.9)	1.4 – 13 (av = 4.7)
% germination	0% - 100% (av = 29%)	0% - 100% (av = 22.7%)

Table 7. Averages obtained for several parameters following reciprocal crosses between tetraploid *R.* x *hybrida* cultivars and a number of diploid wild species (data derived from Van Huylenbroek et al. 2007)

In order to facilitate successful crossing between *R.* x *hybrida* tetraploids and other diploid *Rosa* spp., Meynet et al. (1994) first produced diploid parthenogenetic *R.* x *hybrida* plants through gamma irradiation of *R.* x *hybrida* pollen then used this to pollinate a highly fertile female *R.* x *hybrida* variety (see description of technique in Crespel & Meynet 2003). The embryos that developed were cultured *in vitro* and eventually matured into flowering plants. Resulting diploid plants could be crossed with a number of diploid *Rosa* spp. (*R. gigantea, R. multiflora, R. wichuraiana, R. rugosa, R. laevigata, R. bracteata*) to obtain (following embryo rescue) achenes with viable embryos (El Mokadem et al. 2000).

In the converse to that described above, attempts have also been made to induce mitotic polyploidization of diploid germplasm using mitotic spindle disrupters such as colchicine (Roberts et al. 1990). Lack of reference to this as an adjunct to interspecific hybridization in crosses between a diploid and a tetraploid parent would suggest that its implementation in breeding programmes has not been successful.

Intergeneric crosses have been attempted, the most successful of which resulted in the cultivar 'Tiggles' a hybrid between *Hulthemia persica* (once classified as *R. persica*), a close relative of *Rosa* spp., and *R.* x *hybrida* (Zlesak 2006). Protoplast fusions of *R.* x *hybrida* 'Frensham' with cherry (*Prunus avium* x *pseudocerasus*) and blackberry (*Rubus laciniatus*) resulted in the development of putative somatic hybrid plants (Mottley et al. 1996).

Several laboratory techniques have helped to improve the success of rose breeding via crossing, in particular embryo rescue (Drewes-Alvarez 2003b). For example, this technique has been used to overcome post-fertilization barriers associated with both an interspecific cross (*R. rugosa* x *R. foetida)*(Gudin & Mouchotte 1996) and an intraspecific cross between the English roses *R.* x *hybrida* 'Heritage'® x *R.* x *hybrida* 'Lucetta'® (Marchant et al. 1994).

REFERENCES[5]

Akasaka, M., Ueda, Y., Koba, T. (2003). Karyotype analysis of wild rose species belonging to septets B, C, and D by molecular cytogenetic method. *Breeding Science* **53**: 177-182

Akkaya, A., Ornek, Z., Kaleli, S. (2004). Occupational asthma, eosinophil and skin prick tests and serum total IgE values of the workers in a plant manufacturing rose oil. *Asian Pacific Journal of Allergy and Immunology* **22**: 103-108

Akkerman, A.J.J. (2003). Seedling Rootstocks. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2*. Elsevier pp 656-664.

Amrine Jr., J.W. (2002). Multiflora Rose. In: R Van Driesche, S Lyon, B Blossey, M Hoddle, R Reardon, eds. *Biological Control of Invasive Plants in the Eastern United States*. USDA Forest Service Publication FHTET-2002-04, available online at http://www.invasive.org/eastern/biocontrol/22MultifloraRose.html

Anderson, N., Byrne, D.H. (2007). Methods for *Rosa* germination. *Acta Horticulturae* **751**: 503-507

Anderson, R.G., Woods, T.A. (1999). An economic evaluation of single stem cut rose production. *Acta Horticulturae* **481**: 629-634

André, J.P. (2003). Shoots and Stems. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2*. Elsevier pp 491-497.

APHIS (2008). Field Test Release Applications in the USA (entries under Rose and *Rosa* x *hybrida*). Information Systems for Biotechnology, Database Provided by APHIS Biotechnology Regulatory Services, available online at http://www.isb.vt.edu/cfdocs/fieldtests1.cfm

AQIS (2008). Import Case Details - public listing: *Rosa* spp. as listed. Australian Quarantine and Inspection Service (AQIS), Import Conditions Database - ICON, available online at http://www.aqis.gov.au/icon32/asp/ex_querycontent.asp

Atienza, S.G., Torres, A.M., Millán, TY., Cubero, J.I. (2005). Genetic diversity in *Rosa* as revelaed by RAPDs. *Agriculturae Conspectus Scientificus* **70**: 75-85

Auge, R.M., Shekel, K.A., Wample, R.L. (1986). Osmotic adjustment in leaves of VA mycorrhizal and nonmycorrhizal rose plants in response to drought stress. *Plant Physiology* **82**: 765-770

---

[5] All websites cited in the Reference List were current as of December 2008

Becker, H.F. (1963). The fossil record of the genus *Rosa*. *Bulletin of the Torrey Botanical Club* **90**: 99-110

Bell, R.J. (1988). *Amateurs rose breeder's guide: complete instructions on how to breed new varieties of roses*. Harkaway Victoria.

Biolley, J.P., Jay, M. (1993). Anthocyanins in modern roses: Chemical and colorimetric features in relation to the colour range. *Journal of Experimental Botany* **44**: 1725-1734

Blom, T.J., Tsujita, M.J. (2003). Cut Rose Production. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2*. Elsevier pp 594-600.

