

Review of the Breeding Systems of Wild Roses (*Rosa* spp.)

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ABSTRACT

There are more than 150 wild rose species (*Rosa* spp.) known, but research into breeding systems (sexual reproduction) and pollination relationships has concentrated mostly on cultivars, with only a few exceptions. This review summarizes much of the known information about breeding systems for 94 wild species of rose around the world. Many roses can self-pollinate, a few can reproduce asexually (agamospermy), while some are obligate outcrossers even to the extreme of dioecy; however, many roses show combinations of breeding systems, particularly those that are polyploid. The most common type of breeding system among species is xenogamy, or cross-pollination, which allows for greater genetic variation within populations than methods such as autogamy or self-pollination. This review also presents information on: hip and seed production resulting from different breeding systems for selected species, factors affecting reproductive success including incompatibility, viability, receptivity, ploidy levels, and the *Caninae* meiosis, as well as the debate about the presence of agamospermy, and the features of achenes and seed production in *Rosa*.

Keywords: agamospermy, autogamy, geitonogamy, pollination, reproduction, xenogamy

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INTRODUCTION

The genus *Rosa* (Rosaceae family) contains approximately 150 species (Quest-Ritson and Quest-Ritson 2003), although the number varies, according to authority, from more than 100 species (Ueda and Akimoto 2001; Wissemann 2003; Ugglá 2004) to 200 or more in total (Stewart 1969; Soper and Heimburger 1994). These differences mostly result from the difficulty in identifying roses. Roses can vary greatly in appearance, causing some authors to split a species into multiple species while others lump divergent, closely related populations into a single species. In addition, there are a number of synonyms and cultivars adding to the confusion.

Authorities for taxonomic names in this paper are given in the Tables and after the species name the first time it is listed in the text. They are presented as recorded in the original sources. If the source did not include the authority, no authority is given in the Tables, unless another source for that same species did include an authority, in which case that one is presented here. Synonyms of species are included under the main species name as recognized by Quest-Ritson and Quest-Ritson (2003) or Wissemann (2003). Separation by Sub-genera and Sections follows the classification system as outlined in Wissemann (2003), with additional in-

formation obtained from Darlington and Wylie (1955), Jičínská (1975, 1976), McNeill *et al.* (2006), Rehder (1960), and Ueda and Akimoto (2001).

Roses are an important horticultural crop, receiving much attention from rose breeders, but comparatively little is known about wild roses, particularly their pollination biology, methods of sexual reproduction, and insect visitors (Kevan *et al.* 1990; Kevan 2003; MacPhail 2007). Studies on rose species are scattered throughout the literature and are easily overlooked. This review aims to bring together information from the various studies on wild rose breeding systems and to provide generalizations about the data.

BACKGROUND TO *ROSA*

Wild rose flowers are often fragrant and are commonly rose-colored, although white, or more rarely yellow, flowers do occur in some species (Knuth 1908; Kevan *et al.* 1990; Kevan 2003). Flowers are open and bowl shaped (Knuth 1908; Faegri and van der Pijl 1979), allowing a wide range of flower-visiting insects to access the flower, become dusted with pollen, and touch the stigmas during pollination (Kevan *et al.* 1990; MacPhail 2007).

The flowers of almost all rose species are hermaphroditic (*R. setigera* Michx. is cryptically dioecious) (Kevan *et*

al. 1990; Kemp 1994) and are devoid of nectar (although some species may secrete minute amounts on the edge of the receptacle at the base of the flower between the filaments and the ovary) (Knuth 1908; Taylor and Taylor 1978; Kevan 2003). Lack of nectar is compensated for, as far as pollinators are concerned, by production of abundant pollen as the reward for potential pollinators (Knuth 1908; Kevan *et al.* 1990).

Typically one seed is produced per pistil, and although there is some intra-specific variation in the number of pistils/flower (Cole and Melton 1986), the number is roughly 25-50% that of the number of stamens, which can range from 50-250 (Erlanson 1934; Kevan 2003), or fewer in some cases (e.g. *R. multiflora* Thunb. Ex. Murr., pers. obs.). The hip is made up of the fleshy or pulpy receptacle surrounding the actual fruits (achenes) and may be red, orange, to yellow (depending on species) when mature (Soper and Heimburger 1994). The seed is enclosed in a hard pericarp, and seeds are usually produced every year (Taylor and Taylor 1978). Taylor and Taylor (1978) claim that seed production may be biennial in some rose species, but they do not provide examples.

Only eight to eleven wild species have contributed to the breeding and selection of modern commercial roses: *R. chinensis* Jacq, *R. damascena* Mill., *R. foetida* Herm., *R. gallica* L., *R. giganteana* Coll et Crep., *R. moschata* Herm., *R. multiflora* Thunb. Ex. Murr., and *R. rugosa* Thunb. are the primary ones, although *R. wichurana* Crep., *R. fedtschenkoana* Regel, and yet another species were also involved (Wylie 1954; Stewart 1969; Spethman and Feuerhahn 2003; Zlesak 2006). Recently, a male sterility gene from a female clone of dioecious *R. setigera* has been introgressed into modern rose germplasm (Zlesak *et al.* 2007). Cross- and self-compatibility relationships are important to commercial rose hybridization because commercial cultivars are highly inbred and often have low fertility (Shahare and Shastry 1963; Zlesak 2006). However, not all combinations in crossings are successful. Moreover, the ways in which chromosomes pair and divide in meiosis may preclude fertility (Shahare and Shastry 1963; Jičinská 1976; Kevan 2003) (see discussion on ploidy levels and *Caninae* meiosis below).

POLLINATION AND TYPES OF BREEDING SYSTEMS IN ROSA

Pollination is the transfer of pollen from the anthers of a flower to the stigmas of a flower on a different plant, on the same plant, or within the same flower (Faegri and van der Pijl 1979; Richards 1986; Proctor *et al.* 1996). Pollen is transported to stigmas by vectors such as wind, water, or animals, or by the direct contact between the anthers and stigmas (Kevan and Baker 1983; van Went and Willemsse 1984; Richards 1986; Proctor *et al.* 1996). Breeding systems are distinguished from each other by the source of pollen (or in special cases, the lack of pollen) that can result in successful seed-set. There are five major recognizable types of breeding systems: agamospermy, automatic autogamy, facilitated autogamy, geitonogamy, and xenogamy, and all have been recognized in the genus *Rosa*.

Agamospermy (from Greek, 'unmarried seed') is the process of asexual seed formation (Gustafsson 1946; Nygren 1967; Nogler 1984; Richards 1986; Asker and Jerling 1992; Czapik 1994). Examples of rose species that have been shown to reproduce in this manner are given in **Table 1**. Although the term apomixis includes reproduction in the absence of fertilization by means of seeds and by vegetative structures, it is often used as a synonym for agamospermy (Gustafsson 1946; Nygren 1967). Vegetative reproduction is not discussed in this paper, so the term apomixis is not used.

There are three main types of agamospermy: diplospory, apospory, and adventitious embryony (Gustafsson 1946; Nygren 1967; Nybom 1988; Campbell *et al.* 1991; Czapik 1994). Examples of species of roses showing any type of agamospermy are given in **Table 1**. Diplospory occurs when

the macrospore mother cell (i.e. megasporocyte that fails to complete meiosis) develops into an unreduced embryo sac (Gustafsson 1946; Nygren 1967; Nybom 1988; Campbell *et al.* 1991). In apospory, somatic cells in the nucellus (i.e. archesporal cells) form the unreduced embryo sac (Gustafsson 1946; Nygren 1967; Nybom 1988; Campbell *et al.* 1991). In both those cases a gametophyte is formed with the unreduced ($2n$) chromosome number. As it continues to develop, the egg cell is formed with two synergids, two polar nuclei, and three antipodal cells. If the egg cell develops into an embryo (a sporophyte) without fertilization, the process is known as parthenogenesis; if another cell in the gametophyte develops into an embryo, the process is known as apogamy (Gustafsson 1946; Nygren 1967; Nybom 1988; Campbell *et al.* 1991). Some aposporous or diplosporous species are pseudogamous; although no fertilization of the egg cell takes place, pollination is needed for the endosperm to develop and seeds to be produced (Gustafsson 1946; Nygren 1967).

In adventitious embryony, embryos are formed directly from somatic cells in the nucellus or integuments of the mother sporophyte's ovules (i.e. in a megasporophyte rather than in a megagametophyte) (Gustafsson 1946; Nygren 1967; Campbell *et al.* 1991), while the embryo sac develops in a normal sexual way (Nygren 1967). This form of agamospermy means that the gametophytic stage is skipped entirely (Gustafsson 1946). Adventitious embryony normally leads to the development of more than one embryo (Nygren 1967).

Although plants produce fruits by several types of agamospermy, the result is ovules maturing into seeds without fertilization of the egg and/or central cell from pollen (Richards 1986; Asker and Jerling 1992; Proctor *et al.* 1996). This process results in offspring that usually are genetically identical to the mother plant, and are essentially clones dispersed as seeds (Nogler 1984; Richards 1986; Proctor *et al.* 1996).

