

## Chapter 2

### Subtribe *Spiranthinae*

**Abstract** Breeding systems in *Spiranthes* are diverse. Taxa or populations within taxa can produce seed sexually or asexually or by a combination of sexual and asexual means. Mechanisms include insect pollination, autogamy, and agamospermy. A partial correlation is evident between ploidy level, mode of reproduction, and seed type. The primary pollinators of most sexual or facultatively sexual plants are medium sized to comparatively large, long-tongued bees. Smaller halictine bees are adapted to the pollination of *S. lucida*. Protandry, acropetaly, and pollinator foraging habits favor cross-pollination over geitonogamy in young flowers. Available data on the pollination of *Dichromanthus*, *Deiregyne*, *Schiedeella*, and *Microthelys* are discussed.

**Keywords** *Spiranthes* • *Dichromanthus* • *Deiregyne* • *Schiedeella* • *Microthelys* • Protandry and acropetaly • Sexual and asexual species • Polyembryonic seed • Long- to short-tongued bees and hummingbirds

The subtribe *Spiranthinae* with about 40 genera is mostly confined to the Neotropics (Pridgeon et al. 2003). Five genera, all native, are represented in our flora.

#### *Spiranthes* Richard (Ladies'-Tresses)

*Spiranthes* is a nearly cosmopolitan genus with approximately 45 species worldwide. About 23 are present in North America north of Mexico and Florida. All produce an upright stem bearing a terminal spike of resupinate flowers routinely coiled in a tight to loose spiral of several more or less vertical ranks (Fig. 2.1) (Luer 1975). The flowers are nodding to ascending, tubular or urn shaped (urceolate) to gaping (ringent), and variable in size (Tables 2.1 and 2.2) (Luer 1975; Sheviak and



**Fig. 2.1** *Spiranthes romanzoffiana*. (a) Inflorescence, scale bar = 2 mm; (b) habit, scale bar = 1 cm; (c) flower, exploded view, scale bar = 2 mm

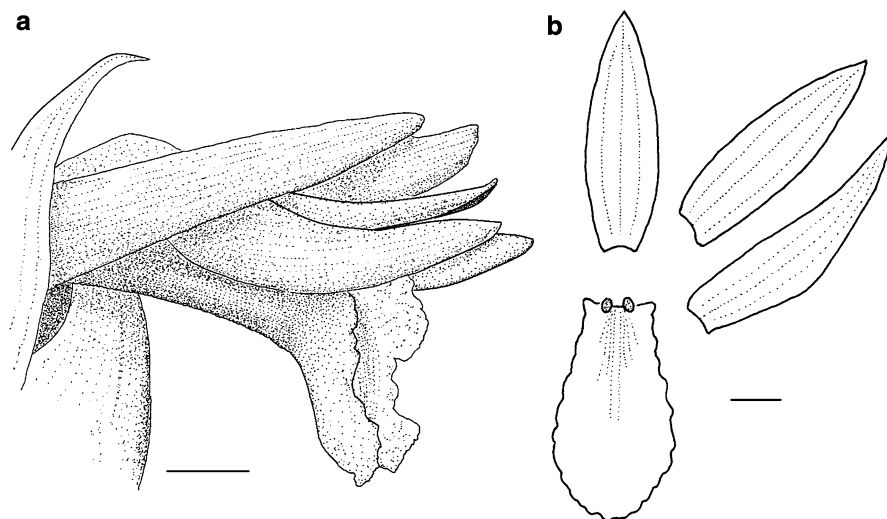
Brown 2002). In our species, they range in color from white or greenish white to cream colored or yellow. The lateral petals are adherent to the dorsal sepal to form a hood over the column (Figs. 2.1 and 2.2). The lateral sepals, with straight to slightly reflexed or upturned tips, may be either spreading or confluent with the lip and lateral petals to produce a floral tube (Catling 1980b). Except for its tip, the lip is often concealed by the other members of the perianth (Fig. 2.1, see below). It is clawed and varies in shape from lanceolate to ovate or sometimes pandurate (violin shaped) and is frequently recurved with a crenulate to lacerate and often crisped apical margin (Figs. 2.1 and 2.2). Paired callosities or nectar glands are present at its base. The dorsal surface of the usually short column bears an erect, bilocular anther containing a pair of deeply cleft, soft, mealy, sectile pollinia (Figs. 2.3 and 2.4).

**Table 2.1** Data on asexual/facultatively sexual species of *Spiranthes* (Sheviak and Brown 2002)

Character	<i>S. casei</i>	<i>S. cernua</i>	<i>S. magnicamporum</i>	<i>S. ochroleuca</i>	<i>S. odorata</i>
Plant height (cm)	4–77	10–50	7–60	10–55	10–100+
Dorsal sepal (mm)	5.2–8	6–12	5–14	6–14	4–18
Lateral sepals (mm)	5.2–8	6–12	5–14	6–14	4–18
Lateral petals (mm)	3.9–7.6	6–12	4.9–13		4–18
Lip (mm)	4.1–8 × 3.2–5.1	6–10.5 × 2–7.5	4.9–12 × 3.3–7	7–12 × 4–7	4–16 × (4–) 7–9.5
Viscidia		Linear to linear-lanceolate	Linear	Linear	Linear to linear-lanceolate

**Table 2.2** Data on uniformly sexual species of *Spiranthes* (Sheviak and Brown 2002)

Character	<i>S. laciniata</i>	<i>S. vernalis</i>	<i>S. lacera</i>	<i>S. romanzoffiana</i>	<i>S. tuberosa</i>	<i>S. lucida</i>	<i>S. diluvialis</i>	<i>S. ovalis</i>
Plant height (cm)	20–95 (–100)	20–65	15–65	8–55	5–30	4–37	20–62	5–40
Dorsal sepal (mm)	6–10×2–3	6–10×2–3	5×1	5.3–12.5	5×1	4.5×5.5	7.5–15	3.5–6.1 to 1–1.5
Lateral sepals (mm)	6–10×2–3	6–10×2–3	5×1	5.3–12.5	5×1	5–6×1–2	7.5–15	3.5–6.1 to 1–1.5
Lateral petals (mm)	7–9×2	6–9×2	5×1	No data	5×1	5–6×2–4	No data	6×1
Lip (mm)	6–9×4	5–8×4	5×2.5	4.8–10×1.6–6.8	5×2.5	5–6×2–4	7–12×2.5–6.8	5×3



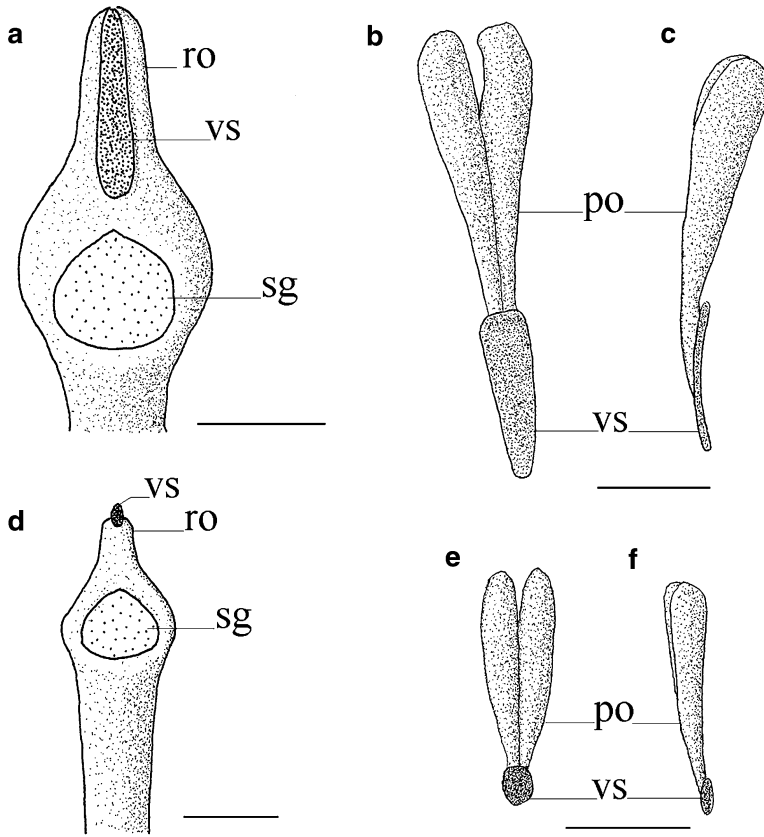
**Fig. 2.2** *Spiranthes magnicamporum*. (a) Flower, oblique lateral view; (b) flower, exploded view, scale bars = 2 mm

These are attached by their apices to a single, usually long viscidium at the distal end of the rostellum, which, when removed, leaves a V-shaped notch (Fig. 2.3) (Luer 1975; Dressler 1993; Johnson and Edwards 2000). A wide, flat, stigmatic surface is positioned on the ventral side of the column behind the rostellum (e.g., Sipes and Tepedino 1995).

Breeding systems are diverse. Taxa or populations within taxa can produce seed sexually or asexually or by a combination of sexual and asexual means. Mechanisms include insect pollination (e.g., Darwin 1862; Godfrey 1922, 1933; Catling 1980b, 1982; Sipes and Tepedino 1995), autogamy (Ridley 1888; Hagerup 1952; Catling 1980a, b, 1982), and agamospermy (e.g., Leavitt 1900, 1901; Schnarf 1929; Swamy 1948; Catling 1979, 1980b, 1982; Schmidt 1987; Schmidt and Antlfinger 1992).

### *Asexual Species or Populations*

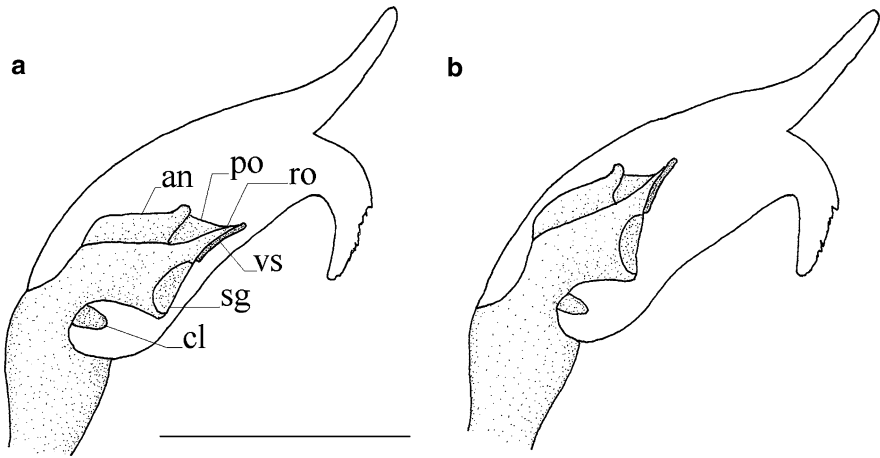
Wholly or partially agamospermous taxa include *S. cernua* (L.) L. C. Richard (nodding ladies'-tresses), *S. ochroleuca* (Rydberg) Rydberg (yellow nodding ladies'-tresses), *S. magnicamporum* Sheviak (Great Plains ladies'-tresses), *S. odorata* (Nuttall) Lindley (fragrant ladies'-tresses), *S. casei* Catling and Cruise var. *casei* (Case's ladies'-tresses), and *S. casei* Catling and Cruise var. *novaescotiae* Catling (Case's ladies'-tresses) (Table 2.1).