Borda, A.M., Nell, T.A., Clark, D.G. (2007). The relationship between floral fragrance and vase life of cut roses. *Acta Horticulturae* **755**: 235-241

Botanic Gardens Trust (2008a). Pests and Diseases of Roses - fact sheet. Botanic Gardens Trust, Sydney - NSW Government Department of Environment and Climate Change, available online at http://www.rbgsyd.nsw.gov.au/plant_info/pests_diseases/fact_sheets/pests_and_disease_of_roses

Botanic Gardens Trust (2008b). Phytophthora root rot - a fact sheet. Botanic Gardens Trust, Sydney - NSW Government Department of Environment and Climate Change, available online at http://www.rbgsyd.nsw.gov.au/plant_info/pests_diseases/fact_sheets/phytophthora_root_rot

Botanic Gardens Trust (2008c). Rose Aphids - fact sheet. Botanic Gardens Trust, Sydney - NSW Government Department of Environment and Climate Change, available online at http://www.rbgsyd.nsw.gov.au/plant_info/pests_diseases/fact_sheets/rose_aphids

Bredmose, N. (2003). Axillary Bud Growth. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 374-381.

Brichet, H. (2003). Australia and New Zealand. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 201-204.

Brickell, C.D., Baum, B.R., Hetterscheid, W.L.A., Leslie, A.C., McNeill, J., Trehane, P., Vrugtman, F., Wiersema, J.H. (2004). *International Code of Nomenclature for Cultivated Plants*. Acta Horticulturae 647, International Society for Horticultural Science

Broertjes, C., van Harten, A.M. (1988). *Applied Mutation Breeding for Vegetatively Propagated Crops*. Elsevier

Bruun, H.H. (2005). *Rosa rugosa* Thunb. ex Murray. *Journal of Ecology* **93**: 441-470

Bryan, W.B., Mills, T.A. (1988). Effect of frequency and method of defoliation and plant size on the survival of Multiflora rose. *Biological Agriculture and Horticulture* **5**: 209-214

Cabrera, R.I. (2001). Effect of NaCl salinity and nitrogen fertilizer formulation on yield and nutrient status of roses. *Acta Horticulturae* **547**: 255-260

Cabrera, R.I. (2002). Rose yield, dry matter partitioning and nutrient status responses to rootstock selection. *Scientia Horticulturae* **95**: 75-83

Cabrera, R.I. (2003). Demarcating salinity tolerance in greenhouse rose production. *Acta Horticulturae* **609**: 51-57

Cairns, T. (2003). Horticultural Classification Schemes. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 117-124.

Carneiro, V.T.C., Dusi, D.M.A., Ortiz, J.P.A. (2006). Apomixis: Occurrence, Applications and Improvements. Chapter 62. In: *Floriculture, Ornamental and Plant Biotechnology, Volume 1*. Global Science Books, available online at http://globalsciencebooks.com/samples/Volume1sample.pdf pp 564-571.

Carr, G.W., Yugovic, J.V., Robinson, K.E. (1992). *Environmental Weed Invasions in Victoria: Conservation and Management Implications*. Department of Conservation & Environment and Ecological Horticulture Pty Ltd Melbourne.

Carruthers, S. (2002). A rosy future. *Practical Hydroponics & Greenhouses* **65**: - available online at http://www.hydroponics.com.au/php/viewtopic.php?t=68

Çelikel, F.G., Reid, M.S. (2005). Temperature and postharvest performance of rose (*Rosa hybrida* L. 'First Red') and Gypsophila (*Gypsophila paniculata* L. 'Bristol Fairy') flowers. *Acta Horticulturae* **682**: 1789-1794

Chaanin, A. (2003). Selection Strategies for Cut Roses. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 33-41.

Channeliére, S., Rivière, S., Scalliet, G., Szecsi, J., Jullien, F., Dolle, C., Vergne, P., Dumas, C., Bendahmane, M., Hugueney, P., Cock, J.M. (2002). Analysis of gene expression in rose petals using expressed sequence tags. *FEBS Letters* **515**: 35-38

Chimonidou, D. (2003). Flower Development and the Abscission Zone. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2*. Elsevier pp 504-512.

Chimonidou-Pavlidou, D. (1996). Effect of water stress at different stages of rose development. *Acta Horticulturae* **424**: 45-51

Chimonidou-Pavlidou, D. (2000). Correlation between internal and external stages of rose development. *Acta Horticulturae* **515**: 233-244

Chrubasik, C., Roufogalis, B.D., Müller-Ladner, U., Chrubasik, S. (2008). A systematic review on the *Rosa canina* effect and efficacy profiles. *Phytotherapy Research* **22**: 725-733

Çinar, I., Çolakoglu, A.S. (2005). Potential health benefits of rose hip products. *Acta Horticulturae* **690**: 253-257

Çinar, Õ.D.K.S. (2005). Rose hip seeds are not waste. *Acta Horticulturae* **690**: 293-297

Cline, M.G. (1997). Concepts and terminology of apical dominance. *American Journal of Botany* **84**: 1064-1069

Collin, H.A. (2003). Extraction and Industrial Processes. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2*. Elsevier pp 726-735.

Condliffe, P.C., Davey, M.R., Power, J.B., Koehorst-van Putten, H., Visser, P.B. (2003). An optimised protocol for rose transformation applicable to different cultivars. *Acta Horticutlurae* **612**: 115-120

Costa, J.M., Van de Pol, P.A. (2003). Own-Rooted Cuttings. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2* Elsevier. pp 607-615.

Cox, J., Pavia, J. (2002). *Landscape with Roses: Gardens, Walkways, Arbors, Containers*. Taunton Press

Cox, P. (1999). *Australian roses: roses and rose breeders of Australia*. Blooming Books Hawthorn, Victoria.

Crespel, L., Meynet, J. (2003). Manipulation of Ploidy Level. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 5-11.