Both autogamy and geitonogamy are forms of self-pollination, and occur when pollen comes into contact with stigmas of flowers on the same plant or genet, allowing individual plants to reproduce in isolation from other plants (i.e. without the need to have other plants nearby to provide pollen) (Richards 1986; Proctor *et al.* 1996). Autogamy ('self-marriage') is a method by which the male and female parts of a single flower interact. There are two main types of autogamy: facilitated autogamy and automatic autogamy. They differ based on how the pollen is transferred from the anthers to the stigmas. In the first, external factors are needed (e.g. pollen must be moved by wind or animals), but in the second, no external factors are needed, and the process is automatic (e.g. filaments bend as the flower ages so that the anthers come into contact with the stigma). Cleistogamy is a type of automatic self-pollination, with the pollen transfer occurring within a closed flower (bud). Geitonogamy ('neighbour-marriage'), on the other hand, involves two flowers from the same plant or genet (in the case of clonal plants), and external vectors are required to transport the pollen from one flower to the other (Faegri and van der Pijl 1979; Richards 1986; Proctor *et al.* 1996). See **Table 1** for examples of roses reproducing through these methods.

In xenogamy ('stranger-marriage'), or cross-pollination, the pollen needed for reproduction must come from a different plant and genet through external vectors (Richards 1986; Proctor *et al.* 1996). Examples of xenogamous roses are given in **Table 1**. This is a prevalent and successful breeding system as it allows for greater genetic recombination and genetic variation than occurs through self-pollinations. That, in turn, translates into greater adaptability to changing habitats and conditions by avoiding inbreeding depression.

Pollination in *Rosa* spp. has not been well studied experimentally (Kevan *et al.* 1990; Kevan 2003; MacPhail 2007). The main mode of reproduction in this genus has been thought to be xenogamy, perhaps through the operation of

Table 1 Breeding systems of 94 *Rosa* spp., as compiled from a literature review.^a

Species	Source(s)	Ploidy ^b	Ag	Autogamy			Ge	Fac Au + Ge	Xe
				Unk Au	Aut Au	Fac Au			
Subgenus Platyrhodon									
<i>R. roxburghii</i>	Erlanson-Macfarlane 1963	2x		N					
<i>R. roxburghii normalis</i> Rehd. et Wils	Ueda and Akimoto 2001	2x					N		
<i>R. roxburghii</i> Tratt. var. <i>hirtula</i> Rehd. et Wils	Ueda and Akimoto 2001	2x					N		
Subgenus Rosa, Section Banksianae									
<i>R. banksiae</i> Ait. var. <i>normalis</i> Regel	Ueda and Akimoto 2001	2x, 4x					N		
<i>R. banksiae</i> f. <i>lutescens</i> Voss	Ueda and Akimoto 2001	2x					N		
<i>R. cymosa</i> Tratt.	Ueda and Akimoto 2001	2x					Y		
Subgenus Rosa, Section Bracteatae									
<i>R. bracteata</i> Wendl.	Cole and Melton 1986; Ueda and Akimoto 2001	2x			N		N		
Subgenus Rosa, Section Caninae									
<i>R. canina</i> L.	Erlanson-Macfarlane 1963; Jičinská 1975 1976; Yeboah Gyan and Woodell 1987; Wissemann and Hellwig 1997; Spethmann and Feuerhahn 2003; MacPhail 2007	5x	Y/N	Y/N	Y		Y		Y ^c
<i>R. caryophyllaceae</i> Besser non Christ	Jičinská 1976	5x			Y				
<i>R. coriifolia</i> Fr. var. <i>froebelii</i> (Lambert) Rehd.	Ueda and Akimoto 2001	5x, 6x					Y		
<i>R. corymbifera</i> Borkh.	Erlanson-Macfarlane 1963; Jičinská 1976; Wissemann and Hellwig 1997	5x	Y	Y/N	Y		Y		Y
<i>R. elliptica</i> Tausch	Jičinská 1976; Wissemann and Hellwig 1997	5x, 6x	Y	Y	Y		Y		Y
<i>R. glauca</i>	Spethmann and Feuerhahn 2003	4x		Y					Y
<i>R. horrida</i> Fisch.	Cole and Melton 1986	5x			N				
<i>R. jundzillii</i> Bess.	Erlanson-Macfarlane 1963; Jičinská 1975 1976; Spethmann and Feuerhahn 2003	6x		Y	Y		Y		Y
<i>R. micrantha</i>	Wissemann and Hellwig 1997	4x, 5x, 6x	Y	Y			Y		Y
<i>R. pycnantha</i> Borb.	Jičinská 1976	5x			Y				
<i>R. rubiginosa</i> L. (syn. <i>R. eglanteria</i> L.)	Erlanson-Macfarlane 1963; Jičinská 1976; Cole and Melton 1986; Wissemann and Hellwig 1997; Ueda and Akimoto 2001; Spethmann and Feuerhahn 2003	5x	Y	Y	Y		Y	Y	Y
<i>R. subcanina</i> (Chr.) Dalla Torre et Sarnth.	Jičinská 1976	5x			Y				
<i>R. tomentosa</i> Sm.	Erlanson-Macfarlane 1963; Jičinská 1976	5x		N	Y				
<i>R. vagina</i> Crep. ex Sagorski	Jičinská 1976	5x			Y				
<i>R. villosa</i> (syn. <i>R. pomifera</i> Herrm.)	Jičinská 1976; Ueda and Akimoto 2001	4x, 8x			Y		Y		
<i>R. vosagiaca</i> Desp.	Jičinská 1976	5x, 6x			Y				
<i>R. zalana</i> Wiesb.	Jičinská 1976	5x			Y				
Subgenus Rosa, Section Gallicanae									
<i>R. centifolia</i>	Erlanson-Macfarlane 1963	4x		N					
<i>R. gallica</i> L.	Jičinská 1975 1976; Ueda and Akimoto 2001	4x			Y		Y	Y	Y
<i>R. gallica</i> var. <i>officinalis</i> Ser.	Ueda and Akimoto 2001	4x					Y		
<i>R. hugonis</i> Hemsl.	Erlanson-Macfarlane 1963; Cole and Melton 1986	2x		N	N				
Subgenus Rosa, Section Indicae									
<i>R. chinensis</i> Jacq. var. <i>spontanea</i> (Rehd. et Wils) Yu et Ku	Ueda and Akimoto 2001	2x, 3x, 4x					N		
<i>R. gigantea</i> Coll et Crep.	Ueda and Akimoto 2001	2x					N		
Subgenus Rosa, Section Laevigatae									
<i>R. laevigata</i> Michx.	Cole and Melton 1986; Ueda and Akimoto 2001	2x			N		N		
Subgenus Rosa, Section Pimpinellifoliae									
<i>R. ecae</i> Ait.	Cole and Melton 1986	2x, 4x			N				
<i>R. foetida</i> Herm. var. <i>bicolor</i> (Jacq.) Wilm	Cole and Melton 1986	4x			N				
<i>R. omeiensis</i> var. <i>pteracantha</i> (Franch.) Rehd et Wilds	Fagerlind 1948; Erlanson-Macfarlane 1963	2x		Y/N					
<i>R. omeiensis</i> Rolfe	Fagerlind 1948	2x		Y					
<i>R. primula</i> Boulenger	Cole and Melton 1986	2x			N				
<i>R. spinosissima</i> L. (syn. <i>R. pimpinellifolia</i>)	Erlanson-Macfarlane 1963; Jičinská 1975, 1976; Ueda and Akimoto 2001; Spethmann and Feuerhahn 2003	4x		N	Y		Y	Y	Y

Table 1 (Cont.)