**Fig. 2.3** Columns and pollinia. (a)–(c) *Spiranthes ochroleuca*; (d)–(f) *S. lucida*. Columns viewed from below (left); pollinia, ventral view (center), lateral view (right), scale bars = 1 mm. *po* pollinia, *ro* rostellum, *sg* stigma, *vs* viscidium

### *Distribution and Habitat*

*S. cernua* commonly forms colonies in usually acidic, sunny areas of marshes, meadows, and woodland openings. It is found from Nova Scotia to Georgia and west to southern Ontario, Minnesota, and Texas (Luer 1975; Catling 1980b; Sheviak and Brown 2002). *S. ochroleuca* prefers dryer and shadier sites than *S. cernua* and occurs in developing woodland or meadows and barrens. It ranges from Nova Scotia to Tennessee and South Carolina west to Michigan and Indiana (Sheviak and Brown 2002). *S. magnicamporum* may be present in wet prairies and fens but is frequently found on dry, grassy uplands in calcareous soil, where it is largely isolated ecologically from *S. cernua* (Catling and Brown 1983; Catling 1990; Sheviak and Brown 2002). It ranges continuously from western Nebraska to Indiana, north to southern Manitoba, and south to Texas, with scattered populations occurring east and west of this region (Luer 1975; Sheviak and Brown 2002; Johnson 2006).



**Fig. 2.4** *Spiranthes vernalis* showing the position of column in newly opened flowers (**a**) and 2–4-day-old flowers (**b**), scale bar=5 mm. *an* anther, *cl* callus, *po* pollinia, *ro* rostellum, *sg* stigma, *vs* viscidium

*S. odorata* is semiaquatic to aquatic, occurring in cypress and hardwood swamps, marshes, and prairies (Sheviak and Brown 2002). According to Luer (1975), two forms occur. One prefers heavily shaded, wet woods and rich, acid humus, the other, full sun in alkaline marshes and wet prairies. It is distributed along the Atlantic and Gulf Coasts from New Jersey to Texas with disjunct populations in Kentucky and Tennessee (Catling 1982; Sheviak and Brown 2002).

*S. casei* var. *casei* grows on mesic to dry, open sites in periodically disturbed, coarse, sandy soils, frequently on barren ridge tops (Catling and Cruise 1974). It is most common from Nova Scotia and northern New England through northern Pennsylvania, southern Quebec, and southern Ontario to Wisconsin (Catling 1990; Sheviak and Brown 2002). *S. casei* var. *novaescotiae* is found on acidic soils on barrens and dry roadsides in southern Nova Scotia (Catling 1981).

## Floral Morphology

The lip is white or ivory colored and may have a darker or yellow center. Flowers of *S. ochroleuca* are variously reported to be strongly fragrant (Sheviak 1973) or to have a very weak and musty odor (Catling and Brown 1983) while those of *S. odorata* are said to have a scent similar to that of coumarin, vanilla, or jasmine (Luer 1975). Flowers of *S. cernua* are either odorless or emit a faint scent resembling that of fresh *Cypripedium* roots (Sheviak 1973; Catling and Brown 1983). *S. magnicarpum*, on the other hand, has flowers that produce a strong, sweet, and coumarin-like fragrance, distinct from that of *S. cernua*. Flowers of agamospermous taxa bloom for 3–10 days and initiate capsule dehiscence within 2 weeks of blooming (Catling 1982).

## ***Compatibility and Breeding System***

Catling (1982) tested taxa from northeastern North America for agamospermy, autogamy, intrafloral selfing, geitonogamy, and xenogamy. He found autonomous agamospermy (i.e., agamospermy without pollination) in widely dispersed populations of *S. casei* var. *casei*, *S. casei* var. *novaescotiae*, and *S. cernua*. Emasculated specimens from these populations enclosed in insect-proof cages developed enlarged ovaries containing abundant seed. Schmidt (1987) obtained similar results for *S. cernua*, and Sheviak (1982) demonstrated normal capsule and seed development in specimens of this species with excised columns.

Autonomous agamospermy was also observed in isolated populations of the otherwise sexual species *S. magnicamporum* and *S. ochroleuca* located near the northeastern limits of their ranges. Agamospermous races of *S. magnicamporum* occurred in extreme southwestern Ontario, eastern Michigan, northern Ohio, and part of Indiana and Illinois, agamospermous races of *S. ochroleuca* in southern Nova Scotia and western Prince Edward Island (Catling 1982). *S. odorata* (*S. cernua* var. *odorata*) was also agamospermic at 12 localities near the northeastern limit of its distribution in New Jersey, Delaware, and northern Virginia (Catling 1982).

The preceding six taxa are members of the *S. cernua* complex (e.g., Catling 1980b). All are similar morphologically, bloom in the autumn, and were formerly included in *S. cernua* (Correll 1978; Catling 1982). *S. odorata*, *S. ochroleuca*, and *S. magnicamporum* are diploid ( $2n=30$ ) (Sheviak 1982). *S. cernua* is tetraploid; a few triploids and aneuploids have also been found (Sheviak 1982). Counts of chromosome numbers for *S. casei* vary between 60 and 75 (Catling 1980b).

Sheviak (1982) established a partial correlation between ploidy level, mode of reproduction, and seed type in this complex. Diploids are sexual, undergo regular meiosis with perfect bivalent formation, and produce monoembryonic seed. Polyploids show variable levels of meiotic irregularity, as well as different levels of agamospermy and polyembryonic seed production, extruded embryos, free embryos, and ruptured embryo sacs.

Contrary to Swamy (1948), Sheviak (1982), among others, reported a high percentage of monoembryonic seed in the agamospermic allotetraploids of this complex. Single embryos were usually present in 40–60% of mature seeds, but their incidence ranged from 20 to 85% (Catling 1980b, 1982). On the other hand, polyembryony is extremely rare or absent in obligately sexual individuals (Sheviak 1982; Schmidt and Antlfinger 1992). Based on these correlations and an examination of some of Catling's material, Sheviak (1982) concluded that the specimens of *S. magnicamporum*, *S. ochroleuca*, and *S. odorata* examined by Catling from near their northeastern range limits were polyploid. However, Catling's (1980b) report of a diploid, agamospermic specimen of *S. magnicamporum*, acknowledged by Sheviak (1982), indicates that the correspondence is not perfect.

Based on direct anatomical studies of *S. casei* var. *casei*, *S. casei* var. *novaescotiae*, *S. cernua*, and an agamospermous race of *S. magnicamporum*, Catling (1982)



**Table 2.3** Pollinators of *Spiranthes casei* and *S. cernua*

Species	Pollinator/state or province	References
<i>S. casei</i>	Apidae	
	<i>Bombus terricola</i> Kirby/NY	Sheviak (1982)
	Halictidae	
	<i>Dialictus versans</i> (Lov.)/ON	Catling (1980b, 1983c)
<i>S. cernua</i>	Apidae	
	<i>B. fervidus</i> (Fabricios)/NH	Sheviak (1982)
	NY	Sheviak (1982)
	VT	Sheviak (1982)
	NS	Catling (1980b, 1983c)
	NH	Luer (1975), p. 120
	<i>B. impatiens</i> Cresson/MA	Sheviak (1982)
	<i>B. terricola</i> Kirby/NY, KS	Sheviak (1982)
	<i>B. sp.</i> /NY, NE	Sheviak (1982)
	NC	Stevenson (1973)
	Halictidae	
	<i>D. sp.</i> /NC	Stevenson (1973)

confirmed earlier reports (Leavitt 1900, 1901; Swamy 1948) that agamospermy in the *S. cernua* complex occurs by adventitious embryony. While the flower is still in bud and at about the time the megasporocyte undergoes its first division, one or two cell layers of the inner integument, usually in an area near the micropylar end of the ovule, start to enlarge and divide (Swamy 1948; Catling 1982). By anthesis or several days thereafter, proliferation in this area has produced 10–30 sometimes greatly enlarged cells, and degeneration of the nucellus has occurred (Catling 1982). Embryo sac development usually fails to proceed beyond the 4-nucleate stage (Swamy 1948; Catling 1980b, 1982; Lakshmanan and Ambegaokar 1984). The enlarged cells ultimately give rise to one or multiple embryos.

Unlike Leavitt (1900), Swamy (1948) found that in a few collections of “*S. cernua*” individual capsules sometimes contained both seeds with adventitious embryos and seeds with embryos derived from the fertilization of normally developed embryo sacs. Although in asexual individuals adventive embryos developed very early, in these so-called “intermediate” individuals their development was delayed until after the normally developed ovules had been fertilized.

The northeastern species of *Spiranthes* studied by Catling (1980b, 1982) differ from many plants with adventitious embryony in not needing pollination to stimulate development of the embryo (pseudogamy), but this does not mean that agamospermy is obligate (Leavitt 1901; Stebbins 1941; Maheshwari 1952; Catling 1982). None of the taxa with adventitious embryony have lost the morphological features required for pollination (Catling 1981, 1982; Sheviak 1982). The flowers remain in anthesis 3–10 days, secrete nectar, are functionally capable of pollen production and reception, may emit a characteristic fragrance (Catling 1980b, 1982), and are frequently pollinated by insects (Tables 2.3–2.9).

**Table 2.4** Pollinators of *Spiranthes magnicamporum*, *S. ochroleuca*, and *S. odorata*

Species	Pollinator/state or province	References
<i>S. magnicamporum</i>	Apidae	
	<i>Bombus fervidus</i> (Fabricus)/ND	Sheviak (1982)
	<i>B. nevadensis</i> var. <i>americanum</i> /WI	Hapeman (1996)
	<i>B. sp.</i> /ON, IL	Catling (1980b, 1983c) <sup>a</sup>
<i>S. ochroleuca</i>	Apidae	
	<i>B. impatiens</i> Cresson/MA	Sheviak (1982)
	<i>B. pennsylvanica</i> (DeGeer)/ne U.S.	Ames (1921), p. 81
	<i>B. vagans</i> /VT	Sheviak (1982)
	<i>B. sp.</i> /PA, MA, ON	Catling (1983c) <sup>a</sup>
<i>S. odorata</i>	Apidae	
	<i>B. pensylvanicus</i> (DeGeer)/FL	Dodson in Luer (1975, p. 120) [as <i>B. americanorum</i> (Fabr.)]
	<i>B. pennsylvanicus</i> /FL	Sheviak (1982)
	<i>B. fervidus</i> /NH	Luer (1975)
	<i>B. impatiens</i> Cresson/MA	Sheviak (1982)
	<i>B. nevadensis</i> Cresson/NC	Stevenson (1973)

<sup>a</sup>Unobserved; likely based on floral morphology and/or flowering pattern

**Table 2.5** Pollinators of *Spiranthes lacera*

	Pollinator/state or province	References
Andrenidae	<i>Calliopsis andreniformis</i> Smith/IL	Robertson (1893, 1929)
Apidae	<i>Bombus americanum</i> (Fabricus)/IL	Robertson (1893, 1929)
	<i>B. perplexus</i> Cresson/ON	Catling (1980b, 1983c)
	<i>B. terricola</i> Kirby/ON	Catling (1980b, 1983c)
	<i>B. vagans</i> Smith/ON	Catling (1980b, 1983c)
	<i>B. sp.</i> /NJ	Catling (1983c) <sup>a</sup>
	<i>Dialictus immitatus</i> (Lov.)/ON	Catling (1980b, 1983c)
Halictidae		
Megachilidae	<i>Anthidium notatum</i> Latreille/FL	Robertson (1893)
	<i>Hoplitis truncata</i> Cresson/ON	Catling (1980b, 1983c)
	<i>Megachile brevis</i> Say/FL	Robertson (1893, 1929)
	<i>M. inermis</i> Prov./ON	Catling (1980b, 1983c)

<sup>a</sup>Unobserved; likely based on floral morphology or flowering pattern

Studies examining population variability and seed morphology are consistent with the occurrence of differing levels of sexuality in agamosperous taxa. In a multivariate analysis of morphological data based on plants from southwestern Ontario, Catling and Brown (1983) found that populations of *S. magnicamporum*, although clearly agamosperous based on their frequent development of polyembryonic seed, were also distinctly more variable than those of *S. cernua*. It is likely that the differences in variability reflect differences in levels of sexuality and that agamospermy is facultative in populations of *S. magnicamporum* at this site (Swamy 1948; Catling 1982; Catling and Brown 1983).