Crespel, L., Zang, D., Meynet, J., Jacob, Y., Gudin, S. (2001). Indentification of appomictic plants in *Rosa hybrida* L. by RFLPs. *Acta Horticulturae* 51-55

CSIRO Entomology (2004). Family Megachilidae. Commonwealth Scientific Industrial & Research Organisation, website based on the CSIRO Handbook of Australian Insect Names, available online at http://www.ento.csiro.au/aicn/system/megachil.htm

Cunningham, S.A., FitzGibbon, F., Heard, T.A. (2002). The future of pollinators for Australian agriculture. *Australian Journal of Agricultural Research* **53**: 896-900

Curtis, C.E., Moran, J.R. (1986). The incidence of Prunus necrotic ringspot virus in commercial cut flower roses grown under cover in Victoria. *Australasian Plant Pathology* **15**: 42-43, available online at http://www.publish.csiro.au/?act=view_file&file_id=APP9860042.pdf

Cutler, R.R. (2003). Culinary Uses and Nutritional Value. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2*. Elsevier pp 707-716.

Dayan, E., Presnov, E., Plaut, Z., Fuchs, M., Matan, E., Solphoy, A. (2001). A model to describe greenhouse crops yield quantity and quality based on morphological parametes. *Acta Horticulturae* **566**: 437-446

de Vries, D.P. (2003). Clonal Rootstocks. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2*. Elsevier pp 651-656.

de Vries, D.P., Dubois, L.A.M. (1983). Pollen and pollination experiments. X. The effect of repeated pollination on fruit- and seed set in crosses between the Hybrid Tea-rose cvs. Sonia and Ilona. *Euphytica* **32**: 685-689

de Vries, D.P., Dubois, L.A.M. (1996). Rose breeding: past, present, prospects. *Acta Horticulturae* **424**: 241-248

de Vries, D.P., Dubois, L.A.M. (2001). Developments in breeding for horizontal and vertical fungus resistance in roses. *Acta Horticulturae* **552**: 103-112

Debener, T., Mattiesch, L. (1999). Construction of a genetic linkage map for roses using RAPD and AFLP markers. *Theoretical and Applied Genetics* **99**: 891-899

Demir, A.U., Karakaya, G., Kalyoncu, A.F. (2002). Allergy symptoms and IgE immune response to rose: an occupational and environmental disease. *Allergy* **57**: 939

Dobson, H.E., Danielson, E.M., van Wesep, I.D. (1999). Pollen odor chemicals as modulators of bumble bee foraging on *Rosa rugosa* Thun. (Rosaceae). *Plant Species Biology* **14**: 153-166

Drewes-Alvarez, R. (2003a). Black Spot. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 148-153.

Drewes-Alvarez, R. (2003b). Early Embryo Breeding. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 3-5.

Dun, E.A., Ferguson, B.J., Beveridge, C.A. (2006). Apical dominance and shoot branching. Divergent opinions or divergent mechanisms? *Plant Physiology* **142**: 812-819

Eastman, J.A. (2003). *The Book of Field and Roadside.* Stackpole Books

El Mokadem, H., Meynet, J., Jacob, Y., Gudin, S. (2000). Utilization of parthenogenetic diploid plants of *Rosa hybrida* L. in interspecific hybridizations. *Acta Horticulturae* **508**: 185-190

Ellstrand, N.C., Whitkus, R., Rieseberg, L.H. (1996). Distribution of Spontaneous Plant Hybrids. *Proceedings of the National Academy of Sciences of the United States of America* **93**: 5090-5093

Eriksson, N.E., Löwhagen, O., Nilsson, J.-E., Norrlind, K., Wihl, J.-Å. (1987). Flowers and other trigger factors in asthma and rhinitis - an inquiry study. *Allergy* **42**: 374-381

Erlanson, E.W. (1938). Phylogeny and polyploidy in *Rosa*. *New Phytologist* **37**: 72-81, available online at http://www3.interscience.wiley.com/cgi-bin/fulltext/119799308/PDFSTART

Ertter, B. (2001). Native California Roses. an On-line Monograph published through the University of California, available online at http://ucjeps.berkeley.edu/ina/roses/roses.html

Esselink, G.D., Smulders, M.J.M., Vosman, B. (2003). Identification of cut rose (*Rosa hybrida*) and rootstock varieties using robust sequence tagged microsatellite site markers. *Theoretical and Applied Genetics* **106**: 277-286

Evans, R. (1998). Improved nitrogen management for greenhouse roses. Growing Points 2[3], 5-6 Department of Environmental Horticulture, University of California, Davis, available online at http://www.plantsciences.ucdavis.edu/eh/Ehweb/Newsltr/1998/GP98sum.pdf

Fiasson, J.-L., Raymond, O., Piola, F., Sanlaville-Boisson, C., Jay, M. (2003). Chemotaxonomy and Molecular Taxonomy. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 127-135.

Filiberti, D. (2005a). Hybrid Tea Roses. available online at http://www.rosegathering.com/hybridteas.html

Filiberti, D. (2005b). Noisettes. available online at http://www.rosegathering.com/noisettes.html

Firoozabady, E., Moy, Y., Courtney-Gutterson, N., Robinson, K. (1994). Regeneration of transgenic rose (*Rosa hybrida*) plants from embryogenic tissue. *Bio/Technology* **12**: 609-613

FSANZ (2006). NUTTAB 2006, Nutrient Data for Australian Foods. Food Standards Australia New Zealand, available online at http://www.foodstandards.gov.au/_srcfiles/Final%20NUTTAB%202006%20Food%20Composition%20Tables%20-%20May%202007.pdf.

García Victoria, N., Eveleens, B., Van Telgen, H.J., Van Weel, P. (2007). Critical success factors for robotized rose harvesting. *Acta Horticultura* **751**: 33-42

Gleason, M.L., Helland, S.J. (2003). Botrytis. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 144-148.