Species	Source(s)	Ploidy ^b	Ag	Autogamy			Ge	Fac Au + Ge	Xe
				Unk Au	Aut Au	Fac Au			
Subgenus Rosa, Section Pimpinellifoliae									
<i>R. spinosissima</i> L. var. <i>altaica</i> (Willd.) Rehd.	Cole and Melton 1986	4x			N				
<i>R. xanthina</i> Lindl.	Cole and Melton 1986	2x			N				
Subgenus Rosa, Sections Pimpinellifoliae and Rosa									
<i>R. x reversa</i> Walds. et Kit. (<i>R.</i> <i>pimpinellifolia</i> x <i>R. pendulina</i>)	Jičínská 1975	4x			Y		Y		Y
Subgenus Rosa, Section Rosa									
<i>R. acicularis</i> Lindl.	Erlanson-Macfarlane 1963; Ueda and Akimoto 2001; Spethmann and Feuerhahn 2003	4x, 8x		N				Y	Y
<i>R. acicularis</i> var. <i>engelmannii</i> Crép. ex Rehd	Ueda and Akimoto 2001	6x						Y	
<i>R. amblyotis</i>	Erlanson-Macfarlane 1963	2x		N					
<i>R. arkansana</i> Porter	Erlanson-Macfarlane 1963; Ueda and Akimoto 2001	4x		Y				Y	
<i>R. blanda</i> Ait.	Erlanson-Macfarlane 1963; Ueda and Akimoto 2001; MacPhail 2007	2x	N	N	Y	Y	Y	Y	Y
<i>R. carolina</i> L.	Erlanson-Macfarlane 1963; Ueda and Akimoto 2001	4x		Y				N	
<i>R. cinnamomea</i> L. (syn <i>R. majalis</i>)	Erlanson-Macfarlane 1963; Jičínská 1976; Ueda and Akimoto 2001; MacPhail 2007	wild: 2x hort: 4x, 8x	N	Y	Y/N	N	N	Y	N
<i>R. cinnamomea</i> var. <i>plena</i> West	Ueda and Akimoto 2001	4x						Y	
<i>R. davurica</i> Pall.	Ueda and Akimoto 2001	2x						N	
<i>R. engelmannii</i>	Erlanson-Macfarlane 1963			N					
<i>R. fedtschenkoana</i> Regel.	Cole and Melton 1986	4x			N				
<i>R. foliolosa</i> Nutt.	Erlanson-Macfarlane 1963; Cole and Melton 1986	2x		Y	N				
<i>R. foliolosa</i> Nutt. ex Torr. et Sarnth.	Ueda and Akimoto 2001	2x						N	
<i>R. forrestiana</i> Bouleng.	Cole and Melton 1986; Ueda and Akimoto 2001	4x				N		N	
<i>R. laxa</i> Froeb.	Cole and Melton 1986	2x			Y				
<i>R. marretii</i> Lev.	Ueda and Akimoto 2001	2x						Y	
<i>R. melina</i> Greene	Ueda and Akimoto 2001	2x						N	
<i>R. moyesii</i> Hemsl. et Wils. 'Geranium'	Ueda and Akimoto 2001	4x						Y	
<i>R. multibracteata</i> Hemsl. et Wils.	Ueda and Akimoto 2001	4x						N	
<i>R. nitida</i> Willd.	Erlanson-Macfarlane 1963; Cole and Melton 1986; Spethmann and Feuerhahn 2003	2x		Y	N				N
<i>R. nutkana</i>	Erlanson-Macfarlane 1963	6x			Y/N				
<i>R. palustris</i> Marsh.	Erlanson-Macfarlane 1963; Ueda and Akimoto 2001	2x			Y			N	
<i>R. pendulina</i> L. (syn. <i>R. alpine</i>)	Fagerlind 1948; Erlanson- Macfarlane 1963; Jičínská 1975, 1976; Ueda and Akimoto 2001	4x			Y/N	Y	Y	Y	Y
<i>R. pendulina</i> var. <i>oxyodon</i> (Boiss.) Rehd.	Ueda and Akimoto 2001	4x						Y	
<i>R. pisocarpa</i> (syn. <i>R. ultramontana</i>)	Erlanson-Macfarlane 1963	2x, 4x			N				
<i>R. rudiuscula</i>	Erlanson-Macfarlane 1963	4x			Y				
<i>R. rugosa</i> Thunb.	Fagerlind 1948; Erlanson- Macfarlane 1963; Jičínská 1976; Cole and Melton 1986; Ueda and Ando 1996; Dobson <i>et al.</i> 1999; Ueda and Akimoto 2001; Spethmann and Feuerhahn 2003	2x	Y	Y/N	N				Y/ N
<i>R. rugosa</i> Thunb. ex Murray f. <i>alba</i> (Ware)	Ueda and Akimoto 2001	2x						Y	
<i>R. setipoda</i> Hemsl. et Wills (syn. <i>R.</i> <i>macrophylla</i>)	Erlanson-Macfarlane 1963; Cole and Melton 1986; Ueda and Akimoto 2001	4x		N	N			N	
<i>R. spaldingii</i> Crep.	Ueda and Akimoto 2001	6x						N	
<i>R. suffulta</i>	Erlanson-Macfarlane 1963				Y				
<i>R. sweginzowii</i> Koehne	Jičínská 1976	6x				Y			
<i>R. virginiana</i> Mill.	Erlanson-Macfarlane 1963; Cole and Melton 1986; Ueda and Akimoto 2001; MacPhail 2007	4x	Y	Y	Y	Y	Y	Y	Y
<i>R. willmottiae</i> Hemsl.	Ueda and Akimoto 2001	2x						N	
Subgenus Rosa, Section Synstylae									
'Polyantha grandiflora' (syn <i>R.</i> <i>gentiliana</i> Lev. et Van.)	Ueda and Akimoto 2001	2x						N	

Table 1 (Cont.)

Species	Source(s)	Ploidy ^b	Ag	Autogamy			Ge	Fac Au + Ge	Xe
				Unk Au	Aut Au	Fac Au			
Subgenus Rosa, Section Synstylae									
<i>R. arvensis</i> Huds.	Fagerlind 1948; Jičinská 1975, 1976; Ueda and Akimoto 2001	2x		Y	N		Y	N	Y
<i>R. filipes</i> Rehd. et Wils.	Jičinská 1976; Ueda and Akimoto 2001	2x			N			N	
<i>R. helenae</i> Rehd. et Wils	Ueda and Akimoto 2001	2x						N	
<i>R. luciae</i> Franch. et Roehbr var. <i>fujisanensis</i> Makino	Ueda and Akimoto 2001	2x						Y	
<i>R. moschata</i> Herrm.	Ueda and Akimoto 2001	2x							N
<i>R. moschata</i> Christ var. <i>nastarana</i> Rehd.	Cole and Melton 1986	2x			N				
<i>R. mulliganii</i> Bouleng	Ueda and Akimoto 2001	2x							N
<i>R. multiflora</i> Thunb. ex. Murr.	Fagerlind 1948; Erlanson-Macfarlane 1963; Jičinská 1976; Stougaard 1983; Spethmann and Feuerhahn 2003; MacPhail 2007	2x, 3x	Y/N ^d	Y	N	N	Y		Y/N
<i>R. multiflora</i> var. <i>adenchaeta</i> (Koidz) Makino	Ueda and Akimoto 2001	2x							N
<i>R. sambucina</i> Koidz.	Ueda and Akimoto 2001	2x							N
<i>R. setigera</i> Michx.	Erlanson-Macfarlane 1963; Cole and Melton 1986; Kevan <i>et al.</i> 1990; Kemp 1994	2x		Y	N				Y
<i>R. soulieana</i> Crep.	Cole and Melton 1986; Ueda and Akimoto 2001	2x			N				N
<i>R. wichurana</i> Crep.	Cole and Melton 1986; Ueda and Akimoto 2001	2x			N				N
<i>R. wichurana</i> Crep. 'hybrid'	Cole and Melton 1986	2x			N				
Subgenus Unknown, Section Unknown									
<i>R. housei</i>	Erlanson-Macfarlane 1963			Y					
<i>R. michiganensis</i>	Erlanson-Macfarlane 1963			Y					
<i>R. naupaulensis</i> Andr.	Cole and Melton 1986	2x			N				
<i>R. ratonensis</i>	Erlanson-Macfarlane 1963			N					
<i>R. x englemannii</i> S. Wats cultivae 'E6'	Cole and Melton 1986	6x			Y				

Legend: An empty entry represents no reported information (i.e. was not tested). "Y" and "N" indicate, respectively, that the species has, or has not, been shown to successfully produce hips and/or seeds through that method of reproduction. "Y/N" indicates that conflicting results have been found in the literature. Ag: agamospermy; Unk Au: unknown type of autogamy; Aut Au: automatic autogamy; Fac Au: facilitated autogamy; Ge: geitonogamy; Fac Au + Ge: facilitated autogamy & geitonogamy (not differentiated by the original authors); Xe: xenogamy.

^a Changes to the original source data were made as follows:

- Data presented by Erlanson-MacFarlane (1963) was summarized as follows: those species recorded as "selfing-strongly" or "selfing-weakly" were recorded as "Y" for unknown autogamy, while those recorded as "non-selfing" were recorded as "N".

^b Ploidy levels ($x=7$) are from Wissemann (2003), with the following exceptions: *R. omeiensis* f. *pteracantha* (Fagerlind 1948); *R. x reversa* (Jičinská 1975); *R. caryophyllaceae*, *R. pycnantha*, *R. vagina*, *R. zalana* (Jičinská 1976); *R. moschata* var. *nastarana*, *R. naupaulensis*, *R. spinosissima* var. *altaica*, *R. wichurana* 'hybrid', *R. x englemannii* cultivae 'E6' (Cole and Melton 1986); *R. cymosa*, *R. gentiliana*, *R. gigantea*, *R. melina*, *R. mulliganii*, *R. multiflora* var. *adenochaeta*, *R. rugosa* f. *alba*, *R. sambucina*, *R. spaldingii* (Ueda and Akimoto 2001); *R. rudiuscula* (Darling and Wylie 1955).