Based on breeding experiments and levels of polyembryonic seed production, Schmidt (1987) and Schmidt and Antlfinger (1992) concluded that agamospermy is

also the predominant mode of reproduction for *S. cernua* near the edge of its range in eastern Nebraska. However, experimental treatments testing for geitonogamy and xenogamy produced a significantly higher proportion of nonpolyembryonic seeds than tests for agamospermy (Schmidt and Antlfinger 1992). They considered that agamospermy was most likely facultative on the assumption that some of the additional nonpolyembryonic seeds were produced sexually. Based on seed morphology in natural populations, the maximum estimates of sexual seed production per capsule ranged from about 20 to 34% in successive years. This would provide sufficient genetic diversity to account for the amount of allozyme variation observed in this population (Schmidt and Antlfinger 1992).

*S. parksii* Correll, described as a facultatively agamospermous tetraploid species endemic to post oak savannas in East Central Texas (Catling and McIntosh 1979; Catling 1990; Sheviak and Brown 2002), is not distinct from *S. cernua* (Dueck 2008; Dueck and Cameron 2008).

### ***Fruiting Success and Limiting Factors***

Schmidt (1987) suggested that the high proportion of agamospermic seeds produced in eastern Nebraska populations of *S. cernua* might be due to pollinator limitation (discussed below under sexual populations) or to the precocious development of adventitious embryos prior to anthesis. Indeed, Sheviak (1982) reported that capsules developed prior to anthesis in some plants of this species, and as noted earlier, Catling (1982) described the initiation of adventitious embryos while the flower was still in the bud stage. Precocious agamospermic reproduction might increase the proportion of asexual embryos by reducing the resources available for the later development of meiotic embryos (e.g., Nogler 1984). If so, any factors that suppress or delay the initiation of asexual reproduction might be expected to permit the maturation of more megagametophytes and hence to increase the level of sexual reproduction (Catling 1982), but such factors have yet to be identified (Schmidt 1987).

Schmidt (1987) and Schmidt and Antlfinger (1992) observed significant yearly fluctuations in the proportion of polyembryonic seeds in unmanipulated plants of *S. cernua* at their study site. Although such fluctuations might be attributed to differences in pollinator availability or to genetic diversity among the plants observed, they might also reflect environmental influences other than those affecting pollinator abundance. Clausen (1954) and Marshall and Brown (1981) considered the level of agamospermy to mirror an interplay of environmental and genetic factors, and Knox (1967), for example, demonstrated that differences in photoperiod at different latitudes correlated with the level of agamospermy in grasses. However, a more complete understanding of interrelationships between asexual and sexual seed production in *S. cernua* must await the results of additional genetic and developmental studies.

Facultative agamospermy is more common and versatile in angiosperms than obligate agamospermy and does not represent the evolutionary blind alley often

associated with the latter (Clausen 1954; Nygren 1966; DeWet and Stalker 1974; Asker 1979; Catling 1981, 1982). When compared with autogamy, agamospermy requires less extreme morphological adaptation (Ornduff 1969) and produces no inbreeding depression (Charlesworth and Charlesworth 1979). At the same time, fertility is assured; the potential for rapid colonization is retained; heterozygosity is maintained; and the fixation of particular patterns of variability (new adaptive gene combinations) may be facilitated (Baker 1955; Antonovics 1968; Jain 1976; Solbrig 1976; Marshall and Weir 1979; Catling 1980b, 1982; Lloyd 1988). Short-term fitness may, thus, be combined with the advantages of genetic recombination (Catling 1982). The latter includes, for example, the ability to recombine new, advantageous mutants, permitting evolutionary responses to changing environmental conditions; the ability of the best-adapted genotypes to escape the accumulation of linked, disadvantageous but nonlethal mutants ("Muller's Ratchet"); and the ability to fill the maximum number of environmental niches through a high level of genetic variation among individuals.

Agamospermy is also thought to confer advantages over sexual reproduction in certain areas, where it may reflect adaptation to isolation or to a reduction in the availability or activity of pollinators (Lloyd 1980, 1988; Manning 1981; Catling 1982; Schmidt and Antlfinger 1992). Such sites include wide expanses of recently glaciated territory, edges of a species range, recently established vegetation zones, or more or less isolated bioclimatic zones (e.g., Bayer and Stebbins 1980; Catling 1982; Schmidt and Antlfinger 1992). For example, the three species, *S. magnicamporum*, *S. ochroleuca*, and *S. odorata*, which appear to be sexual over most of their distributions, reveal an apparent association between agamospermy and range limits, particularly northeastern range limits (Catling 1982). *S. casei* is distributed within formerly glaciated territory (Prest 1970; Ives et al. 1975; Catling 1990), and *S. casei* var. *novascotiae* lies in the relatively isolated bioclimatic zone of southern Nova Scotia (Fernald 1921; Roland and Smith 1962–1969; Catling 1981, 1982, 1990). The association of agamospermy with northeastern range limits, glaciated territory, and isolated bioclimatic zones, its augmentation of other isolating mechanisms, and its presence in a complex of closely related taxa suggest that it has been a significant factor in the production of new species (Catling 1982, 1983a).

## *Sexual Species or Populations*

This section examines sexual reproduction in uniformly sexual species of *Spiranthes* and the facultatively agamospermous populations of the *S. cernua* complex whose asexual reproduction was discussed above. Uniformly sexual species include: *S. lacera* (Rafinesque) Rafinesque var. *lacera* (northern slender ladies'-tresses), *S. lacera* var. *gracilis* (Bigelow) Luer (southern slender ladies'-tresses), *S. tuberosa* Rafinesque (little ladies'-tresses), *S. vernalis* Engelman and Gray (spring ladies'-tresses), *S. laciniata* (Small) Ames (lace-lip ladies'-tresses), *S. romanzoffiana* Chamisso (hooded ladies'-tresses), *S. diluvialis* Sheviak (Ute ladies'-tresses), *S. lucida* (H. H. Eaton)

Ames (wide-leaved ladies'-tresses), *S. ovalis* Lindley var. *erostellata* Catling (oval ladies'-tresses), and *S. ovalis* var. *ovalis* (oval ladies'-tresses) (Table 2.2).

### ***Distribution and Habitat***

Most species are variously distributed in the eastern USA from the Atlantic to Saskatchewan, Nebraska, Kansas, and Texas. The range of *S. romanzoffiana*, however, extends across Canada from Newfoundland to the Aleutian Islands and at elevation to New Mexico, Arizona, Nevada, and California. *S. diluvialis* is an amphiploid ( $2n=74$ ) resulting from hybridization of *S. romanzoffiana* ( $2n=44$ ) and *S. magnicamporum* ( $2n=30$ ), probably during the last glacial period (Sheviak 1984; Arft and Ranker 1998). A rare riparian species, it is confined to mesic or wet meadows and marshes near permanent drainage systems, springs, or large lakes scattered from Nebraska and Montana to Nevada and Washington (Sipes et al. 1993; Sheviak and Brown 2002; Bjork et al. 2008). *S. lucida*, *S. romanzoffiana*, and *S. laciniata* are also frequently found in wet to mesic sites from calcareous fens and shorelines to meadows (Luer 1975; Catling 1980b; Sheviak and Brown 2002). The remaining species occur in a wide range of situations, including open forests, grassy meadows, old fields, and roadside ditches (Luer 1975; Sheviak and Brown 2002).

### ***Floral Morphology***

The lip varies from white, often with a yellowish tinge or a yellowish or greenish center, to rich saffron yellow with green tints in *S. lucida*. The column lacks a rostellum and viscidium in *S. ovalis* var. *erostellata* (Catling 1983b).

The flowers of *S. diluvialis* have a faint, coumarin-like scent while those of *S. romanzoffiana* are said to produce a weak and musty-sweet or vanilla-like odor (Sheviak 1984; Larson and Larson 1990). Flowers of sexual species bloom for 10–40 days and initiate capsule dehiscence 14 (7–21) days after pollination (Catling 1982). Flowers over 30 days old are no longer functional. *S. lucida* blooms much earlier than the other sexual species and is further distinguished by a number of floral features, including the shape of its viscidium, the location of its nectar, and the orientation of its stigma (see below) (Catling 1983c, 1990).

### ***Compatibility and Breeding System***

Catling (1982) found that there was no expansion of the ovary or development of seed in caged, unmanipulated flowers of *S. lacera* var. *lacera*, *S. lucida*, *S. romanzoffiana*, *S. vernalis*, or populations of *S. ochroleuca* from Pennsylvania and New York

or *S. magnicamporum* from western Illinois. Observations of other species of *Spiranthes* maintained in insect-proof cages indicated that *S. laciniata*, *S. lacera* var *gracilis*, and *S. tuberosa* were also uniformly sexual (Catling 1980b, 1982).

Experimental self-pollination, geitonogamous pollination, and cross-pollination in examined species all usually led to full ovary expansion. However, when compared to self- and geitonogamous pollinations, cross-pollinations produced a higher percentage of ovaries with seeds (Catling 1980b, 1982). Catling attributed the difference to partial self-incompatibility or postzygotic embryo abortion (e.g., Brink and Cooper 1939, 1947).

Embryo development followed a similar pattern. Although highly variable, the percentage of seeds with well-developed embryos was reduced in cases of self-pollination and geitonogamous pollination when compared to cross-pollination (Catling 1980b, 1982). Catling (1980b, 1982) suggested that this might be related to the rate of pollen-tube growth and/or a reduced rate of pollen germination in intraplant pollinations (e.g., Weller and Ornduff 1977). Seed development and capsule dehiscence occurred up to 5 days earlier in cross-pollinated as compared to self-pollinated individuals (Catling 1980b). In addition, seed development only occurred in the upper portion of the ovary in cases of geitonogamous and self-pollination, especially in populations of *S. lacera* var. *lacera* and *S. lucida* (Catling 1980b, 1982). Thus, it appears that some interference with the development of the pollen tubes occurred in these treatments. Inbreeding depression in *S. lucida* was also suggested by a reduction in the size of the embryo in many seeds resulting from self- or geitonogamous pollinations, often to one-quarter or less of the usual size (Catling 1982). No small embryos were produced in cross-pollinated ovaries: all seed coats contained either large embryos or no embryos at all (Catling 1980b, 1982).

Unlike *S. ovalis* var. *ovalis* (an outcrossing or geitonogamous plant), the absence of a rostellum in *S. ovalis* var. *erostellata* permits the pollinia to develop in direct contact with the stigmatic surface (Catling 1983b). The seeds are monoembryonic, and routine experimental tests suggest that the flowers are autogamous, although pseudogamy cannot be entirely excluded (Catling 1980b, 1983b). In addition, the flowers are partly open, and a limited amount of outcrossing might be possible (Catling 1983b; Sheviak and Brown 2002).

Autogamy can confer advantages pertinent to plants colonizing disturbed or successional sites, and *S. ovalis* var. *erostellata* has recently become more common in old-field and second growth woodland habitats in some northern parts of its distribution (Sheviak 1974). Like agamospermy, the level of autogamy can be responsive to both genetic and environmental factors (Uphof 1938; Jain 1976; Frankel and Galun 1977) and is, therefore, subject to selection (Catling 1983a). Mixed mating systems may be highly adaptive to characteristics of the local environment, such as the availability of pollinators. As in facultative agamospermy, protracted adjustment of autogamy and outcrossing may reach equilibrium, balancing short-term fitness with the advantages of genetic recombination (Catling 1982). In addition, distinct modifications in floral morphology, associated with restricted gene flow, accompany autogamy (see Ornduff 1969) and may be related to the development or augmentation of ethological isolating mechanisms (Levin 1971).