Gonnet, J.-F. (2008). Origin of the colour of cv. Rhapsody in Blue rose and some other so-called "blue" roses. *Journal of Agricultural and Food Chemistry* **51**: 4990-4994

Groves, R.H., Hosking, J.R., Batianoff, G.N., Cooke, D.A., Cowie, I.D., Johnson, R.W., Keighery, G.J., Lepschi, B.J., Mitchell, A.A., Moerkerk, M., Randall, R.P., Rozefelds, A.C., Walsh, N.G., Waterhouse, B.M. (2003). *Weed categories for natural and agricultural ecosystem management.* Bureau of Rural Sciences Canberra, available online at affashop.gov.au/PdfFiles/PC12781.pdf

Gudin, S. (1994). Embryo rescue in *Rosa hybrida* L. *Euphytica* **72**: 205-212

Gudin, S. (1995). Rose improvement, a breeder's experience. *Acta Horticulturae* **420**: 125-128

Gudin, S. (2000). Rose: Genetics and Breeding. Chapter 17. In: J Janick, ed. *Plant Breeding Reviews, Volume 17*. John Wiley & Sons, Inc. pp 159-189.

Gudin, S. (2001). Rose breeding technologies. *Acta Horticulturae* **547**: 23-26

Gudin, S. (2003a). Breeding Overview. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 25-33.

Gudin, S. (2003b). Seed Propagation. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2*. Elsevier pp 620-623.

Gudin, S., Arene, L., Bulard, C. (1991). Influence of season on rose pollen quality. *Sexual plant reproduction* **4**: 113-117

Gudin, S., Mouchotte, J. (1996). Integrated research in rose improvement - a breeder's experience. *Acta Horticulturae* **424**: 285-291

Gumbert, A., Kunze, J., Chittka, L. (1999). Floral colour diversity in plant communities, bee colour space and a null model. *Proceedings of the Royal Society of London B* **266**: 1711-1716

Gupta, M.N., Shukla, R. (1971). Mutation breeding of garden roses. *Japanese Journal of Breeding* **21**: 129-136

Guterman, I., Shalit, M., Menda, N., Piestun, D., Dafny-Yelin, M., Shalev, G., Bar, E., Davydov, O., Ovadis, M., Emanuel, M., Wang, J., Adam, Z., Pichersky, E., Lewinsohn, E., Zamir, D., Vainstein, A., Weiss, D. (2002). Rose scent: genomics approach to discovering novel floral fragrance-related genes. *The Plant Cell* **14**: 2325-2338

Haas, R.H., Lehman, S.K., Morton, H.L. (1970). Influence of mowing and spraying dates on herbicidal control of Macartney rose. *Weed Science* **18**: 33-37

Harborne, J.B., Williams, C.A. (2000). Advances in flavonoid research since 1992. *Phytochemistry* **55**: 481-504

Harden, G.J. (2000). *Flora of New South Wales Volume 1*. Harden, G.J. (eds). University of New South Wales Press

Hartmann, H.T., Kester, D.E. (1975). *Plant Propagation, Principles and Practices.* Prentice-Hall, New Jersey

Hassall & Associates Pty Ltd (2001). Hydroponics as an Agricultural Production System. RIRDC Publication NO. 01/141, Rural Industries Research and Development Corporation, Canberra, available online at http://www.rirdc.gov.au/reports/Ras/01-141.pdf

Hatton, T.J. (1989). Spatial patterning of sweet briar (*Rosa rubiginosa*) by two vertebrate species. *Austral Ecology* **14**: 199-205

Hert, A.P., Jones, J.B. (2003). Crown Gall. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 140-144.

Hess, G., Byrne, D.H., Zhang, H. (2007). Toward positional cloning of everblooming (*evb*) in plants: A BAC library of *Rosa chinensis* cv. Old Blush. *Acta Horticulturae* **751**: 169-174

Higson, H. (2007). The History and Legacy of the China Rose. Quarryhill Botanical Gardens, Glen Ellen, California, available online at http://www.quarryhillbg.org/page14.html

Horridge, J.S., Cockshull, K.E. (1974). Flower initiation and development in the glasshouse rose. *Scientia Horticulturae* **2**: 273-284

Hosafci, H., Arslan, N., Sarihan, E. (2005). Propagation of dog roses (*Rosa canina* L.) by seed. *Acta Horticulturae* **690**: 159-164

Hubbard, M., Kelly, S., Rajapakse, S., Abbott, A., Ballard, R. (1992). Restriction fragment length polymorphisms in rose and their use for cultivar identification. *HortScience* **27**: 172-173

Hurst, C.C. (1925). Chromosomes and characters in *Rosa* and their significance in the origin of species. *Experiments in Genetics* **37**: 534-550

Jackson, G.A., Blundell, J.B. (1963). Germination in *Rosa*. *Journal of Horticultural Science* **38**: 310-320

Jacob, Y., Ferrero, F. (2003). Pollen Grains and Tubes. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2*. Elsevier pp 518-523.

Jacob, Y., Pierret, V. (2000). Pollen size and ploidy level in the genus *Rosa*. *Acta Horticulturae* **508**: 289-292

Jay, M., Biolley, J.-P., Fiasson, J.-L., Fiasson, K., Gonnet, J.-F., Grossi, C., Raymond, O., Viricel, M.-R. (2003). Anthocyanins and Other Flavonoid Pigments. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 248-255.

JBCH (2008a). Approved Type 1 Use Regulation: Rose variety with modified flavonoid biosynthesis pathway (F3'5'H, 5AT, *Rosa hybrida* WKS82/130-4-1). Japan Biosafety Clearing House, available online at http://www.bch.biodic.go.jp/download/en_lmo/130_4_1_2008enRi.pdf

JBCH (2008b). Approved Type 1 Use Regulation: Rose variety with modified flavonoid biosynthesis pathway (F3'5'H, 5AT, *Rosa hybrida* WKS82/130-9-1). Japan Biosafety Clearing House, available online at http://www.bch.biodic.go.jp/download/en_lmo/130_9_1_2008enRi.pdf

Jesse, L.C., Moloney, K.A., Obrycki, J.J. (2006). Insect pollinators of the invasive plant, *Rosa multiflora* (Rosaceae), in Iowa, USA. *Weed Biology and Management* **6**: 235-240

Johns, L., Stevenson, V. (1979). *The Complete Book of Fruit.* Angus and Robertson Publishers Sydney.