^c Xenogamy data for *R. canina* from Yeboah-Gyan and Woodell (1987) is actually the combined result of xenogamy and open-pollination combined (i.e. flowers were hand pollinated and exposed to insect visitors).

^d MacPhail (2007) did have one hip produced (out of 30 flowers tested) through agamospermy in 2004, but did not have hips any produced in 2005 (out of 66 flowers tested), and so did not consider it an accurate reflection of *R. multiflora*'s breeding systems. This discrepancy between years is represented by the "Y/N" in the agamospermy column.

incompatibility systems (Ueda and Akimoto 2001), but there are discrepancies in reports concerning self-incompatibility of various rose species (see **Table 1** and e.g. Erlanson-Macfarlane 1963; Jičinská 1975, 1976; Stougaard 1983; Cole and Melton 1986; Ueda *et al.* 1996). There is also high variability in fruit and seed production, both within and between species, when different breeding systems have been tested experimentally (see **Tables 2-3** and e.g. Ueda and Akimoto 2001; MacPhail 2007).

The results of a diversity of breeding systems tested are presented in **Tables 1-3** and emphasize the need for more extensive studies. **Table 1** summarizes, from many sources of widely disparate quality, the known information about the breeding systems of 94 rose species (including a few cultivars). **Table 1** also includes the ploidy levels for each species. The percent hip-sets (# hips set/# flowers tested * 100) are shown in **Table 2**, while the mean number or percent seed-set per hip is listed in **Table 3**, for species for which information is available. A summary of the data can be found in **Table 4**.

We have made extensive efforts to standardize the reporting of data from across sources and, by the use of footnotes in the table, offer some clarifications when needed.

For detailed information about the particular methods used by a researcher, please refer to the original source paper(s). Almost all the information in **Table 1** is based on papers that report results of experimental manipulative studies, but a few are vague with conclusions unsupported by experimental studies (i.e. the author(s) reported their impressions and/or findings from previous work). All data in **Tables 2** and **3** are supported by quantified results.

Because not all authors investigated each of the five major recognizable types of breeding systems, there are many gaps in the data. Also, because some authors did not describe their methods adequately for us to determine the type of selfing actually tested, we report two additional categories of breeding systems, 1) unknown autogamy and 2) facultative autogamy + geitonogamy. However, when categories are clear and consistency in experimental design is apparent and follows standard techniques, such as described in Dafni *et al.* (2005), we are more definitive in the presentation of data. Treatments to test for agamospermy generally include the use of bags and the removal of stamens (emasculation), and in some cases, even stigmas, to assure no pollen reaches the stigma. To test for autogamy, flowers are bagged to prevent external pollen sources from

Table 2 Percent hip-set (# hips set/# flowers tested *100, ± standard error (SE) when available) for various breeding systems of 80 *Rosa* spp., as compiled from a literature review^a.

Species	Source(s)	Ag	Autogamy			Ge	Fac Au + Ge	Xe ^b
			Unk Au	Aut Au	Fac Au			
Subgenus Platyrhodon								
<i>R. roxburghii normalis</i> Rehd. et Wils	Ueda and Akimoto 2001						0	
<i>R. roxburghii</i> Tratt. var. <i>hirtula</i> Rehd. et Wils	Ueda and Akimoto 2001						0	
Subgenus Rosa, Section Banksianae								
<i>R. banksiae</i> Ait. var. <i>normalis</i> Regel	Ueda and Akimoto 2001						0	
<i>R. banksiae</i> f. <i>lutescens</i> Voss	Ueda and Akimoto 2001						0	
<i>R. cymosa</i> Tratt.	Ueda and Akimoto 2001						6.2	
Subgenus Rosa, Section Bracteatae								
<i>R. bracteata</i> Wendl.	Cole and Melton 1986; Ueda and Akimoto 2001			0			0	
Subgenus Rosa, Section Caninae								
<i>R. canina</i> L.	Jičínská 1975 1976; Yeboah Gyan and Woodell 1987; MacPhail 2007	0		40, 48.0 ± 16.2, 82.2, 83.2		28.0 ± 10.2, 50	82.3	37.8, 72, 88
<i>R. caryophyllaceae</i> Besser non Christ	Jičínská 1976			90.2				
<i>R. coriifolia</i> Fr. var. <i>froebelii</i> (Lambert) Rehd.	Ueda and Akimoto 2001						100	
<i>R. corymbifera</i> (syn. <i>R. dumetorum</i>)	Jičínská 1976			96				
<i>R. elliptica</i> Tausch	Jičínská 1976			86.1				
<i>R. horrida</i> Fisch.	Cole and Melton 1986			0				
<i>R. jundzillii</i> Bess.	Jičínská 1975 1976			87.2, 95.9		89.4	87.2	84.5
<i>R. pycnantha</i> Borb.	Jičínská 1976			88.9				
<i>R. rubiginosa</i> L. (syn. <i>R. eglanteria</i> L.)	Jičínská 1976; Cole and Melton 1986; Ueda and Akimoto 2001			(yes), 84.9			95.2	
<i>R. subcanina</i> (Chr.) Dalla Torre et Sarnth.	Jičínská 1976			90				
<i>R. tomentosa</i> Sm.	Jičínská 1976			41.3				
<i>R. vagina</i> Crep. ex Sagorski	Jičínská 1976			78.3				
<i>R. villosa</i> (syn. <i>R. pomifera</i> Herrm.)	Jičínská 1976; Ueda and Akimoto 2001			45.1			14.7	
<i>R. vosagiaca</i> Desp.	Jičínská 1976			95.3				
<i>R. zalana</i> Wiesb.	Jičínská 1976			75.5				
Subgenus Rosa, Section Gallicanae								
<i>R. gallica</i> L.	Jičínská 1975 1976; Ueda and Akimoto 2001			11.3		52.7	11.3, 55	85
<i>R. gallica</i> var. <i>officinalis</i> Ser.	Ueda and Akimoto 2001						8.7	
<i>R. hugonis</i> Hemsl.	Cole and Melton 1986			0				
Subgenus Rosa, Section Indicae								
<i>R. chinensis</i> Jacq. var. <i>spontanea</i> (Rehd. et Wils) Yu et Ku	Ueda and Akimoto 2001						0	
<i>R. gigantea</i> Coll et Crep.	Ueda and Akimoto 2001						0	
Subgenus Rosa, Section Laevigatae								
<i>R. laevigata</i> Michx.	Cole and Melton 1986; Ueda and Akimoto 2001			0			0	
Subgenus Rosa, Section Pimpinellifoliae								
<i>R. ecae</i> Ait.	Cole and Melton 1986			0				
<i>R. foetida</i> Herm. var. <i>bicolor</i> (Jacq.) Wilm	Cole and Melton 1986			0				
<i>R. primula</i> Boulenger	Cole and Melton 1986			0				
<i>R. spinosissima</i> L. (syn. <i>R. pimpinellifolia</i>)	Jičínská 1975 1976; Ueda and Akimoto 2001			14.8, 24.5		63	14.8, 75.8	67.3
<i>R. spinosissima</i> L. var. <i>altaica</i> (Willd.) Rehd.	Cole and Melton 1986			0				
<i>R. xanthina</i> Lindl.	Cole and Melton 1986			0				
Subgenus Rosa, Section Pimpinellifoliae and Rosa								
<i>R. x reversa</i> Walds. et Kit. (<i>R. pimpinellifolia</i> x <i>R. pendulina</i>)	Jičínská 1975			55.9		47	56.6	40
Subgenus Rosa, Section Rosa								
<i>R. acicularis</i> Lindl.	Ueda and Akimoto 2001						40	
<i>R. acicularis</i> var. <i>engelmannii</i> Crep. ex Rehd	Ueda and Akimoto 2001						57.7	
<i>R. arkansana</i> Porter	Ueda and Akimoto 2001						50	
<i>R. blanda</i> Ait.	Ueda and Akimoto 2001; MacPhail 2007	0, 0		3.0 ± 3.0, 5.0 ± 5.0	3.3	3.0 ± 3.0, 15.0 ± 15.0	5	31.0 ± 20.2, 70.0 ± 19.1
<i>R. carolina</i> L.	Ueda and Akimoto 2001						0	
<i>R. cinnamomea</i> L. (syn. <i>R. majalis</i>)	Jičínská 1976; Ueda and Akimoto 2001; MacPhail 2007	0, 0		0, 0, 8.5	0, 0	0, 0	25	0, 0
<i>R. cinnamomea</i> var. <i>plena</i> West	Ueda and Akimoto 2001						44	

Table 2 (Cont.)