The absence of a rostellum and the occurrence of autogamy are unknown among other North American species of *Spiranthes* (Catling 1980b, 1983b). However, among European and Asiatic members, autogamy is present in northern Danish populations of *S. spiralis* (L.) Chev. (Hagerup 1952), at least some Australian populations of *S. sinensis* (Pers.) Ames (Darwin 1862; Fitzgerald 1876; Ridley 1888) and Hong Kong populations of *S. hongkongensis* Hu and Barr (Hu 1977). The column also lacks a rostellum in some populations of *S. sinensis* (Ridley 1888) and a viscidium in *S. hongkongensis* (Hu 1977; Sun 1996), and the pollinia come into direct contact with the stigma in both.

Another type of mixed mating system based on varying levels of selfing and outcrossing is found in the rare orchid *S. diluvialis* at sites in Colorado and Utah (Sipes and Tepedino 1995). Experimental self-pollination, geitonogamous pollination, and cross-pollination produced no statistically significant differences in fruit and seed set (Sipes 1995; Sipes and Tepedino 1995). Thus, no indication of self-incompatibility or inbreeding depression is present in this species, and although outcrossing is favored by protandry, acropetally, and pollinator foraging habits (see below), male and female phases overlap and facilitated selfing and geitonogamy occur. Tests for autogamy and agamospermy led to no fruit production, and no polyembryonic seeds were found in any of the populations examined (Sheviak 1984; Sipes and Tepedino 1995). As in other nonautogamous members of *Spiranthes* (Catling 1982), autogamy is precluded by the structure of the column which prevents contact between the pollinium and stigma in the absence of a pollinator (Fig. 2.4) (Sipes and Tepedino 1995).

Various factors contribute to the maintenance of species integrity in taxa with overlapping distributions (Sheviak and Brown 2002). Phenology is highly variable, but may be of some significance in the isolation of particular species. For example, in southwestern Ontario, *S. ochroleuca* and *S. magnicamporum* bloom simultaneously after *S. cernua* has passed its peak (Catling and Brown 1983). Both can cross with *S. cernua* but, like most members of the *S. cernua* complex, are more or less genetically isolated from one another (Sheviak 1982). They tend to be spatially isolated by soil pH as well, *S. ochroleuca* preferring acidic conditions and *S. magnicamporum* alkaline (Catling and Brown 1983). In addition to a degree of phenological isolation, *S. cernua* is also partly isolated from *S. magnicamporum* and *S. ochroleuca* by a preference for relatively moist sites (Catling and Brown 1983). Differences in ploidy level may also restrict introgressive hybridization between *S. cernua* with  $2n=60$  chromosomes and *S. ochroleuca* or *S. magnicamporum* with  $2n=30$  (Sheviak 1976; Catling 1980b; Sheviak and Catling 1980). Occasional crosses do occur, however, and it is likely that hybridization between *S. cernua* and related diploids accounts for a large part of the variability observed in this species (Sheviak 1982; Catling 1990; Johnson 2006).

Sheviak (1973, 1982) suggested that pollinator discrimination might further isolate *S. cernua* and *S. magnicamporum*. Although this hypothesis has not been corroborated by subsequent studies (Sheviak 1976, 1982; Catling 1983c) and both species share at least one common pollinator in eastern North America (Tables 2.3 and 2.4), the flowers and inflorescences of these plants differ in appearance, and



as already noted the flowers of *S. magnicamporum* have a strong and distinctive fragrance (Sheviak 1973, 1976, 1982). Catling and Brown (1983) think that pollinators in mixed populations of these species may very well respond to these differences. At the same time, a general similarity in floral morphology may serve to attract and reinforce the behavior of pollen vectors as in *Goodyera* (Kallunki 1981; Catling and Brown 1983).

## ***Pollinators and Pollination Mechanisms***

The primary pollinators of this genus are medium sized (ca. 9-mm long) to comparatively large (15–20-mm long), long-tongued bees, particularly species of *Bombus* and to lesser extent members of the Megachilidae (Tables 2.3–2.9) (Darwin 1862; Robertson 1893, 1929; Ames 1921; Godfery 1931, 1933; Catling 1980b, 1983c; Sheviak 1982). Smaller halictine bees (species of *Lasioglossum* (*Dialictus* Robertson) and *Augochlorella*) are adapted to the pollination of *S. lucida* (Table 2.7); visits of these bees to other species are often erratic and associated with inefficient pollen transfer (see below) (Catling 1980b, 1983c). Among the few remaining tabulated insects, the importance of the andrenid *Calliopsis andreniformis* as a pollinator of *S. lacera* (Table 2.5) remains to be determined. The same may be said of the long-tongued bees of the genus *Anthophora* and the typhiid wasp, *Myzinum*, reported as pollinators of *S. diluvialis* (Table 2.8). Sipes and Tepedino (1995) only rarely observed them bearing any pollinaria, and they have not been implicated in the pollination of other species of *Spiranthes* (Catling 1983c).

In most *Spiranthes*, the nectar glands (calli) secrete their nectar into the base of the floral tube (Fig. 2.5a) (Ames 1921; Correll 1978; Catling 1982, 1983c). The relatively long, curved galea and projecting tongue of *Bombus* species and Megachilidae are well-adapted to reach this nectar source. The galea is hinged to the Stipes and when extended it reaches well forward of the head. As the insect inserts its head into the flower to obtain the nectar, it brings the dorsal surface of the flat-topped galea into contact with the viscidium (Fig. 2.5b) (Catling 1983c). The viscidium is elongated and rigid in all northeastern species of *Spiranthes*, except *S. lucida* (Fig. 2.3) (see below), and attaches readily to the stiff, flat-topped galea (Fig. 2.5c) (Catling 1980b, 1983c; Catling and Catling 1991). It is oriented parallel to the long axis of the proboscis and adheres to the middle or proximal upper surface in bees with a short galea and to the distal upper surface in bees with a long galea. A similar mode of attachment was reported for *Bombus* pollinators of *S. romanzoffiana* and *S. diluvialis* (see below) in western North America (Tables 2.6 and 2.8) (Larson and Larson 1987; Sipes and Tepedino 1995) and *S. spiralis* in England (Darwin 1862; Godfery 1933).

The flowers open first near the base of the spike, and blooming proceeds upward in sequence (e.g., Darwin 1862; Catling 1983c; Sipes and Tepedino 1995). Individual flowers are protandrous. In newly opened flowers, the lip and column are close together and the stigma hidden (Fig. 2.4a). At this male stage, incoming pollinia



**Table 2.6** Pollinators of *Spiranthes romanzoffiana*

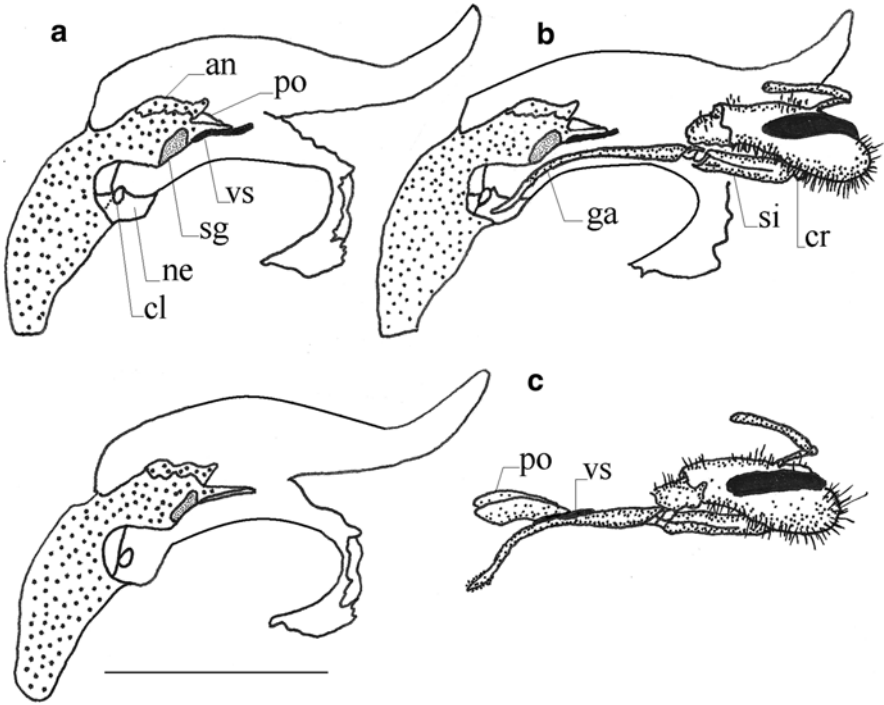
	Pollinator/state or province	References
Apidae	<i>Apis mellifera</i> L./BC	Larson and Larson (1987)
	<i>Bombus bifarius</i> Cresson/BC	Larson and Larson (1987, 1990)
	<i>B. borealis</i> Kirby/ON	Catling (1980b, 1983c)
	<i>B. flavidus</i> (Fabricius)/ON	Catling (1980b, 1983c)
	<i>B. flavifrons</i> Cresson/BC	Larson and Larson (1987, 1990)
	<i>B. cf. insularis</i> (Smith)/NL	Catling (1980b, 1983c)
	<i>B. perplexus</i> Cresson/ON	Catling (1980b, 1983c)
	<i>B. vagans</i> Smith/QC	Godfery (1933), p. 96
	/ON, QC	Catling (1980b, 1983c)
	<i>B. vagans</i> ssp. <i>bolsteri</i> Franklin/NL	Catling (1980b, 1983c)
	<i>B. terricola</i> Kirby/NL, ON	Catling (1980b, 1983c)
	<i>B. terricola occidentalis</i> Greene/BC	Larson and Larson (1987, 1990)
	<i>B. ashtoni</i> (Cresson)/NL	Catling (1980b, 1983c)
Halictidae	<i>B. insularis</i> (Smith)/BC	Larson and Larson (1987)
	“ <i>Chloryalictus smilacini</i> ” presents identity unknown/QC	Godfery (1933), p. 96
	<i>Halictus confusus</i> Smith (as <i>H. provancheri</i> D.T.)/QC	Godfery (1933), p. 96
Megachilidae	<i>Lasioglossum zonulum</i> (Smith)/NL	Catling (1980b, 1983c)
	<i>Megachile melanophea</i> Smith/NL	Catling (1980b, 1983c)

**Table 2.7** Pollinators of *Spiranthes laciniata*, *S. lucida*, *S. ovalis* var. *ovalis*, and *S. parksii* (= *S. cernua*)

Species	Pollinator/state or province	References
<i>S. laciniata</i>	Apidae	
	<i>Bombus</i> sp./FL	Catling (1980b) <sup>a</sup>
<i>S. lucida</i>	Halictidae	
	<i>Augochlorella aurata</i> (Smith)/ON	Catling (1980b, 1983c)
	<i>Dialictis immitatus</i> (Smith)/ON	Catling (1983c)
<i>S. ovalis</i> var. <i>ovalis</i>	Apidae	
	<i>B. sp.</i> /?	Catling (1980b) <sup>a</sup>
	Halictidae /?	Catling (1980b) <sup>b</sup>
<i>S. parksii</i> (= <i>S. cernua</i> )	Unknown/TX	Catling and McIntosh (1979), Catling 1990; Sheviak and Brown (2002)

<sup>a</sup>Unobserved; likely based on floral morphology and/or flowering pattern<sup>b</sup>Confirmation needed<sup>c</sup>Study sites were not given, and therefore no data are available**Table 2.8** Pollinators of *Spiranthes diluvialis*

	Pollinator/state or province	References
Anthophoridae	<i>Anthophora terminalis</i> Cresson/CO	Sipes and Tepedino (1995)
	<i>Anthophora</i> Latreille sp./UT	Sipes and Tepedino (1995)
Apidae	<i>Bombus fervidus</i> /UT	Sipes and Tepedino (1995)
	<i>B. morrisoni</i> Cresson/UT	Sipes and Tepedino (1995)
Tiphiidae	<i>Myzinum</i> Latreille sp./UT	Sipes and Tepedino (1995)



**Fig. 2.5** *Spiranthes romanzoffiana* and *Bombus vagans*. (a) Lateral view of flower with part of the perianth removed; (b) bee removing nectar, showing the position of head and mouthparts; (c) lateral view of flower following removal of the pollinarium and the head of *B. repens* with the pollinarium attached to its galea, scale bar = 5 mm. *an* anther, *cl* callus, *cr* cardo, *ga* galea, *ne* nectar, *po* pollinia, *sg* stigma, *si* stipes, *vs* viscidium. After Catling 1983c, ©2008 of NCR Canada. Reproduced with permission

attached to the upper surface of a bumblebee's proboscis cannot readily reach the stigmatic surface but are instead diverted above and around the column by the downward pointing rostellum at its tip (Fig. 2.4a) (Catling 1980b, 1983c). However, the galea of probing bees can easily contact the exposed viscidia at the tip of the rostellum and extract the pollinia (Fig. 2.5) (Catling 1980b, 1983c). After 2–4 days, the column and lip separate and the stigma is exposed so that pollinia are easily deposited on its surface (Fig. 2.4b). In some species (e.g., *S. lacera* var. *lacera* from Ontario, *S. vernalis* from New Jersey), the stigmatic surface becomes stickier after the column separates from the lip (Catling 1983c).