Joublan, J.P., Rios, D. (2005). Rose culture and industry in Chile. *Acta Horticulturae* **690**: 65-69

Karakaya, G., Kalyoncu, A.F. (2003). A case of anaphylaxis due to rose pollen ingestion. *Allergol et Immunopathol* **31**: 91-93

Karlik, J.F. (2008). Roses in the Garden and Landscape: Cultural Practices & Weed Control. Pest Notes, Publication 7465, University of California, Agriculture and Natural Resources, available online at http://www.ipm.ucdavis.edu/PMG/PESTNOTES/pn7465.html

Katsumoto, Y., Fukuchi-Mizutani, M., Fukui, Y., Brugliera, F., Holton, T.A., Karan, M., Nakamura, N., Yonekura-Sakakibara, K., Togami, J., Pigeaire, A., Tao, G.-Q., Nehra, N.S., Lu, C.-Y., Dyson, B.K., Tsuda, S., Ashikari, T., Kusumi, T., Mason, J.G., Tanaka, Y. (2007). Engineering of the rose flavonoid biosynthetic pathway successfully generated blue-hued flowers accumulating delphinidin. *Plant and Cell Physiology* **48**: 1589-1600

Kemp, J.R., Kevan, P.G., Posluszny, U. (1993). Morphological differences and changes of the gynoecium in short-lived flowers of *Rosa setigera* Michaux and their relationship to dioecy. *International Journal of Plant Sciences* **154**: 550-556

Kevan, P.G. (2003). Pollination. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2*. Elsevier pp 456-460.

Khosh-Khui, M., Bassiri, A., Niknejad, M. (1976). Effects of temperature and humidity on pollen viability of six rose species. *Canadian Journal of Plant Science* **56**: 517-523

Kim, H.-J., Kim, K., KIm, N.-S., Lee, D.-S. (2000). Determination of floral fragrances of *Rosa hybrida* using solid-phase trapping-solvent extraction and gas chromatography-mass spectrometry. *Journal of Chromatography A* **902**: 389-404

Kwaselow, A., Rowe, M., Sears-Ewald, D., Owenby, D. (1990). Rose hips: a new occupational allergen. *Journal of Allergy and Clinical Immunology* **85**: 704-708

L.H.Bailey Hortorium (1976). *Hortus Third - A Concise Dictionary of Plants Cultivated in the United States and Canada.* Macmillan New York, USA. pp -1290.

Lavid, N., Wang, J., Shalit, M., Guterman, I., Bar, E., Beuerle, T., Menda, N., Shafir, S., Zamir, D., Adam, Z., Vainstein, A., Weiss, D., Pichersky, E., Lewinsohn, E. (2002). *O*-methyltransferases involved in the biosynthesis of volatile phenolic derivatives in rose petals. *Plant Physiology* **129**: 1899-1907

Lazarides, M., Cowley, K., Hohnen, P. (1997). *CSIRO Handbook of Australian Weeds.* CSIRO Canberra, ACT. pp 1-264.

Li, X., Gasic, K., Cammue, B., Broekaert, W., Korban, S.S. (2003). Transgenic rose lines harboring an antimicrobial protein gene, *Ace-AMP1*, demonstrate enhanced resistance to powdery mildew (*Spaerotheca pannosa*). *Planta* **218**: 226-232

Lieth, H. (1998). To pinch or bend? Manipulating cut rose quantity and quality in greenhouse production. Growing Points 2[3], 2-4 Department of Environmental Horticulture, University of California, Davis, available online at http://www.plantsciences.ucdavis.edu/eh/Ehweb/Newsltr/1998/GP98sum.pdf

Linde, M., Mattiesch, L., Debener, T. (2004). *Rpp1*, a dominant gene providing race-specific resistance to rose powdery mildew (*Podosphaera pannosa*): molecular mapping,SCAR development and confirmation of disease resistance data. *Theoretical and Applied Genetics* **109**: 1261-1266

Linde, M., Shishkoff, N. (2003). Powdery Mildew. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 158-165.

Lindenbaum, S., Ginzburg, C., Halevey, A.H. (1975). A morphological study of the 'bullhead' malformation in the Baccara rose. *Annals of Botany* **39**: 219-223

Lohaus, E., Zenger, C., Rüdiger, W. (1985). Natural inhibitors of germination and growth, III New α-pyrones from seeds of *Rosa canina*. *Verlag der Zeitschrift für Naturforschung* **40C**: 490-495

Lorenzo, H., Cid, M.C., Siverio, J.M., Ruano, M.C. (2000). Effects of sodium on mineral nutrition in rose plants. *Annals of Applied Biology* **137**: 65-72

Maas, F.M., Hofman-Eijer, L.B., Hulsteijn, K. (1995). Flower morphogenesis in *Rosa hybrida* 'Mercedes' as studied by cryo-scanning electron and light micrsocopy. Effects of light and shoot position on a branch. *Annals of Botany* **75**: 199-205, available online at http://aob.oxfordjournals.org/cgi/content/abstract/75-2/199

MacPhail, V.J., Kevan, P.G. (2007). Reproductive success and insect visitation in wild roses (*Rosa* spp.) - preliminary results from 2004. *Acta Horticulturae* **751**: 381-388

Marchant, R., Power, J.B., Davey, M.R., Chartier-Hollis, J. (1994). Embryo rescue, for the production of F1 hybrids, in English rose. *Euphytica* **74**: 187-193

Marchant, R., Power, J.B., Lucas, J.A., Davey, M.R. (1998). Biolistic transformation of rose (*Rosa hybrida* L.). *Annals of Botany* **81**: 109-114

Marriott, M. (2003). Modern (Post-1800). In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 402-409.