Species	Source(s)	Ag	Autogamy			Ge	Fac Au + Ge	Xe ^b
			Unk Au	Aut Au	Fac Au			
Subgenus Rosa, Section Rosa								
<i>R. davurica</i> Pall.	Ueda and Akimoto 2001						0	
<i>R. fedtschenkoana</i> Regel.	Cole and Melton 1986			0				
<i>R. foliolosa</i> Nutt.	Cole and Melton 1986			0				
<i>R. foliolosa</i> Nutt. ex Torr. et Sarnth.	Ueda and Akimoto 2001						0	
<i>R. forrestiana</i> Bouleng.	Cole and Melton 1986; Ueda and Akimoto 2001			0			0	
<i>R. laxa</i> Froeb.	Cole and Melton 1986			(yes)				
<i>R. marretii</i> Lev.	Ueda and Akimoto 2001						0	
<i>R. melina</i> Greene	Ueda and Akimoto 2001						52	
<i>R. moyesii</i> Hemsl. et Wils. 'Geranium'	Ueda and Akimoto 2001						33.3	
<i>R. multibracteata</i> Hemsl. et Wils.	Ueda and Akimoto 2001						0	
<i>R. nitida</i> Willd.	Cole and Melton 1986			0				
<i>R. palustris</i> Marsh.	Ueda and Akimoto 2001						0	
<i>R. pendulina</i> L. (syn. <i>R. alpina</i>)	Jičínská 1975 1976; Ueda and Akimoto 2001			0, 2		1.4	2, 34.8	8.1
<i>R. pendulina</i> var. <i>oxyodon</i> (Boiss.) Rehd.	Ueda and Akimoto 2001						70	
<i>R. rugosa</i> Thunb.	Jičínská 1976; Cole and Melton 1986; Ueda <i>et al.</i> 1996; Dobson <i>et al.</i> 1999; Ueda and Akimoto 2001	(yes)	0	0, 0, (yes)				62.4, (yes)
<i>R. rugosa</i> Thunb. ex Murray f. <i>alba</i> (Ware)	Ueda and Akimoto 2001						13.3	
<i>R. setipoda</i> Hemsl. et Wills (syn. <i>R. macrophylla</i>)	Cole and Melton 1986; Ueda and Akimoto 2001			0			0	
<i>R. spaldingii</i> Crep.	Ueda and Akimoto 2001						0	
<i>R. sweginzowii</i> Koehne	Jičínská 1976			5.4				
<i>R. virginiana</i> Mill.	Cole and Melton 1986; Ueda and Akimoto 2001; MacPhail 2007	3.1 ± 3.1, 15.1 ± 5.1		(yes), 18.8 ± 12.0, 28.8 ± 9.5	50.0 ± 10.2	34.4 ± 15.6, 71.2 ± 7.2	90	65.6 ± 7.9, 83.0 ± 5.9
<i>R. willmottiae</i> Hemsl.	Ueda and Akimoto 2001						0	
Subgenus Rosa, Section Synstylae								
'Polyantha grandiflora' (syn. <i>R. gentiliana</i> Lev. et Van.)	Ueda and Akimoto 2001						0	
<i>R. arvensis</i> Huds.	Jičínská 1975 1976; Ueda and Akimoto 2001			0, 0		2.4	0	3.6
<i>R. filipes</i> Rehd. et Wils.	Jičínská 1976; Ueda and Akimoto 2001			0			0	
<i>R. helenae</i> Rehd. et Wils	Ueda and Akimoto 2001						0	
<i>R. luciae</i> Franch. et Rochebr var. <i>fujisanensis</i> Makino	Ueda and Akimoto 2001						17.9	
<i>R. moschata</i> Herm.	Ueda and Akimoto 2001						0	
<i>R. moschata</i> Christ var. <i>nastarana</i> Rehd.	Cole and Melton 1986			0				
<i>R. mulliganii</i> Bouleng	Ueda and Akimoto 2001						0	
<i>R. multiflora</i> Thunb. ex. Murr.	Jičínská 1976; Stougaard 1983; MacPhail 2007	0, 3.3 ± 3.3		0, 0, 0.2	0, 0, 12.1	1.5 ± 1.5, 6.7 ± 4.2		29.1 ± 8.4, 43.3 ± 17.4, 83.7
<i>R. multiflora</i> var. <i>adenchaeta</i> (Koidz) Makino	Ueda and Akimoto 2001						0	
<i>R. sambucina</i> Koidz.	Ueda and Akimoto 2001						0	
<i>R. setigera</i> Michx.	Cole and Melton 1986; Kevan <i>et al.</i> 1990			0, 0				74
<i>R. soulieana</i> Crep.	Cole and Melton 1986; Ueda and Akimoto 2001			0			0	
<i>R. wichurana</i> Crep.	Cole and Melton 1986; Ueda and Akimoto 2001			0			0	
<i>R. wichurana</i> Crp. 'hybrid'	Cole and Melton 1986			0				
Subgenus Unknown, Section Unknown								
<i>R. naupaulensis</i> Andr.	Cole and Melton 1986			0				
<i>R. x englemannii</i> S. Wats cultivae 'E6'	Cole and Melton 1986			(yes)				

Legend: An empty entry represents no reported information (i.e. was not tested); multiple entries indicate data from multiple sources and/or years, listed in ascending order. Numbers are rounded to one decimal place when applicable. Ag: agamospermy; Unk Au: unknown type of autogamy; Aut Au: automatic autogamy; Fac Au: facilitated autogamy; Ge: geitonogamy; Fac Au + Ge: facilitated autogamy & geitonogamy (not differentiated by the original authors); Xe: xenogamy.

^a Changes to the original source data were made as follows:

- Stougaard (1983) reported results from eight clones of *R. multiflora*; this data was averaged before presenting in this table.

- It is assumed that 0 hips were produced when 0% seed set was reported by Cole and Melton (1986). When Cole and Melton (1986) reported >0% seed set, hip set was recorded in the table as (yes).

- Dobson *et al.* (1999) did not present information on hip set for *R. rugosa*, but did have hips set through agamospermy, automatic autogamy, and xenogamy as she reports seed-set (see Table 3). This is reflected in the table as (yes).

^b Xenogamy data for *R. canina* from Yeboah-Gyan and Woodell (1987) is actually the combined result of xenogamy and open-pollination combined (i.e. flowers were hand pollinated and exposed to insect visitors). For *R. setigera* (Kevan *et al.* 1990), it is for natural (open) cross-pollination by hand.

Table 3 Mean number of seeds per hip^a (\pm standard error (SE) when available) or percent seed set (# seeds set/# pistils *100, represented by “%”) for various breeding systems of 26 *Rosa* spp., as compiled from a literature review^b.

Species	Source(s)	Ag	Autogamy			Ge	Fac Au + Ge	Xe ^c
			UnkAu	Aut Au	Fac Au			
Subgenus Rosa, Section Banksianae								
<i>R. cymosa</i> Tratt.	Ueda and Akimoto 2001						15%	
Subgenus Rosa, Section Caninae								
<i>R. canina</i> L.	MacPhail 2007			38.3 \pm 4.7		36.9 \pm 4.8		40.1 \pm 3.6
<i>R. coriifolia</i> Fr. var. <i>froebelii</i> (Lambert) Rehd.	Ueda and Akimoto 2001						77.6%	
<i>R. rubiginosa</i> L. (syn. <i>R. eglanteria</i> L.)	Cole and Melton 1986; Ueda and Akimoto 2001			16.6%			79.9%	
<i>R. villosa</i> (syn. <i>R. pomifera</i> Herrm.)	Ueda and Akimoto 2001						3%	
Subgenus Rosa, Section Gallicanae								
<i>R. gallica</i> L.	Ueda and Akimoto 2001						6.9%	
<i>R. gallica</i> var. <i>officinalis</i> Ser.	Ueda and Akimoto 2001						21.9%	
Subgenus Rosa, Section Pimpinellifoliae								
<i>R. spinosissima</i> L. (syn. <i>R. pimpinellifolia</i>)	Ueda and Akimoto 2001						58.7%	
Subgenus Rosa, Section Rosa								
<i>R. acicularis</i> Lindl.	Ueda and Akimoto 2001						17.2%	
<i>R. acicularis</i> var. <i>engelmannii</i> Crep. ex Rehd	Ueda and Akimoto 2001						25.1%	
<i>R. arkansana</i> Porter	Ueda and Akimoto 2001						6%	
<i>R. blanda</i> Ait.	Ueda and Akimoto 2001; MacPhail 2007			32 \pm ., 38 \pm ., 28 \pm .		35 \pm ., 47.3 \pm 3.0	20%	31.1 \pm 3.6, 38 \pm 2.0
<i>R. cinnamomea</i> L. (syn. <i>R. majalis</i>)	Ueda and Akimoto 2001						5.9%	
<i>R. cinnamomea</i> var. <i>plena</i> West	Ueda and Akimoto 2001						30.2%	
<i>R. laxa</i> Froeb.	Cole and Melton 1986			45%				
<i>R. melina</i> Greene	Ueda and Akimoto 2001						11.3%	
<i>R. moyesii</i> Hemsl. et Wils. 'Geranium'	Ueda and Akimoto 2001						80.9%	
<i>R. pendulina</i> L.	Ueda and Akimoto 2001						24.4%	
<i>R. pendulina</i> var. <i>oxyodon</i> (Boiss.) Rehd.	Ueda and Akimoto 2001						27.6%	
<i>R. rugosa</i> Thunb.	Dobson <i>et al.</i> 1999	1.5 \pm 6.1% SD		2.2 \pm 6.7% SD				84.3 \pm 16.8% SD
<i>R. rugosa</i> Thunb. ex Murray f. <i>alba</i> (Ware)	Ueda and Akimoto 2001						35.1%	
<i>R. virginiana</i> Mill.	Cole and Melton 1986; Ueda and Akimoto 2001; MacPhail 2007	39.9 \pm 1.6, 71.0 \pm .,		46.4 \pm 1.7, 53.8 \pm 5.3; 16%	45.8 \pm 1.0	45.8 \pm 1.0, 47.4 \pm 2.1	7.9%	45.8 \pm 1.4, 52.2 \pm 1.6
Subgenus Rosa, Section Synstylae								
<i>R. luciae</i> Franch. et Rochebr var. <i>fujisanensis</i> Makino	Ueda and Akimoto 2001						10%	
<i>R. multiflora</i> Thunb. ex. Murr.	Stougaard 1983; MacPhail 2007 7 \pm .,			1.4	1	5.5 \pm 1.5, 7 \pm .,		8, 8 \pm 0.4, 9
<i>R. setigera</i> Michx.	Kevan <i>et al.</i> 1990							25.3 \pm 3.0 SD
Subgenus Unknown, Section Unknown								
<i>R. x englemanni</i> S. Wats cultivae 'E6'	Cole and Melton 1986			0.1%				