Because of the bumblebee's tendency to move from the base toward the top of the inflorescence, in full anthesis the older, functionally female flowers at the base of the inflorescence are visited first and receive pollen from other plants (e.g., Darwin 1862; Gray 1862a; Catling 1980b, 1983c; Corbet et al. 1981; Willems and Lahtinen 1997). The younger flowers near the top are functionally male and donate pollen prior to the maturation and exposure of their stigmas (Catling 1983c).

The bumblebees that arrive as pollen donors, thus, depart as pollen recipients, and selfing and geitonogamous pollination are reduced while cross-pollination is promoted (Catling 1983c). The effectiveness of protandry has now been demonstrated experimentally (Jersakova and Johnson 2007).

Darwin (1862) first drew attention to protandry and sequential flowering as factors promoting cross-pollination in *S. spiralis*. This flowering pattern has now been confirmed for *S. spiralis* (Willems and Lahtinen 1997) and reported for other species, including *S. cernua* and *S. lacera* var. *gracilis* (Gray 1862b), *S. romanzoffiana* (Godfery 1933; Summerhayes 1951; Larson and Larson 1987, 1990), *S. sinensis* (Coleman 1933), and *S. diluvialis* (Sipes and Tepedino 1995).

In addition, Catling (1980b, 1982, 1983c) confirmed the association of this flowering pattern with pollination by *Bombus*, a few other Apidae, and some Megachilidae. The relationship is documented for North American species of *S. cernua* var. *cernua* from southeastern Ontario, southwestern Quebec, and New England; *S. lacera* var. *lacera* from Ontario, Quebec, Nova Scotia, and Pennsylvania; *S. romanzoffiana* from Ontario, New Brunswick, Newfoundland, and Quebec; *S. vernalis* from New Jersey, Florida, and Georgia; and, based on more limited data, *S. odorata* from the southern Coastal Plain. Floral morphology, acropetal flowering, and protandry imply that bumblebees are also the primary pollinators of northeastern North American species of *S. lacera* var. *gracilis* in New Jersey; *S. laciniata* in central Florida; *S. magnicamporum* in southwestern Ontario (facultatively agamospermic population) and western Illinois (sexual population); *S. ochroleuca* in Pennsylvania, Massachusetts, and southwestern Ontario; and *S. tuberosa* in New Jersey (Catling 1980b, 1982, 1983c).

The upward movement of bumblebees on the inflorescence of *Spiranthes* has been verified in North America for *Bombus terricola* Kirby, *B. vagans* ssp. *vagans* Smith, *B. vagans* ssp. *bolsteri* (Franklin) (= *B. vagans* Smith), *B. flavifrons* Cresson, *B. bifarius* Cresson, *B. morrisoni* Cresson, *B. fervidus* (Fabricius), and 15 other unidentified *Bombus* species (Catling 1983c; Larson and Larson 1987, 1990; Sipes et al. 1993; Sipes and Tepedino 1995). Consistent movement in one direction may benefit the forager by reducing its chances of revisiting newly emptied flowers (e.g., Pyke 1978; Heinrich and Waddington 1979). Corbet et al. (1981) found that bees moved upward when flowers of the inflorescence were visited head up and downward when they were visited head down. Floral morphology in *Spiranthes* requires that bees of the Apidae and Megachilidae visit the flower in an upright position to extract nectar (Catling 1983c). In addition, it is probably more difficult for large bees to crawl down a spike than up (Catling 1983c). Although Corbet et al. (1981) found bee movements to be independent of the vertical pattern of reward, Catling (1983c) maintained that the presence of more nectar in older flowers at the base of the inflorescence makes it more energy efficient for bees to visit these flowers first.

Changes in the perianth may sometimes permit bees to identify the flowers at the base of the inflorescence that contain the largest amounts of nectar. Thus, for example, two characteristic brown spots appear on the lips of old or pollinated flowers of *S. vernalis* (Luer 1975; Catling 1980b). In most species, pollination simply leads to a halt in nectar secretion followed by a wilting and fading of flower color within 1–3

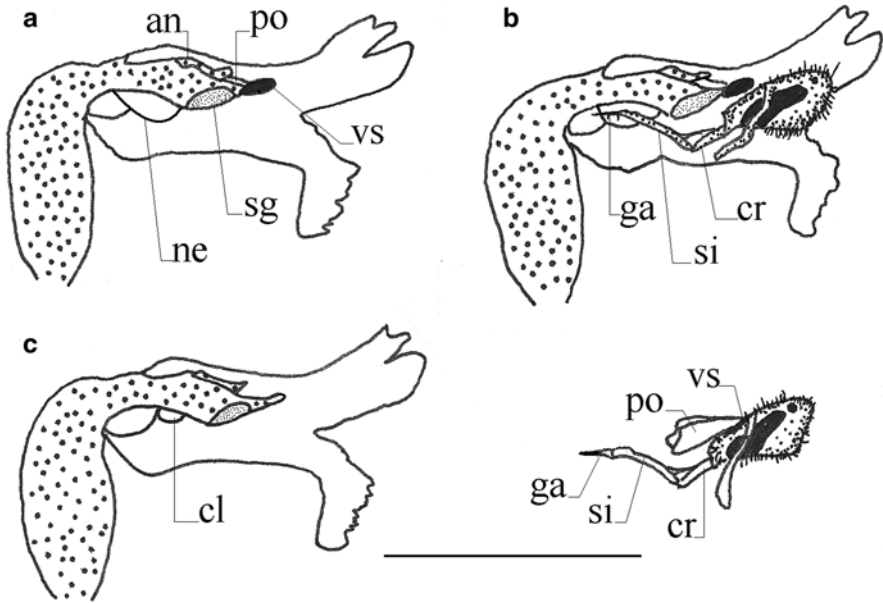
days. In *S. ochroleuca*, however, 30–40-day-old, unpollinated flowers with a dry stigma, nonfunctioning viscidium, and dead ovules still contain nectar and remain fresh looking (Catling 1983c). Catling (1980b, 1983c) suggested that these flowers might improve the chances of pollination in other nearby plants of *S. ochroleuca* by rewarding and, thus, reinforcing pollinator visitations. Selection for this condition might occur within a genet or in populations of closely related plants.

Depending on the species and the weather, all flowers in a spike become functionally female after 5–30 days. However, a functional viscidium can still be present (e.g., Catling 1983c). Thus, although outcrossing is initially favored by protandry, acropetally, and the predominantly upward movements of bumblebees on the inflorescences, circumstances change if the pollinia are still in place a number of days after the beginning of anthesis. Flowers then contain exposed, receptive stigmas and fully viable pollen, and pollinators may effect self-pollination (Sipes and Tepedino 1995). The level of selfing may consequently be dependent on the frequency of pollinator visits (Sipes 1995; Sipes and Tepedino 1995). For example, when visitation rates were low in populations of *S. diluvialis* from Colorado and Utah, more flowers reached the female stage with a functional viscidium, and a higher percentage of pollinaria (>80%) were removed during this hermaphroditic stage. When rates were high, only 16% of pollinaria were removed during this stage (Sipes and Tepedino 1995). Of course, the number of pollinations per visit would be higher in an inflorescence with functionally hermaphroditic flowers than in one with flowers in separate male and female stages (Sipes 1995). As compared to obligate outcrossing, this circumstance could provide a selective advantage in species with low levels of self-incompatibility and few pollinator visitors (Sipes and Tepedino 1995).

Unlike the other examined taxa of *Spiranthes*, *S. lucida* is specifically adapted to pollination by halictine bees (Table 2.7) (Catling 1983c). The elongated viscidium and protandry associated with bumblebee and megachilid pollination are absent: the viscidium is oval (Fig. 2.3), and the inflorescence is relatively short and not protandrous or only weakly so (Catling 1980b, 1983c). The stigma is glutinous and more upright and accessible in newly opened flowers, and pollinaria are easily removed at this stage (Catling 1983c).

Due to the relatively greater length of its column and the short claw of its lip, the calli in *S. lucida* secrete nectar onto the ventral surface of the column rather than into the base of the floral tube (Fig. 2.6) (Catling 1983c). It is here more easily reached by a short-tongued bee. In direct contrast with the Megachilidae and Apidae, the basal parts of the proboscis in halictines are relatively long with a well-developed cardo, prementum, and stipes (Fig. 2.6) (Catling 1980b, 1983c). At the same time, the terminal parts, including the galea, palpus, and glossa, are small (Catling 1980b, 1983c). This morphology appears to be well-adapted to reach the nectar on the ventral surface of the column behind the stigma. As the bee inserts its head into the relatively open flower, the clypeus, between the eyes and below the antennae, contacts the oval viscidium (Fig. 2.6b), and the pollinia are extracted as the bee withdraws (Fig. 2.6c) (Catling 1983c).

Catling (1980b, 1983c) observed *Augochlorella aurata* [as *A. stricta* (Prov.)] and *Lasioglossum imitatum* (Smith) [= *Dialictus immitatus* (Smith)] pollinating this species in Ontario. Species of *Bombus* were present in the study area, but none



**Fig. 2.6** *Spiranthes lucida* and *Augochlorella aurata*. (a) Lateral view of flower with part of perianth removed. (b) Bee removing nectar, showing the position of head and mouthparts. (c) Lateral view of flower after removal of the pollinarium and head of *A. aurata* with pollinarium attached to the clypeus (forehead), scale bar=5 mm. an anther, cl callus, cr cardo, ga galea, ne nectar, po pollinia, sg stigma, si stipes, vs viscidium. After Catling (1983c), ©2008 of NCR Canada. Reproduced with permission

carried pollinaria of *S. lucida*. *A. aurata* usually visited only a single flower in each inflorescence, even though the spikes normally bore a number of fully open blooms. When visits to a second adjacent flower occurred, they always involved flight. In no case did the bee begin its exploration on the lowermost open flower. Compared to *Bombus*, halictine visits to a spike were less systematic and involved much less crawling and fewer flower visits.

Other species of *Spiranthes*, particularly taxa having relatively small, amply-distended flowers, often with small viscidia and pollinia, are also sometimes pollinated by halictines (e.g., *S. casii* var. *casii*, *S. lacera* var. *lacera*, *S. lacera* var. *gracilis*, *S. tuberosa*) (Tables 2.3, 2.5, 2.9) (Stevenson 1973; Catling 1980b, 1983c). The pollinia of *S. casii* var. *casii* are occasionally found attached between the compound eyes of *Lasioglossum versans* (Lovell) [= *Dialictus versans* (Lovell)] (Catling 1983c). However, this is probably abnormal, and except for *S. lucida* it is likely that halictines usually enter the flowers of *Spiranthes* upside down in order to reach the nectar at the base of the floral tube (Catling 1980b, 1983c). The viscidium is then attached to the underside of the prementum or to the ventral edges of the stipes. Catling (1980b, 1983c) observed a *L. imitatum* (= *Dialictus immitatus*) pollinating *S. lacera* var. *lacera* in this manner, but considered it a rare event.