Massey University (2008). Sweet Brier *Rosa rubiginosa*. Massey University, New Zealand Weeds database, available online at http://weeds.massey.ac.nz/weeds.asp?pid=59&sf=common

Mercure, M., Bruneau, A. (2008). Hybridization between the escaped *Rosa rugosa* (Rosaceae) and native *R. blanda* in eastern North America. *American Journal of Botany* **95**: 597-607

Meynet, J., Barrade, R., Duclos, A., Siadous, R. (1994). Dihaploid plants of roses (*Rosa* x *hybrida* cv 'Sonia') obtained by parthenogenesis induced using irradiated pollen and *in vitro* culture of immature seeds. *Agronomie* **2**: 169-175

Moe, R. (1988). Growth and flowering in roses. *Acta Horticulturae* **218**: 121-130

Moe, R., Kristofferson, T. (1969). The effect of temperature and light on growth and flowering of *Rosa* 'Baccara' in greenhouses. *Acta Horticulturae* **14**: 157-163

Mottley, J., Yokoya, K., Matthews, D., Squirrell, J., Wentworth, J.E. (1996). Protoplast fusion and its potential role in the genetic improvement of roses. *Acta Horticulturae* **424**: 393-397

Munger, G.T. (2002). *Rosa multiflora*. In: *Fire Effects Information System, [Online]*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, available online at http://www.fs.fed.us/database/feis/plants/shrub/rosmul/all.html

Noriega, C., Söndahl, M.R. (1991). Somatic embryogenesis in Hybrid Tea roses. *Bio/Technology* **9**: 991-993

Nybom, H., Werlemark, G., Esselink, D.G., Vosman, B. (2005). Sexual preferences linked to rose taxonomy and cytology. *Acta Horticulturae* **690**: 21-27

OECD (2006). Points to Consider for Consensus Documents on the Biology of Cultivated Plants. ENV/JM/MONO(2006)1, Organisation for Economic Co-operation and Development, available online at http://www.olis.oecd.org/olis/2006doc.nsf/LinkTo/NT00000B8E/$FILE/JT03206674.PDF

Ogata, J., Kanno, Y., Itoh, Y., Tsugawa, H., Suzuki, M. (2005). Anthocyanin biosynthesis in roses. *Nature* **435**: 757-758

OGTR (2006). Risk Assessment and Risk Management Plan for DIR 060/2005: Limited and controlled release of three imported GM rose lines. Document prepared by the Australian Government Office of the Gene Technology Regulator, available online at http://www.ogtr.gov.au/internet/ogtr/publishing.nsf/Content/dir060-2005

Oregon State University (2008). Rose (*Rosa* and hybrids) - Armillaria root rot. Oregon State University Extension Service, available online at http://plant-disease.ippc.orst.edu/disease.cfm?RecordID=978

Parsons, W.T., Cuthbertson, E.G. (2001). *Noxious Weeds of Australia*. CSIRO Publishing (2nd Edition) & Inkata Press (1st Edition) Collingwood, Victoria.

Pertwee, J. (2000). *Production and Marketing of Roses*. Elsevier, partial book content available online at http://www.pathfastpublishing.com/Rose%20Book%20Contents.htm

Phillips, R., Rix, M. (1988). *Roses*. Pan Books Ltd London.

Pionnat, S., Keller, H., Héricher, D., Bettachini, A., Dessaux, Y., Nesme, X., Poncet, C. (1999). Ti plasmids from *Agrobacterium* characterize rootstock clones that initiated a spread of Crown Gall disease in Mediterranean countries. *Applied and Environmental Microbiology* **65**: 4197-4206

Rajasekharan, P.E., Ganeshan, S. (1994). Freeze preservation of rose pollen in liquid nitrogen: feasibility, viability and fertility status after long-term storage. *Journal of Horticultural Science* **69**: 565-569

Randall, R.P. (2002). *A Global Compendium of Weeds*. R.G. & F.J. Richardson Meredith, Victoria. pp 1-905.

Randall, R.P. (2007). *The Introduced Flora of Australia and its Weed Status*. CRC for Australian Weed Management, available online at http://www.weedscrc.org.au/documents/intro_flora_australia.pdf

Reid, A. (2005). Common Problems of Roses. Government of Western Australia, Department of Agriculture Garden Note, available online at http://www.agric.wa.gov.au/content/PW/GARD/COMROSPROB.PDF

Ritz, C.M., Schmuths, H., Wissemann, V. (2005). Evolution by reticulation: European dogroses originated by multiple hybridization across the genus *Rosa*. *Journal of Heredity* **96**: 4-14

Roberts, A.V., Blake, P.S. (2003). Floral Induction. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 381-386.

Roberts, A.V., Blake, P.S., Lewis, R., Taylor, J.M., Dunstan, D.I. (1999). The effect of gibberellins on flowering in roses. *Journal of Plant Growth Regulation* **18**: 113-119

Roberts, A.V., Debener, T., Gudin, S. (2003). *Encyclopedia of Rose Science*. Elsevier

Roberts, A.V., Lewis, R. (2003). Mutation. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 312-318.

Roberts, A.V., Lloyd, D., Short, K.C. (1990). *In vitro* procedures for the induction of tetraploidy in a diploid rose. *Euphytica* **49**: 33-38

Roberts, A.V., Schum, A. (2003). Micropropagation. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 57-66.