Legend: An empty entry represents no reported information (i.e. was not tested or no hips had been produced); multiple entries indicate data from multiple sources and/or years, listed in ascending order. Numbers are rounded to one decimal place when applicable. Ag: agamospermy; Unk Au: unknown type of autogamy; Aut Au: automatic autogamy; Fac Au: facilitated autogamy; Ge: geitonogamy; Fac Au + Ge: facilitated autogamy & geitonogamy (not differentiated by the original authors); Xe: xenogamy; SD: standard deviation; \pm . indicates no SE because only one hip had been produced.

^aNote that for calculations involving number of seeds per hip, Kevan *et al.* (1990) and MacPhail (2007) included the smaller, sometimes shriveled achenes in the totals used above (although they also presented data in their papers about just the larger-sized achenes), while Cole and Melton (1986) did not. Dobson *et al.* (1999) only included "normal" seeds (based on visual appearance and size), which suggests the smaller achenes were excluded. It is unknown what method Stougaard (1983). As well, some of the mean numbers of seeds may be misleading, as standard errors are not presented here for all sources (e.g. if only one hip was produced and it had a high seed count).

^bChanges to the original source data were made as follows:

- Stougaard (1983) reported results from eight clones of *R. multiflora*; this data was averaged before presenting in this table.

- 0% seed set, as reported by Cole and Melton (1986), was not included in the above table.

^cXenogamy data for *R. canina* from Yeboah-Gyan and Woodell (1987) is actually the combined result of xenogamy and open-pollination combined (i.e. flowers were hand pollinated and exposed to insect visitors). For *R. setigera* (Kevan *et al.* 1990), it is for natural (open) cross-pollination by hand.

contaminating the test flowers that are either left in isolation (automatic autogamy) or briefly un-bagged to allow the researcher to manually transfer pollen from the anthers to stigmas (facilitated autogamy). Flowers used to test for geitonogamy and xenogamy treatments are emasculated, bagged, and then later pollinated with pollen from a flower of the same plant or genet (geitonogamy) or from a different plant or genet (xenogamy). The control flowers are marked and left open to the whims of nature.

FACTORS INFLUENCING REPRODUCTIVE SUCCESS OF BREEDING SYSTEMS

As mentioned above, plants reproduce by seed using many types of breeding systems; however, there are many intrinsic and extrinsic factors that can influence reproductive success. Intrinsic factors include the age of the flower being pollinated, available resources (including competition), ploidy levels, and incompatibility systems. Extrinsic factors

include the type, condition, and amount of pollen applied, the time of pollination, and environmental conditions (temperature, humidity, time of flowering season when the flower is produced) (Faegri and van der Pijl 1979; Stephenson 1981; DeVries and Dubois 1983; Richards 1986; Lee 1988; Lloyd and Schoen 1992; Proctor *et al.* 1996). The main factors that are discussed below include incompatibility, periods of pollen viability and stigma receptivity, ploidy levels, and *Caninae* meiosis.

Incompatibility

The most common way by which plants can avoid self-fertilization is through a physiological barrier, defined as self-incompatibility, or the inability of a fertile hermaphrodite seed plant to produce zygotes after self-pollination (de Nettancourt 1977; Richards 1986; Proctor *et al.* 1996; Barrett 2003). Incompatibility systems affect 1) pollen-stigma interactions, more specifically, pollen germination on the stigma, 2) the growth of the pollen tube towards the ovule, and 3) the fusion of nuclei (de Nettancourt 1977; Faegri and van der Pijl 1979; Richards 1986; Barrett 2003). Gametophytic incompatibility mechanisms, in which the self-incompatibility phenotype of the pollen is determined by its own genotype, are well known in Rosaceae, including the genus *Rosa* (Brewbaker 1959; Stougaard 1983; Cole and Melton 1986; Richards 1986; Barrett 2003).

Periods of pollen viability and stigma receptivity

Anthesis, the period when a chasmogamous flower is open and functional, occurs when anthers and stigmas are exposed to pollinators (versus a cleistogamous flower, in which sexual function takes place in the bud). However, in chasmogamous flowers, the anthers and stigmas may not be functional simultaneously (Faegri and van der Pijl 1979; Richards 1986). In a homogamous flower, anther dehiscence and stigma receptivity co-occur. In dichogamous flowers, the two sexual phases occur at different times (Richards 1986). Flowers which shed their pollen before the stigmas are ready for pollination are protandrous, whereas those in which the stigma matures first are protogynous (Faegri and van der Pijl 1979; Richards 1986).

There is confusion in the literature as to whether roses are homogamous or dichogamous (protandrous or protogynous). Matsson (1912, cited in Wissemann and Hellwig, 1997), Schwertschlagler (1915, cited in Wissemann and Hellwig 1997), and Fagerlind (1954) indicated that *Caninae* roses are self-pollinated before the flower even opens (cleistogamy), although Wissemann and Hellwig (1997) found no open anthers at the beginning of anthesis for these roses to support claims for cleistogamy. Spethmann and Feuerhahn (2003) state that the stigmas of roses are receptive when they show a shiny secretion, which usually occurs when the flower is still closed but the petals are slightly colored. Although they suggest rose pollen is not usually viable or available at this stage, they point out that *R. nitida* Willd. and *R. rugosa* may be cleistogamous. Protandry is indicated by Erlanson-Macfarlane (1963) who believed that 1) pollen matures before the embryo sac and egg cells, 2) that most pollen is available when the petals first open, and 3) although second-day flowers are the ones which are most receptive for pollination, third-day flowers may still self-fertilize. Similarly, Dobson *et al.* (1999) indicated protandry in *R. rugosa*, but there are conflicting reports about self-pollination in this species that have not been corroborated by experimentation (See **Tables 1-3**).

Variation is also reported in other studies. Kemp (1994) found that, although *R. setigera* is receptive to pollen over the three days in which the petals remain on the flowers of the female plants, most pollination occurs during the first morning that the flowers are open. Dobson *et al.* (1999) indicated that second-day *R. rugosa* flowers contained some pollen and were receptive, implying that both pollen and stigmas are at their prime on first-day flowers. Ueda and

Akimoto (2001) conducted pollinations the day of flower opening, so it is logical to assume that this is the period when they believed receptivity was highest. MacPhail (2007) made receptivity tests using hydrogen peroxide on variously aged flowers and found that *R. blanda* Ait., *R. canina* L., and *R. multiflora* were most receptive during the second day of bloom, but *R. cinnamomea* L. and *R. virginiana* Mill. were most receptive during the first day. Clearly, there is not one scheme of intra-floral phenology for all rose species, so researchers planning pollination trials should make their own observations on pollen liberations and stigmatic viability and receptivity. Recommended techniques for this are detailed in Dafni *et al.* (2005), and include the testing of stigmatic receptivity using hydrogen peroxide and pollen viability using particular sugar solutions or stains.