**Table 2.9** Pollinators of *Spiranthes tuberosa* and *S. vernalis*

Species	Pollinator/state or province	References
<i>S. tuberosa</i>	Apidae	
	<i>Bombus</i> sp. !?	Catling (1980b) <sup>a</sup>
	Halictidae	
	<i>Augochlorella pura</i> (Say)/NC	Stevenson (1973)
<i>S. vernalis</i>	Unknown bee, possibly Halictidae !?	Catling (1980b)
	Apidae	
	<i>Apis mellifera</i> L./GA	Catling (1980b, 1983c)
	<i>B. impatiens</i> /NC	Stevenson (1973)
	<i>B. pennsylvanicus</i> /NC	Stevenson (1973)
	<i>B. sp.</i> !?	Catling (1980b)

<sup>a</sup>Unobserved; likely based on floral morphology and/or flowering pattern

<sup>?</sup>Study sites were not given, and therefore no data are available

The available evidence indicates a lower level of pollinator specificity among most northeastern species of *Spiranthes* (Catling 1983c). Sheviak (1982), for example, noted that in greenhouse-grown specimens, *B. impatiens* moved between *S. cernua* and *S. odorata* and between *S. cernua* and *S. ochroleuca* effecting pollination. A similar lack of specificity in natural populations is clearly evident from the tabulation of *Spiranthes* species and their known pollinators (Table 2.3–2.9). Thus, for example, Catling (1980b, 1983c) identified *B. perplexus* Cresson, *B. terricola*, and *B. vagans* as pollinators of *S. lacera* var. *lacera* (Table 2.5) and *S. romanzoffiana* (Table 2.6) even though these orchids differ in the size and structure of their flowers (Catling 1983c). Hybrids are known and the resulting nothospecies is recognized as *S. × simpsonii* Catling and Sheviak (Simpson and Catling 1978; Catling 1980b; Catling and Sheviak 1993). In general, the granular pollinia in *Spiranthes* permit the deposition of pollen from a single pollinium on several successively visited flowers, augmenting any potential for hybridization (Catling 1983c).

Larson and Larson (1987, 1990) studied the foraging behavior of bumblebees on *S. romanzoffiana* at three sites on Vancouver Island. Although they also found low levels of pollinator specificity, visitation rates were usually high, possibly in response to a continuous and/or abundant nectar reward. Within a 5 × 12-m study plot of a dozen sparsely distributed plants, the pollinators, principally *B. bifarius*, zigzagged along a clearly directional flight path and were attracted to conspicuous, tall plants with long inflorescences more frequently than to short plants with smaller inflorescences, which they often bypassed. An association between larger inflorescences and higher pollinator visitation rates is not uncommon (e.g., Schmid-Hempel and Speiser 1988). In the case of *S. romanzoffiana*, a foray by a single bee did not usually involve repeat visits to any one plant; however, in a series of forays, bees revisited the four most “conspicuous” plants at frequencies that may have exceeded the optimal foraging behavior wanted to maximize nectar rewards (Larson and Larson 1990).

Visits were also correlated at a lower level with nearest neighbor distance and the number of open flowers per inflorescence (Larson and Larson 1990). Other studies have also shown increased pollinator visits in populations with closely

spaced inflorescences (e.g., Rathcke 1983). However, when the inflorescences are nonclonal, competition between plants could also be higher and the number of flowers visited per plant might decrease (Klinkhamer and De Jong 1990). Duffy and Stout (2008), in a study in western Ireland, found that intraspecific competition among inflorescences of *S. romanzoffiana* increased and visitation rates per inflorescence decreased at high densities. At the same time, they reported a positive relationship between the number of pollinator visits to *S. romanzoffiana* and total floral density in mixed patches of this and other rewarding plants, the so-called magnet species effect.

Many *Spiranthes* species congregate in patches, and outcrossing may be restricted because pollen transport is usually undirected and occurs chiefly among densely spaced plants that are likely to be closely related (Ackerman 1975; Larson and Larson 1987). However, Larson and Larson (1987, 1990) found that when bees finished foraging on *S. romanzoffiana* at their study site, they consistently moved on to other scattered patches of this orchid in the adjacent forest. This, along with their clearly directional flight path within plots, suggests that the bees may trapline through the forest, effecting some level of gene flow between patches (Heinrich 1976).

Some parallels between *S. cernua* in northeastern North America and *G. tessellata* are noteworthy. Both are polyploid (apparently of hybrid origin) and sympatric with two closely related diploid species. Like *G. tessellata*, *S. cernua* blooms before the diploids, and this phenological separation may be a statistically significant obstacle to hybridization (Catling and Brown 1983). Northeastern North American species of *Spiranthes* (14 of 15 taxa) also resemble *Goodyera* in column structure as well as mode of viscidia attachment, and both genera are protandrous with sequential acropetal flowering (Darwin 1862; Ames 1921; Hagerup 1952; Kipping 1971; Ackerman 1975; Catling 1980b, 1983c).

### ***Fruiting Success and Limiting Factors***

Extensive studies are available on the reproduction of Nebraska populations of *S. cernua*. According to Schmidt (1987), artificially crossed plants produced a significantly higher proportion of monoembryonic seeds than unmanipulated (control) plants. This suggests that pollinator limitation may influence the proportion of agamospermic seeds produced. Schmidt (1987) also found that the frequency of polyembryonic and monoembryonic seeds did not differ significantly for emasculated, bagged, and unbagged plants. Presumably, if there was no pollinator limitation, a higher proportion of monoembryonic seeds would be expected in the unbagged treatment.

Sheviak (1982), Catling (1980a, 1983a, c), and Schmidt and Antlfinger (1992) saw few pollinators visiting the flowers, and few pollinaria were removed. Factors that might limit pollinator visits have yet to be identified. This species might simply be less attractive to pollinators than other fall-flowering taxa (Anderson and Schelfhout 1980; Kaul and Rolfsmeier 1987) or fragmentation of the prairie may



have decreased pollinator populations (Schmidt 1987). In either case, the mating system of *S. cernua* might provide independence from pollinators, permitting it to colonize and survive in small numbers on isolated remnants of its prairie habitat (Schmidt and Antlfinger 1992).

Although a large percentage of the stored reserves in Nebraska populations of *S. cernua* was allocated to reproduction, the demographic data suggested that the effects on subsequent flowering and growth, at least in larger individuals, were lower than in some other orchid genera with similar reproductive effort (Whigham 1984; Schmidt 1987; Snow and Whigham 1989; Primack and Hall 1990; Calvo 1993; Primack et al. 1994; Antlfinger and Wendel 1997). Less than half of the Nebraska population produced inflorescences in a given season (Antlfinger 1991), but of the plants that flowered two-thirds were reproductive for at least 2 years in a row and one-fourth of these for 3 or more years in a row (Antlfinger and Wendel 1997). In fact, as compared to nonflowering plants, those that flowered in 1 year were usually more likely to produce flowers again the next year (Antlfinger and Wendel 1997). Similar results have been reported for *S. delitescens* Sheviak (McClaran and Sundt 1992).

Plant size was a significant factor. Seed production, flower number, and inflorescence size were positively correlated with plant size as estimated by dry weight and leaf area (Antlfinger and Wendel 1997). Plant size was also correlated between years. The production of inflorescences had relatively little effect on subsequent reproductive effort in large plants producing 31 or more flowers per year. A cost of reproduction was not observed in these plants for several years, and it remains unclear if reproductive effort or below-average rainfall during the study period contributed most significantly to a progressive decrease in leaf size, stored photosynthate, and eventual transition to a vegetative state (Antlfinger and Wendel 1997). Smaller plants producing 16–30 flowers showed a smaller increase or a reduction in size a year after flowering compared to those that did not flower and a more frequent reversion to a vegetative state for a year or more after flowering. The reproductive cost was highest in the smallest plants, those producing 1–15 flowers. Although highly variable, this group was the one most likely to remain vegetative or to be absent following a year of flowering, presumably because they had fewer stored reserves than larger plants (Antlfinger and Wendel 1997). If larger plants consistently produce more flowers and capsules, the effective size of the population is reduced. Schmidt (1987) believes that this could lead to inbreeding and genetic drift with changes in the population's gene pool.

Antlfinger (1991) considers that frequent flowering in *S. cernua* may be worth the cost. Formation of the inflorescence in a facultative apomict assures the production of a large number of seeds even where sexual reproduction may be pollinator limited (Schmidt and Antlfinger 1992; Antlfinger and Wendel 1997). Schmidt (1987), for example, found that 92% of surviving flowers produced capsules at his study site in Nebraska. In addition, the inflorescence in *S. cernua*, a species with often fugaceous leaves, is photosynthetically active and plays a role in carbon assimilation (an estimated 8.4% of the season total) that may contribute significantly to a reduction in the cost of reproduction (Antlfinger and Wendel 1997). This carbon assimilation may, in



fact, account for nearly half of the requirement for inflorescence production and maintenance, the remainder presumably coming from stored carbohydrates.

Many species of *Spiranthes* may persist as mycorrhizomes and be dependent on fungal associates for nourishment for many years before leaves differentiate and photosynthesis begins (Summerhayes 1951; Wells 1981). However, *S. cernua* is capable of initiating photosynthesis shortly after germination (Stoutamire 1974; Schmidt 1987). Flowering may follow within 2 or 3 years (Ames 1921; Stoutamire 1974). Thousands of seeds are dispersed by the wind in October and November in Nebraska (Schmidt 1987), and although further studies are needed, success in the establishment of new populations might benefit from an association between agamospermy and frequent flowering if it leads to a disproportionate representation of these genotypes in the seed bank and in colonizing individuals (Antlfinger and Wendel 1997).

Some species of *Spiranthes* appear to differ from *S. cernua* in reproductive investment and resource allocation. For example, Willems and Dorland (2000) conducted demographic studies on *S. spiralis*, a sexual, Old World species totally dependent on insects for its reproduction (Willems and Lahtinen 1997). Here, more than 80% of flowering plants failed to flower again the next year, and this result was independent of the age structure of the population (cf. Wells 1967). Flowering had a negative effect on the size of the rosette the following year, but it also reduced leaf size in the year of flowering due to allocation of limited underground resources to both the developing inflorescence and the rosette (Willems and Dorland 2000). Thus, the cost of reproduction exceeded the resources available in a given flowering year. Most plants required only 1 year to accumulate the reserves needed to flower again, but plants that flowered for 2 or more successive years required longer recovery times (Willems and Dorland 2000). Longevity is unknown for *S. cernua*, but *S. spiralis* may live several decades (Wells 1967; Tamm 1972), and life span must be factored into the balance between current reproductive investment and future fitness with long-lived species spreading their reproductive output more or less evenly over the course of their lifetime.

Other species appear to differ from *S. cernua* in pollinator recruitment. Sipes et al. (1993) found no reduction in the mean number of fertile seeds produced in open-pollinated compared to hand-pollinated flowers in *S. diluvialis*. They concluded that seed production is not limited by pollinator visitation rates. Natural fruit set may, however, be affected by the position of the flower on the inflorescence. Fruits were produced by a higher percentage of flowers (85%) from the bottom half of the inflorescence than from the top half (50%) (Sipes and Tepedino 1995). This result might be expected based on protandry and the acropetal movement of bumblebees. Schmidt (1987) also reported the occurrence of larger capsules at the bottom of the inflorescence in *S. cernua*, but this occurred in artificially pollinated plants and was related to factors other than the frequency of pollination.