Rosati, C., Simoneau, P. (2006). Metabolic engineering of flower color in ornamental plants: a novel route to a more colorful world. *Journal of Crop Improvement* **18**: 301-324

Rose, J. (1999). *375 Essential Oils and Hydrosols*. Frog Books

Ross, D. (1991). *The Ross Guide to Rose Growing*. Lothian Publishing Company Pty Ltd Port Melbourne,Victoria.

Rout, G.R., Samantaray, S., Mottley, J., Das, P. (1999). Biotechnology of the rose: a review of recent progress. *Scientia Horticulturae* **81**: 201-228

Roxburgh, N. (2008). Leaf Yellowing on Roses - Part 2: Chlorosis. Garden Grapevine (online magazine) Government of Western Australia, available online at http://www.westone.wa.gov.au/toolbox6/hort6/html/resources/nursery/gvine/leaf_yellow2.htm

Safi, M.I. (2005). Flower production related to re-blooming time of three *Rosa hybrida* cultivars in response to rootstock type. *ScienceAsia* **31**: 179-181

Salgado, C., Cepero, M.C., Realpe, E., Restrepo, S. (2007). Histological analyses of the fungal endophytes in *Rosa hybrida*. *Revista Iberoamericana de Micologia* **24**: 323-324

SAMDBNRMB (2008). Weed Sheet: Dog Rose & Sweet Briar Rose. Government of South Australia, South Australian Murray-Darling Basin Natural Resources Management Board, available online at http://www.samdbnrm.sa.gov.au/Portals/7/DOG%20Rose.pdf

Scalliet, G., Piola, F., Douady, C.J., Rèty, S., Raymond, O., Baudino, S., Bordji, K., Bendahmane, M., Dumas, C., Cock, J.M., Hugueney, P. (2008). Scent evolution in Chinese roses. *Proceedings of the National Academy of Sciences* **105**: 5927-5932

Schum, A. (2003). Mutation breeding in ornamentals: an efficient breeding method? *Acta Horticulturae* **612**: 47-60

Schum, A., Dohm, A. (2003). In Vitro Regeneration Techniques. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 76-90.

Schum, A., Preil, W. (1998). Induced Mutations in Ornamental Plants. Chapter 17. In: SM Jain, DS Brar, BS Ahloowalia, eds. *Somaclonal Variation and Induced Mutations in Crop Improvement*. Springer pp 333-366.

Shalit, M., Guterman, I., Volpin, H., Bar, E., Tamari, T., Menda, N., Adam, Z., Zamir, D., Vainstein, A., Weiss, D., Pichersky, E., Lewinsohn, E. (2003). Volatile ester formation in roses. Identification of an acetyl-coenzyme A. geraniol/citronellol acetyltransferase in developing rose petals. *Plant Physiology* **131**: 1868-1876

Shattock, R.C. (2003). Rust. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 165-169.

Shaw, J. (1983). Gardening with species roses. *Arnoldia* **43**: 3-16, available online at http://arnoldia.arboretum.harvard.edu/pdf/articles/1148.pdf

Skytt Andersen, A., Fuchs, H.W.M. (2003). Roots. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2*. Elsevier pp 512-518.

Solís-Pérez, A.R., Cabrera, R.I. (2007). Evaluating counter-ion effects on greenhouse roses subjected to moderately high salinity. *Acta Horticulturae* **751**: 375-380

Souq, F., Coutos-Thevenot, P., Yean, H., Delbard, G., Maziere, Y., Barbe, J.P., Boulay, M. (1996). Genetic transformation of roses, 2 examples: one on morphogenesis, the other on anthocyanin biosynthetic pathway. *Acta Horticulturae* **424**: 381-388

Spethmann, W., Feuerhahn, B. (2003). Species Crosses. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 299-312.

Spoerke, D.G., Smolinske, S.C. (1990). *Toxicity of Houseplants.* CRC Press

Stace, C.A., Thompson, H. (1997). *New Flora of the British Isles.* Cambridge University Press

Syrett, P. (1990). The rose seed chalcid *Megastigmus aculeatus* Swederus (Hymenoptera: Torymidae) on sweet brier, *Rosa rubiginosa*, in the South Island tussock country. *New Zealand Entomologist* **13**: 34-38

Tanaka, Y., Fukuchi-Mizutani, M., Mason, J.G. (2003). Cloned Genes. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 341-350.

Torre, S. (2003). Leaves. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2*. Elsevier pp 497-504.

Ueda, Y. (2003). Seed Maturation and Germination. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2*. Elsevier pp 623-626.

Ueda, Y., Akimoto, S. (2001). Cross- and self-incompatibility in various species of the genus *Rosa*. *Journal of Horticultural Science and Biotechnology* **76**: 392-395

Uggla, M., Nybom, H. (1999). Domestication of a new crop in Sweden - Dogroses (*Rosa* Sect. *Caninae*) for commercial rose hip production. *Acta Horticulturae* **484**: 147-151

Ünlü, M., Sahin, U., Yariktas, M., Demirci, M., Akkaya, A., Öztürk, M., Orman, A. (2001). Allergic rhinitis in *Rosa domescena* cultivators: a novel type of occupational allergy? *Asian Pacific Journal Allergy Immunology* **19**: 231-235

Urban, L. (2003). Influences of Abiotic Factors in Growth and Development. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 369-374.