Ploidy levels and *Caninae* meiosis

Wild species in the genus *Rosa* comprise a polyploid complex with a base chromosome number of seven. Many species are diploid ($2n=2x=14$) or tetraploid ($2n=4x=28$), and others may be triploid, pentaploid, hexaploid, or octaploid ($2n=3x$, $5x$, $6x$, or $8x$, respectively). Most species occur at only one ploidy level, but a few form a polyploid series (see **Table 1**; Wissemann 2003). The effect that ploidy level has on sexual reproduction in roses is uncertain (Cole and Melton 1986; Ueda and Akimoto 2001), but it is ventured that higher ploidy leads to greater inter-specific diversity in breeding systems (Ratsek *et al.* 1941; Cole and Melton 1986). Triploids, often formed from crosses between diploid and tetraploid roses or diploids where one produces a $2n$ gamete, commonly have reduced fertility (Rowley 1960, cited in Zlesak 2006). Self-pollination appears to be more common at higher ploidy levels (see **Table 4**), possibly reflecting reduced influence of incompatibility genes and the competitive interaction of *S*-alleles in diploid and triploid pollen (Cole and Melton 1986; Debener and Mattiesch 1999; Ueda and Akimoto 2001; Spethmann and Feuerhahn 2003).

In most plant species with the same, even-numbered ploidy level, the seed parent and the pollen parent transmit approximately the same amount of genetic material to their offspring, resulting in offspring that have traits of both parents (Werlemark 2003). However, for pentaploidy (in e.g. many *Caninae* species), another method of genetic division and formation of gametophytes occurs, with the uneven distribution of genetic material (Werlemark 2003; Nybom 2007), known as the *Caninae* meiosis. This was discovered by Täckholm (1920).

Pentaploid *Caninae* roses (i.e. those with 35 chromosomes) contain 14 paired chromosomes (7 bivalents) and 21 unpaired chromosomes (3 sets of 7 univalents) in each somatic cell. However, meiosis results in uneven distribution of chromosomes as gametophytes are formed. The univalents are only included in the egg cells but not in the pollen cells, which contain only half of the separated bivalents. Therefore, the pollen is monoploid, containing 7 chromosomes, while the eggs are tetraploid, containing 28 chromosomes (the 21 univalent chromosomes plus one set of seven chromosomes from the separated bivalents). When fertilization occurs, the chromosomes combine and restore the original pentaploid number ($x=35$) (Wissemann and Hellwig 1997; Kevan 2003; Werlemark 2003; Nybom *et al.* 2004, 2006; Nybom 2007). Interestingly, tetraploid and hexaploid *Caninae* roses ($x=28$ and 42 chromosomes, respectively) follow a similar pattern, with the pollen containing 7 chromosomes and the egg cells containing 21 or 35 chromosomes, depending on the ploidy level (Kevan 2003; Nybom 2007). Because most of the genetic information in these roses is from the seed parent (e.g. 80% for pentaploids), offspring from species in the *Caninae* section appear morphologically identical to their mother. Indeed, Nybom *et al.* (2004) found that the genomes of offspring from crossed *Caninae* were often identical or essentially so to the maternal parent, and that bivalent formation prefer-

Table 4 The effect of ploidy level on various breeding systems of 94 *Rosa* spp., as compiled from a literature review^a.

Successful Breeding System?	# of Diploid (2x) Species	# of Polyploid (3x, 4x, 6x, 8x) Species	# of Uncertain or Unknown Ploidy ^b Species	Total # of Species Tested
For Agamospermy				
Yes	1	5		6
Yes/No		1	1	2
No	1		1	2
Total # of species tested	2	6	2	10
For Autogamy (Unk. Au, Aut. Au, and Fac. Au combined)				
Yes	3	20	3	26
Yes/No	7	6	2	15
No	13	8	4	25
Total # of species tested	23	32	9	66
For Geitonogamy				
Yes	2	11	1	14
Yes/No				0
No			1	1
Total # of species tested	2	11	2	15
For Facilitated Autogamy and Geitonogamy^c				
Yes	5	14	1	20
Yes/No				0
No	21	5	2	28
Total # of species tested	26	19	3	48
For Autogamy (Unk. Au, Aut. Au, and Fac. Au combined), Geitonogamy, Facilitated Autogamy and Geitonogamy				
Yes	6	25	3	34
Yes/No	8	8	2	18
No	27	9	6	42
Total # of species tested	41	42	11	94
For Xenogamy				
Yes	3	13		16
Yes/No	1		1	2
No	1		1	2
Total # of species tested	5	13	2	20

Legend: An empty entry represents no reported information (i.e. was not tested). "Yes" and "No" indicate, respectively, that the species has, or has not, been shown to successfully produce hips through that method of reproduction. "Yes/No" indicates that conflicting results have been found in the literature. Unk Au: unknown type of autogamy; Aut Au: automatic autogamy; Fac Au: facilitated autogamy.

^a See Table 1 for the data and sources used to compile this summary.

^b Uncertain ploidy refers to species that potentially have both diploid and polyploid individuals in the population and it is unknown what the ploidy of tested individuals were. Unknown ploidy refers to species where a ploidy level could not be found in the papers referenced (see note in Table 1).

^c This category includes information on species where the original investigators did not distinguish between facilitated autogamy and geitonogamy; it does not include papers already included under the separate autogamy or geitonogamy categories.

entially takes place between chromosomes that share the same microsatellite alleles (i.e. whose genomes are very similar). These effects have led to a general suspicion of asexual and clonal reproduction.

CONCERNING THE PRESENCE OF AGAMOSPERMY IN ROSA SPP.

Although agamospermy is common in many rosaceous genera (e.g. Gustafson 1946, 1947; Stebbins 1963; Nygren 1967; Nogler 1984; Richards 1986; Nybom 1988; Campbell *et al.* 1991; Nybom *et al.* 2006), the occurrence of agamospermy within *Rosa* spp. has been much debated. Several authors (see Table 1 and Fagerlind 1940, cited in Jičinská 1975; Ratsek *et al.* 1941; Fagerlind 1942, cited in Jičinská 1975; Gustafsson 1942; Gustafsson and Håkansson 1942; Cole and Melton 1986) found no evidence of it in the genus. However, according to other researchers (see Tables 1-3 and Täckholm 1920; 1922 cited in Fagerlind 1954; Gustafsson 1937, cited in Nybom 2007; Gustafsson 1944; Kroon and Zelinga 1974; Wissemann and Hellwig 1997; Werlemark *et al.* 1999; Crespel *et al.* 2001; Werlemark and Nybom 2001; Werlemark 2000, 2003; Nybom *et al.* 2004, 2006; MacPhail 2007; MacPhail and Kevan 2007; Nybom 2007), agamospermy is a valid means of seed production in some *Rosa* sections. Results from all studies must be interpreted with care as they can be affected by the techniques used. For instance, the process of emasculation damages the bloom and the prevention of pollination may interfere with the production of hormones and other factors that could influence endosperm, embryo, and hip formation (Young 1982; Stougaard 1983; Cruden and Lyon 1989; Stone *et al.*

1995). As well, despite the removal of anthers at a period before anticipated anthesis, accidental selfing may have occurred (Werlemark *et al.* 1999; MacPhail 2007; Nybom 2007).

Much of the debate over the presence of agamospermy centers in the section *Caninae*. The distribution of chromosomes during meiosis in the *Caninae* (see discussion above) can result in progeny that resemble their seed parent in all almost all aspects (e.g. Werlemark 2003; Nybom 2007). This has led to the erroneous conclusion by many authors that the plants originated by agamospermy (e.g. Gustafsson and Håkansson 1942; Werlemark 2003). However, recent studies using RAPD and microsatellite analyses on pairs of reciprocal crosses suggest that at least some roses in the *Caninae* may be facultative agamosperms (Werlemark *et al.* 1999, 2000; Werlemark 2000; Werlemark and Nybom 2001; Nybom *et al.* 2004, 2006; Nybom 2007). There is not enough published data to allow comment on why or when facultative agamospermy takes place.

Roses were believed to be pseudogamous (i.e. requiring the influence of pollen to cause the endosperm to develop with the embryo in the ovules) by Gustafsson (1937, cited in Werlemark 2003 and Nybom 2007), as is the case in many other apomictic Rosaceae (e.g. Gustafsson 1946; Asker 1977; Nogler 1984; Campbell *et al.* 1991; Nybom 2007). However, Gustafsson (1942) later stated, along with Wissemann and Drewes-Alvarez (1997, cited in Wissemann 1997), that there was no evidence of this in *Rosa*.

A characteristic of agamospermy often looked for in studies is the appearance of unreduced embryo sacs. Although studies by Fagerlind (1940 cited in Werlemark 2003) and Gustafsson and Håkansson (1942) did not find

any, Crespel and Gudin (2003) found that tetraploid roses (e.g. cultivars of *R. hybrida* L.) can produce unreduced gametes, which in turn develop into 4x progeny. El Mokadem *et al.* (2001) found that a tetraploid *R. canina*, obtained through an induced parthenogenesis treatment, produced tetraploid (2n) eggs. Nybom *et al.* (2006) also found evidence suggesting that unreduced egg cells sometimes form in the *Caninae* roses.