Pollinator limitation was also not apparent in *S. romanzoffiana* from British Columbia. Bees visited each inflorescence an average of about once every 4 min (Larson and Larson 1987, 1990), an unusual rate, particularly for an orchid (Ackerman 1975, 1981; Heinrich 1976, 1979a, b; Pyke 1978; Hodges and Miller 1981; Zimmerman 1982; Catling 1983c). Over 75% of the flowers produced seed,

and all the plants examined bore capsules (10–45/plant) containing seed. Larson and Larson (1987, 1990) suggested that the level of visitation at their study site might be in response to a continuous or rich nectar supply. This was apparently not the case for this orchid in western Ireland, where Duffy and Stout (2008) could establish no correlation between nectar reward and visitation rates.

Additional factors influencing reproductive success in *Spiranthes* include fire, which may stimulate flower production (Sheviak 1982) and predation, which can be significant in some areas. Schmidt (1987) found that in Nebraska populations of *S. cernua*, predators destroyed 55% of the plants with flower buds prior to anthesis. Antlfinger and Wendel (1997) also found an overall loss of 22–39% of the inflorescences of this species to herbivores, probably to voles. Other possible causes of mortality in eastern Nebraska included interspecific competition and the loss of associated fungi.

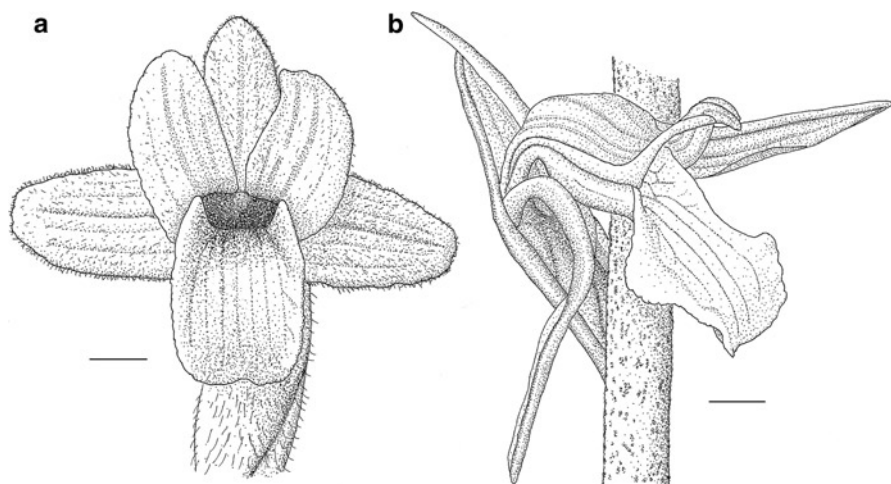
## Additional Species of *Spiranthes*

Ten other *Spiranthes* taxa occur in North America north of Florida and Mexico: *S. porrifolia* Lindley (creamy ladies'-tresses), *S. stellata* P. M. Brown, Dueck, and Cameron (no common name), *S. infernalis* Sheviak (ash meadows ladies'-tresses), *S. delitescens* Sheviak (reclusive ladies'-tresses), *S. longilabris* Lindley (giant spiral ladies'-tresses), *S. brevilabris* Lindley (texas ladies'-tresses), *S. floridana* (Wherry) Cory (florida ladies'-tresses), *S. eatonii* Ames ex P. M. Brown (eaton's ladies'-tresses), *S. praecox* (Walter) S. Watson (greenvein ladies'-tresses), and *S. sylvatica* P. M. Brown (woodland ladies'-tresses), although the latter may not be distinct from *S. praecox* (Dueck and Cameron 2008). Nothing is yet known of their pollination biology. However, the presence of a narrow, elongated viscidium in *S. praecox* suggested to Catling (1980b) that it is protandrous and pollinated by *Bombus*. In addition, *S. infernalis* is very similar to *S. porrifolia*, and Sheviak (1989) believes that it may have evolved from it. *S. porrifolia*, in turn, was formerly recognized as a variety of *S. romanzoffiana*, an otherwise uniformly sexual species. Finally, Sheviak and Brown (2002) and Brown et al. (2008) reported that these taxa produce exclusively monoembryonic seeds, implying that the breeding system is sexual in the populations they examined.

## Other Spiranthinae

### *Dichromanthus* Garay

*Dichromanthus* includes three species distributed from the southern USA through Mexico to Honduras. Two are present in our flora.



**Fig. 2.7** (a) *Dichromanthus michuacanus*, flower, front view; (b) *Deiregyne confusa*, flower, oblique view, scale bars = 3 mm

*Dichromanthus cinnabarinus* (Llave and Lexarza) Garay (= *S. cinnabarina* (LaLave and Lexarza) Hemsl.) (cinnabar ladies'-tresses) is found from southwest Texas to Guatemala (Brown 1998) and *D. michuacanus* (LaLave and Lexarza) Salazar and Soto Arenas (= *Stenorrhynchos michuacanum* (LaLave and Lexarza) Lindley or *Spiranthes michuacana* (LaLave and Lexarza) Hemsl.) (michoacan ladies'-tresses) from southeastern Arizona and southwest Texas to Mexico (World Checklist of Monocotyledons 2008). Balogh and Greenwood (1982) originally suggested without elaboration that *D. cinnabarinus* might be pollinated by bees. However, the flowers are odorless and along with the entire spike are bright red to yellow–orange, features which suggest hummingbird pollination (Luer 1975; Brown 2002a; Pridgeon et al. 2003). According to Light (1998), the perianth is very hard and may curb the efforts of nectar-robbing insects and birds to puncture the flower base. Pollination rates are low. Coleman et al. (2006) found only three maturing capsules in one population from Brewster County, Texas.

*D. michuacanus* (Fig. 2.7a), on the other hand, usually has white, cream-colored, or pale green flowers with dark green stripes (nectar guides) and during the day produces a strong lemony and faintly urine-like scent (e.g., Luer 1975; Catling and Brown 2002). An exception is forma *armeniacus* R. A. Coleman, which has flowers with a rich, apricot-yellow background color and a stronger, sweet odor (Coleman 2009). Regardless of color, the plants are large with robust flowers and may be pollinated by bumblebees or carpenter bees. Coleman (2005) monitored four sites in Arizona over a period of 9 years. He found that about 60% of plants initiating inflorescences over this period failed to reach anthesis, mostly as a result of herbivory. About 52% of plants that attempted to bloom in 1 year also attempted to bloom again the following year. Relatively, few plants attempted to bloom more than 2 years in a row. Plants not flowering again a year after a blooming event were often

either stunted or failed to emerge, sometimes for 1 or 2 years, usually reappearing, if at all, as small plants. The availability of stored energy reserves may, therefore, play a role in limiting the reproductive success of this orchid.

### *Deiregyne Schlechter*

*Deiregyne* is a genus of about 15–20 species largely confined to the mountains of Mexico and Guatemala. One species *D. confusa* Garay (confusing ladies'-tresses) (Fig. 2.7b), however, extends into Texas in the Chisos Mountains of Brewster County. Its flowers produce nectar and a diurnal fragrance, and their size, shape, and color suggest pollination by bumblebees (Pridgeon et al. 2003).

In a study in the state of Durango, Mexico, Luer (1975) noted bumblebee pollination of a plant identified as *S. durangensis* Ames and Schweinfurth (= *Deiregyne durangensis* (Ames and Schweinfurth) Garay = *Schiedeella saltensis* Schlechter). Although Kew's World Checklist of Monocotyledons places this taxon in south Texas, Garay (1982), in his study of Spirantheae, referred all specimens of *S. durangensis* that he examined, including those from Texas, to *D. confusa*. Brown (2002c) also recognizes this taxon as *D. confusa* in the Flora of North America. (Although Garay and Brown are followed here, the World Checklist of Monocotyledons (2008) recognizes the species as *Schiedeella confusa* (Garay) Espejo and Lopez-Ferr.) Luer described the bumblebee as a huge, yellow and black queen that moved slowly upward in the spicate inflorescence, grasping the lateral sepals and thrusting its head far down into each flower in search of nectar. In the process, its head contacted the viscidia, and pollinaria were extracted.

### *Schiedeella Schlechter*

*Schiedeella*, a genus of nine (Brown 2002b) to 15 (Pridgeon et al. 2003) species is found from the southern USA to Panama (except Belize) and the Caribbean (Cuba, Hispaniola). One species, *S. arizonica* P. M. Brown (red-spot ladies'-tresses), occurs in the USA from Arizona to Texas (Brown 2002b). There are no published observations on the pollination of this orchid. Among related species, Szlachetko (1993) reported autogamy in *S. romeroana* Szlach. from Mexico. A rostellum is lacking or poorly developed in this species, and the pollinia come to lie in direct contact with the stigma at anthesis. However, the pollinia in *Schiedeella* are usually attached dorsally to a well-developed, sheathing, ventral viscidium. Thus, for example, *S. llaveana* (Lindl.) Schltr. and *S. trilineata* (Lindl.) Burns-Bal., from Mexico and Central America, are xenogamous and thought to be pollinated by foraging bees, possibly bumblebees, based on the size, color, and odor of the flowers (Pridgeon et al. 2003).

## *Microthelys* Garay

*Microthelys* is a genus of about ten species once thought to be restricted to scattered montane habitats in Mexico, Central America, and Ecuador (Pridgeon et al. 2003). However, *M. rubrocallosa* (Robins and Greenm.) Garay (green medusa orchid) was recently discovered in the Sacramento Mountains in New Mexico (R. A. Coleman and Baker 2006). No detailed studies have been published on its pollination, but some plants or populations are apparently autogamous. The putatively self-pollinating individuals include forms with both poorly developed and normal-appearing rostellata. The pollinia lie in direct contact with the rim of the stigma in both (Pridgeon et al. 2003).

## References

- Ackerman JD (1975) Reproductive biology of *Goodyera oblongifolia* (Orchidaceae). Madrono 23:191–198
- Ackerman JD (1981) Pollination biology of *Calypso bulbosa* var. *occidentalis* (Orchidaceae): a food-deception system. Madrono 28:101–110
- Ames O (1921) Notes on New England orchids. I. *Spiranthes*. Rhodora 23:3–85
- Anderson RC, Schelfhout S (1980) Phenological patterns among tallgrass prairie plants and their implications for pollinator competition. Am Midl Nat 104:253–263
- Antlfinger AE (1991) Temporal patterns of reproduction and above ground growth in the terrestrial orchid, *Spiranthes cernua*. Am J Bot (Suppl.)78:47 (abstract)
- Antlfinger AE, Wendel LF (1997) Reproductive effort and floral photosynthesis in *Spiranthes cernua* (Orchidaceae). Am J Bot 84:769–780
- Antonovics J (1968) Evolution in closely adjacent plant populations. V. Evolution and self-fertility. Heredity 23:219–238
- Arft AM, Ranker TA (1998) Allopolyploid origin and population genetics of the rare orchid *Spiranthes diluvialis*. Am J Bot 85:110–122
- Asker S (1979) Progress in apomixis research. Hereditas 91:231–240
- Baker HG (1955) Self-compatibility and establishment long after ‘long distance’ dispersal. Evolution 9:347–349
- Balogh P, Greenwood EW (1982) *Cutsis* Balogh, Greenwood, and Gonzalez, a new genus from Mexico. Phytologia 51:297–298
- Bayer RJ, Stebbins GL (1980) Geographic distribution of chromosome numbers, sex ratios, and apomictic reproduction in the *Antennaria* of the eastern United States. In: Second international congress of systematic and evolutionary biology, University of British Columbia, No. 413 (abstract)
- Bjork CR, McIntosh T, Hall R (2008) Noteworthy collections: British Columbia. Madrono 54:366–367
- Brink RA, Cooper DC (1939) Somatoplastic sterility in *Medicago sativa*. Science 90:545
- Brink RA, Cooper DC (1947) The endosperm in seed development. Bot Rev 13:423–477
- Brown PM (1998) Checklist of the orchids of North America north of Mexico. N Am Nat Orchid J 4(1):61–99
- Brown PM (2002a) *Dichromanthus*. In: Flora of North America Editorial Committee (ed) Flora of North America North of Mexico, vol 26. Oxford University Press, Oxford, pp 524–525
- Brown PM (2002b) *Schiedeella*. In: Flora of North America Editorial Committee (ed) Flora of North America North of Mexico, vol 26. Oxford University Press, Oxford, p 530