Vainstein, A., Ben-Meir, H., Zuker, A., Watad, A.A., Scovel, G., Ahroni, A., Ovadis, M. (1995). Molecular markers and genetic transformation in the breeding of ornamentals. *Acta Horticulturae* **420**: 65-67

Vainstein, A., Lewinsohn, E., Pichersky, E., Weiss, D. (2001). Floral fragrance. New inroads into an old commodity. *Plant Physiology* **127**: 1383-1389

Van de Pol, P.A. (2003). Stenting. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 2*. Elsevier pp 615-620.

van der Salm, T.P.M., van der Toorn, C.J.G., Bouwer, R., Hänisch ten Cate, C.H., Dons, H.J.M. (1997). Production of *ROL* gene transformed plants of *Rosa hybrida* L. and characterization of their rooting ability. *Molecular Breeding* **3**: 39-47 van der Salm, T.P.M., van der Toorn, C.J.G., Hänisch ten Cate, C.H., Dons, J.M. (1996). Somatic embryogenesis and shoot regeneration from excised adventitious roots of the rootstock *Rosa hybrida* L. 'Moneyway'. *Plant Cell Reports* **15**: 522-526

Van Huylenbroek, J., Eeckhaut, T., Leus, L., Werlemark, G., De Riek, J. (2007). Introduction of wild germplasm in Modern Roses. *Acta Horticulturae* **751**: 285-290

Van Tuyl, J.M., Lim, K.-B. (2003). Interspecific hybridisation and polyploidisation as tools in ornamental plant breeding. *Acta Horticulturae* **612**: 13-22

van Weel, P.A., de Dood, J., Woittiez, R.D. (1992). Cut-rose production in closed systems with emphasis on environmental aspects. *Acta Horticulturae* **303**: 15-21

Visser, T., de Vries, D.P., Scheurink, J.A.M., Welles, G.W.H. (1977). Hybrid Tea - rose pollen. II. Inheritance of pollen viability. *Euphytica* **26**: 729-732

Walsh, N.G., Entwisle, T.J. (1996). *Flora of Victoria - Volume 3 Dicotyledons, Winteraceae to Myrtaceae.* Walsh, N.G., Entwisle, T.J. (eds). Inkata Publishing pp - 1093.

Walther, F., Sauer, A. (1986). *In vitro* mutagenesis in roses. *Acta Horticulturae* **189**: 37-46

Wang, G. (2007). A study of the history of Chinese roses from ancient works and images. *Acta Horticulturae* **751**: 347-351

Weidema, I. (2006). NOBANIS - Invasive Alien Species Fact Sheet - *Rosa rugosa*. Online Database of the North European and Baltic Network on Invasive Alien Species - NOBANIS, available online at http://www.nobanis.org/files/factsheets/Rosa_rugosa.pdf

Werlemark, G., Nybom, H. (2001). Skewed distribution of morphological character scores and molecular markers in three interspecific crosses in *Rosa* section *Caninae*. *Hereditas* **134**: 1-13

Werlemark, G., Nybom, H. (2005). The importance of being mother - inheritance in Dogroses, *Rosa* section *Caninae*. *Acta Horticulturae* **690**: 113-118

Widenfelt, S.E., Wifstrand, S., Berg, E. (1975). *Favorite Swedish Recipes.* Courier Dover Publications

Williams, D., Pullman, K. (2000). Pests of Roses. State of Victoria, Department of Primary Industries, available online at http://www.dpi.vic.gov.au/dpi/nreninf.nsf/9e58661e880ba9e44a256c640023eb2e/2e692c4dadc0c66dca256f3c0002b2d3/$FILE/AG0516.pdf

Winkel-Shirley, B. (2001). Flavonoid Biosynthesis. A Colorful Model for Genetics, Biochemistry, Cell Biology, and Biotechnology. *Plant Physiology* **126**: 485-493

Wissemann, V. (2003). Conventional Taxonomy (Wild Roses). In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science*. Elsevier B.V. Oxford. pp 111-117.

Wissemann, V., Ritz, C.M. (2007). Evolutionary patterns and processes in the genus *Rosa* (Rosaceae) and their implications for host-parasite co-evolution. *Plant Systematics and Evolution* **266**: 79-89

Xu, X., Pettit, T. (2003). Downy Mildew. In: AV Roberts, T Debener, S Gudin, eds. *Encyclopedia of Rose Science, Volume 1*. Elsevier pp 154-158.

Yamaguchi, H., Nagatomi, S., Morishita, T., Degi, K., Tanaka, A., Shikazono, N., Hase, Y. (2003). Mutation induced with ion beam irradiation in rose. *Nuclear Instruments and Methods in Physics Research B* **206**: 561-564

Yambe, Y., Hori, Y., Takeno, K. (1992). Levels of endogenous abscisic acid in rose achenes and leaching with activated charcoal to improve seed germination. *Journal of the Japanese Society for Horticultural Science* **61**: 383-387

Yambe, Y., Takeno, K. (1992). Improvement of rose achene germination by treatment with macerating enzymes. *HortScience* 1018-1020

Yambe, Y., Takeno, K., Saito, T. (1995). Light and phytochrome involvement in *Rosa multiflora* seed germination. *Journal of the American Society for Horticultural Science* **120**: 953-955

Yokoya, K., Roberts, A.V., Mottley, J., Lewis, R., Brandham, P.E. (2000). Nuclear DNA amounts in roses. *Annals of Botany* **85**: 557-561

Younis, A., Riaz, A., Ahmed, R., Raza, A. (2007). Effect of hot water, sulphuric acid and nitric acid on the germination of rose seeds. *Acta Horticulturae* **755**: 105-108

Zamski, E., Oshri, S., Zieslin, N. (1985). Comparative morphology and anatomy of axillary buds along a rose shoot. *Botanical Gazette* **146**: 208-212

Zieslin, N. (1988). Postharvest control of vase life and senescence of rose flowers. *Acta Horticulturae* **261**: 257-264

Zlesak, D.C. (2006). Rose *Rosa* x *hybrida*. Chapter 26. In: NO Anderson, ed. *Flower Breeding and Genetics: Issues, Challenges and Opportunities for the 21st Century*. Springer Dordrecht. pp 695-738.