Additionally, although *R. rugosa* repeatedly has been reported as self-incompatible (Fagerlind 1944, cited in Brunn 2005; Jičinská 1976; Ueda *et al.* 1996), two recent studies found evidence of agamospermy. Ueda and Akimoto (2001) report that 13% of flowers of *R. rugosa* Thunb. Ex. Murray f. *alba* (Ware) produced hips through automatic autogamy (self-pollination), with an average of 35% seed-set (seeds/pistil) per hip. As well, Dobson *et al.* (1999) found that flowers of *R. rugosa* bagged before opening produced small hips with few (mean percent = 2.2, SD = 6.7, n = 19) normal achenes (based on appearance and size), and that bagged, emasculated, flowers produced hips of similar size, containing a similar number of normal achenes (mean percent = 1.5, SD = 6.1, n = 18). Spethmann and Feuerhahn (2003) therefore suggest that *R. rugosa* may reproduce by agamospermy, or its stigmas may be receptive while the flower is still in bud and can self-pollinate then (cleistogamy). Viability of seeds produced through their agamospermy trials was not reported by Dobson *et al.* (1999) or Ueda and Akimoto (2001), so it is uncertain if the seeds had the potential to develop into new plants.

Two other species not normally thought of as agamospermic include *R. virginiana* and *R. multiflora*. Although *R. virginiana* was known to be able to both self- and cross-pollinate (Tables 1-3), MacPhail (2007) found that it produced small numbers of hips in tests for agamospermy: 1 out of 32 flowers tested in the first year of her study, and 10 out of 66 in the second year. When viability was examined, using a tetrazolium test in the second year of her study, 2 of the 10 hips produced each contained two viable seeds (MacPhail 2007). She also had 1 hip out of 30 flowers tested possibly produced by agamospermy for *R. multiflora* in the first year of her study, but because there were no hips produced in the next year (out of 66 flowers tested), she suggested that perhaps it was a result of experimental error, such as an anther being missed during emasculation, rather than a valid breeding system.

FEATURES OF ACHENE AND SEED PRODUCTION IN ROSA

Achene and seed production are not always equivalent measures of reproduction (Fagerlind 1954). Achene production can be a sign that fertilization has occurred, but it is not evidence that seeds have developed to maturity and are viable; embryos often degenerate before the achenes have matured, at least in the *Caninae* (Fagerlind 1948, 1954). Achenes, which from their external morphology appear fully normal, may develop but in reality are either empty or contain shrivelled remains (Erlanson 1931; Fagerlind 1948, 1954; MacPhail 2007). MacPhail (2007) compared the viability of seeds, using a tetrazolium test, from *R. blanda*, *R. multiflora*, and *R. virginiana* to the appearance of their achenes, and found that all small achenes were brown and shrivelled, as were the seeds inside. MacPhail's (2007) hypothesis that all larger achenes would contain viable seeds was not valid. Although many of the larger achenes had fully formed seeds, in some cases the seeds were misshapen, brown, and/or shrivelled. Her results, presented here in greater detail than in her 2007 paper, showed that the mean number of viable seeds was significantly smaller than the mean number of large and medium achenes, respectively, in *R. blanda* (28 hips; mean=5.82 SE=0.66 vs. mean=12.43 SE=1.0), *R. multiflora* (63 hips; mean=2.06 SE=0.23 vs. mean=4.67 SE=0.32), and *R. virginiana* (100 hips; mean=11.12 SE=0.08 vs. mean=16.45 SE=1.51). Therefore rose seed viability would have to be tested by the more time-consuming me-

thods of staining (e.g. tetrazolium test), x-ray, and/or germination, rather than by visual size classification alone.

CONCLUSION

Wild roses, like many other flowering plants, can reproduce vegetatively, asexually, and sexually, although the relative success of each means of reproduction may be affected by diverse extrinsic and intrinsic factors, such as the period of anthesis, incompatibility systems, and ploidy level. These factors may work in isolation or together; for example, some roses are essentially self-incompatible, but the incompatibility system may be overcome as the flower ages or if it is exposed to high temperatures (e.g. Richards 1986; Gudin *et al.* 1991; Gudin 2000; Zlesak 2006). This may also help to explain why varying results are found between studies; of the 94 species in this review tested for self-pollination, 34 were clearly self-compatible, while 18 had conflicting reports in the literature (Table 4).

The most common type of sexual breeding system in wild species of *Rosa* is xenogamy or cross-pollination. It is interesting to note that some species of *Rosa* (i.e. *R. nitida*, *R. cinnamomea*, *R. rugosa*, *R. multiflora*) are reported, in at least one paper, to have not produced hips or seeds through xenogamy, even though they did through self-pollination (Table 1). These strange results beg for further research. Although self-pollination (autogamy and geitonogamy) is quite common, notably in polyploid species (Tables 1, 4), it is evident that xenogamy produces more hips in several species (*R. blanda*, *R. spinosissima*, *R. rugosa*, *R. virginiana*, *R. multiflora*, and of course, the dioecious *R. setigera*) (Table 2). But exceptions do occur, such as in *R. canina*, where no differences were reported (Table 2). In some species hips produced through self-pollination have equal numbers of seeds as through xenogamy (e.g. *R. canina*, *R. blanda*, *R. virginiana*), while sometimes autogamy resulted in fewer seeds (e.g. *R. multiflora*) (Table 3).

Geitonogamy has been found to be more effective in hip and seed production than autogamy for *R. virginiana*, *R. blanda*, and *R. spinosissima* (Tables 2-3), even though both are means of self-pollination. This may be a result of greater pollen transfer through geitonogamy than autogamy. Dichogamy may also reduce the effectiveness of autogamy. Facilitated autogamy has been found to be more effective than automatic autogamy in *R. virginiana* and *R. multiflora* (but not in *R. blanda*, where both are equally effective) (Tables 2-3), supporting the idea of the importance of high pollen dosing to the stigma.

Agamospermy may be rare in the genus, but it clearly exists in a few species, including 7 or 8 of the 10 species specifically tested for it (Table 4). Our review has not uncovered any rose species that are exclusively agamospermous, but more studies are needed to see if this generality holds throughout *Rosa*. Thus our review indicates that facultative agamospermy operates in a number of species. For example, in *R. virginiana* and *R. multiflora*, agamospermy was, of all the breeding systems examined, the least effective means of producing hips (Tables 2-3).

There is little information in the literature on the effects of breeding system on other characteristics besides hip- and seed-set, such as hip weights or seed viabilities (but see MacPhail (2007) for discussions on several species). It is strongly encouraged that this gap be addressed. The information would be of particular interest for those species producing seeds asexually, and as a comparison between species.

Ploidy levels in roses do affect the breeding system as is known in plants generally (Stebbins 1963; Richards 1986). As ploidy levels increase there is a greater tendency towards autogamy and agamospermy, even though xenogamy is represented throughout (Table 4). For example, 20 of 32 polyploid species, but only 3 of 23 diploid species, show autogamy, and 5 of 6 polyploids, but only 1 of 2 diploids, show agamospermy (Table 4). This tendency has not been investigated sufficiently with respect to geitonogamy to

comment, as the 11 polyploids and 2 diploid species tested were all successful (only 1 species of uncertain/unknown ploidy did not produce hips) (Table 4). When information from autogamy, geitonogamy, and facilitated autogamy, and geitonogamy trials are combined, ploidy is clearly shown to have a strong effect: 25 of 42 polyploids versus 6 of 41 diploids set hips through self-pollination (Table 4).

It is clear that many species require the transfer of pollen for greatest hip- and seed-set, whether through facilitated autogamy, geitonogamy, or xenogamy. Although not discussed in this paper, attention must be paid to the external pollen vectors, in particular insects, their diversity and behaviours, of which few studies exist for roses (exceptions: Knuth 1908; Stougaard 1983; Yeboah Gyan and Woodell 1987; Kevan *et al.* 1990; Kemp 1994; Kevan 2003; MacPhail 2007; MacPhail and Kevan 2007). MacPhail (2007) summed up much of the known research and claimed that bees and syrphid (flower) flies are likely the best pollinators of *Rosa* spp. These insects make frequent visits to many flowers, becoming dusted with pollen, which transfers from their hairy bodies to stigmas as they go. Although other insects visit rose flowers, most appear to be rather ineffective pollinators. For instance, beetles often stay on one flower for long periods of time. Other insects, such as ants, butterflies, and true bugs often do not carry much pollen, make many visits among flowers, and/or often avoid contact with the receptive stigmas.

The breeding systems in the genus *Rosa* are complex. The generalizations we have been able to make, when sufficient information seemed available, need to be tested by further and more thorough investigations into the species discussed here, as well as into more species and populations. It is particularly important that investigators determine the actual breeding systems of their species by rigorous experimentation. We recommend that the pollination partnerships with insects, and the details of pollen-transfer, be an integral part of such studies.

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