- Brown PM (2002c) *Deiregyne*. In: Flora of North America Editorial Committee (ed) Flora of North America North of Mexico, vol 26. Oxford University Press, Oxford, pp 499–523
- Brown PM, Dueck LA, Cameron KM (2008) *Spiranthes stellata* (Orchidaceae), a new species of ladies'-tresses from the western United States. *N Am Nat Orchid J* 14:3–21
- Calvo RN (1993) Evolutionary demography of orchids-Intensity and frequency of pollination and the cost of fruiting. *Ecology* 74:1033–1042
- Catling PM (1979) Breeding systems of northeastern *Spiranthes* spp. *Can Bot Assoc Bull* 12:37 (abstract)
- Catling PM (1980a) Autogamy in northeastern North American orchids. Publication of Abstracts, Canadian Botanical Association 1980, Botanical Society of America, Miscellaneous Series Publication, No. 158, p. 20 (abstract)
- Catling PM (1980b) Systematics of *Spiranthes* L. C. Richard in northeastern North America. Ph.D. thesis, University of Toronto, Toronto
- Catling PM (1981) Taxonomy of autumn flowering *Spiranthes* species of southern Nova Scotia. *Can J Bot* 59:1253–1270
- Catling PM (1982) Breeding systems of northeastern North American *Spiranthes* (Orchidaceae). *Can J Bot* 60:3017–3039
- Catling PM (1983a) Autogamy in eastern Canadian Orchidaceae: a review of current knowledge and some new observations. *Naturaliste Canadien* 110:37–54
- Catling PM (1983b) *Spiranthes ovalis* var. *erostellata* (Orchidaceae), a new autogamous variety from the eastern United States. *Brittonia* 35:120–125
- Catling PM (1983c) Pollination of northeastern North American *Spiranthes* (Orchidaceae). *Can J Bot* 61:1080–1093
- Catling PM (1990) Biology of North American representatives of the subfamily Spiranthoideae. In: Sawyers C (ed) North American native orchid propagation and production. Brandywine Conservancy/Mt. Cuba Center/New England Wildflower Society, Chadds Ford, PA, pp 49–67
- Catling PM, Brown JR (1983) Morphometrics and ecological isolation in sympatric *Spiranthes* (Orchidaceae) in southwestern Ontario. *Can J Bot* 61:2747–2759
- Catling PM, Brown JR (2002) *Stenorhynchos*. In: Flora of North America Editorial Committee (ed) Flora of North America North of Mexico, vol 26. Oxford University Press, Oxford, p 545
- Catling PM, Catling VR (1991) A synopsis of breeding systems and pollination in North American orchids. *Lindleyana* 6:187–210
- Catling PM, Cruise JE (1974) *Spiranthes casei*, a new species from northeastern North America. *Rhodora* 76:526–536
- Catling PM, McIntosh KL (1979) Rediscovery of *Spiranthes parksii* Correll. *Sida* 8:188–193
- Catling PM, Sheviak CJ (1993) Taxonomic notes on some North American orchids. *Lindleyana* 8:77–81
- Charlesworth B, Charlesworth D (1979) A model for the evolution of dioecy and gynodioecy. *Am Nat* 112:975–997
- Clausen J (1954) Partial apomixis as an equilibrium system in evolution. *Caryologia* 6(Suppl):469–479
- Coleman E (1933) Further notes on the pollination of *Spiranthes sinensis*. *Victoria Nat* 50:61–64
- Coleman RA (2005) Population studies in *Dichromanthus* and *Hexaletris* in southeastern Arizona. *Selbyana* 26:246–250
- Coleman RA (2009) A yellow form of *Dichromanthus michuacanus* (Llave and Lex.) Salazar and SotoArehas in Arizona. *Native Orchid Conf J* 6:17–20
- Coleman RA, Baker M (2006) *Microthelys rubocallosa* (Robins. And Greenm.) Garay (Orchidaceae): a new orchid for the United States. *Native Orchid Conf J* 3:18–20
- Coleman RA, Sirotinak J, Leavitt A (2006) The hunt for *Deiregyne confusa*. *Native Orchid Conf J* 3:7–13
- Corbet SA, Cuthill I, Fallows M, Harrison T, Hartley G (1981) Why do nectar foraging bees and wasps work upwards in inflorescences? *Oecologia* 51:79–83
- Correll DS (1978) Native orchids of North America North of Mexico. Stanford University Press, Stanford, CA

- Darwin C (1862) On the various contrivances by which British and foreign orchids are fertilized by insects. John Murray, London
- DeWet MJM, Stalker HT (1974) Gametophytic apomixis and evolution in plants. *Taxon* 23:689–697
- Dressler RL (1993) Phylogeny and classification of the orchid family. Dioscorides, Portland, OR
- Dueck LA (2008) The *Spiranthes* formerly known as *parksii*. *N Am Nat Orchid J* 14:143–199
- Dueck LA, Cameron KM (2008) Molecular evidence on the species status and phylogenetic relationships of *Spiranthes parksii*, an endangered orchid from Texas. *Conserv Genet* 9:1617–1631
- Duffy KJ, Stout JC (2008) The effects of plant diversity and nectar reward on bee visitation to the endangered orchid *Spiranthes romanzoffiana*. *Acta Oecol* 34:131–138
- Fernald ML (1921) The Gray herbarium expedition to Nova Scotia. *Rhodora* 23:89–111, 130–152, 153–171, 184–195, 223–246, 257–258, 284–300
- Frankel R, Galun E (1977) Pollination mechanisms, reproduction, and plant breeding. Monographs on theoretical and applied genetics, 2. Springer, New York
- Fritzgerald RD (1876) Australian orchids, vol 1, part 2. Government Printer, Sidney
- Garay LA (1982) A generic revision of the Spiranthinae. *Bot Mus Leaflet Harv Univ* 28:278–379
- Godfrey MJ (1922) *Spiranthes romanzoffiana*. *Orchid Rev* 30:261–264
- Godfrey MJ (1931) The pollination of *Coeloglossum*, *Nigritella*, *Serapias*, etc. *J Bot* 69:129–130
- Godfrey MJ (1933) Monograph and iconograph of native British Orchidaceae. Cambridge University Press, Cambridge, UK
- Gray A (1862a) Enumeration of the plants of Dr. Parry's collection in the Rocky Mountains. *Am J Sci Ser 2*, 34:249–261
- Gray A (1862b) Fertilization of orchids through the agency of insects. *Am J Sci Ser 2* 34: 420–429
- Hagerup O (1952) Bud autogamy in some northern orchids. *Phytomorphology* 2:51–60
- Hapeman JR (1996) Orchids of Wisconsin. An interactive flora. Available at [www.botany.wisc.edu/orchids/magnicamporum.html](http://www.botany.wisc.edu/orchids/magnicamporum.html)
- Heinrich B (1976) The foraging specializations of individual bumblebees. *Ecol Monogr* 46:105–128
- Heinrich B (1979a) Bumblebee economics. Harvard University Press, Cambridge, MA
- Heinrich B (1979b) Resource heterogeneity and patterns of movement by foraging bumblebees. *Oecologia* 40:235–245
- Heinrich B, Waddington KD (1979) The foraging movements of bumblebees on vertical inflorescences: an experimental analysis. *J Comp Physiol* 134:113–117
- Hodges CM, Miller RB (1981) Pollinator flight directionality and the assessment of pollen returns. *Oecologia* 50:376–379
- Hu S-y (1977) The Genera of Orchidaceae in Hong Kong. The Chinese University Press, Hong Kong
- Ives JD, Andrews JT, Barry RG (1975) Growth and decay of the Laurentide ice sheet and comparisons with Fennoscandia. *Naturwissenschaften* 62:118–125
- Jain SK (1976) The evolution of inbreeding in plants. *Annu Rev Ecol Syst* 7:469–495
- Jersakova J, Johnson SD (2007) Protandry promotes male pollination success in a moth-pollinated orchid. *Funct Ecol* 21:496–504
- Johnson GP (2006) Exclusion of *Spiranthes magnicamporum* for Arkansas: three strikes and your out. *Nat Orchid Conf J* 3:1–5
- Johnson SD, Edwards T (2000) The structure and function of orchid pollinaria. *Plant Syst Evol* 222:243–269
- Kallunki JA (1981) Reproductive biology of mixed-species populations of *Goodyera* (Orchidaceae) in northern Michigan. *Brittonia* 33:137–155
- Kaul RB, Rolfsmeier SB (1987) The characteristics and phytogeographic affinities of the flora of Nine-Mile Prairie, a western tall-grass prairie in Nebraska. *Trans Nebraska Acad Sci* 15:23–35
- Klinkhamer PGL, De Jong TJ (1990) Effects of plant size, plant density and sex differential nectar reward on pollinator visitation in the protandrous *Echium vulgare*. *Oikos* 57:399–405

- Kipping JL (1971) Pollination studies of native orchids. MS Thesis, San Francisco State College, San Francisco, CA, USA
- Knox RB (1967) Apomixis: seasonal and population differences in a grass. *Science* 157:325–326
- Lakshmanan KK, Ambegaokar KB (1984) Polyembryony. In: Johri M (ed) *Embryology of angiosperms*. Springer, New York, pp 445–474
- Larson RJ, Larson KS (1987) Observations on the pollination biology of *Spiranthes roman-zoffiana*. *Lindleyana* 2:176–179
- Larson KS, Larson RJ (1990) Lure of the locks: Showiest ladies-tresses orchids, *Spiranthes roman-zoffiana*, affect bumblebee, *Bombus* spp., foraging behavior. *Can Field Nat* 104:519–525
- Leavitt RG (1900) Polyembryony in *Spiranthes cernua*. *Rhodora* 2:227–228
- Leavitt RG (1901) Notes on the embryology of some New England orchids. *Rhodora* 3(61–63):202–205
- Levin DA (1971) The origin of reproductive isolating mechanisms in flowering plants. *Taxon* 20:91–113
- Light HMS (1998) Promise of reward-scent, nectar and pollen. *Orchid Rev* 106:330–336
- Lloyd DG (1980) Demographic factors and mating in angiosperms. In: Solbrig OT (ed) *Demography and evolution in plant populations*. Blackwell Scientific, Oxford, pp 67–88
- Lloyd DG (1988) Benefits and costs of biparental and uniparental reproduction in plants. In: Michod RE, Levin BR (eds) *The evolution of sex*. Sinauer, Sunderland, MA, pp 233–252
- Luer CA (1975) *The native orchids of the United States and Canada excluding Florida*. The New York Botanical Garden, New York
- Maheshwari P (1952) Polyembryony in angiosperms. *Paleo-botanist (Lucknow)* 1:319–329
- Manning JT (1981) The “survivor effect” and the evolution of parthenogenesis and self-fertilization. *J Theor Biol* 93:491–493
- Marshall DR, Brown ADH (1981) The evolution of apomixis. *Heredity* 47:1–15
- Marshall DR, Weir BS (1979) Maintenance of genetic variation in apomictic plant populations. *Heredity* 42:159–172
- McClaran MP, Sundt PC (1992) Population dynamics of the rare orchid, *Spiranthes delitescens*. *Southwest Nat* 37:299–333
- Nogler GA (1984) Gametophyte apomixis. In: Johri BM (ed) *Embryology of angiosperms*. Springer, New York, pp 474–518
- Nygren A (1966) Apomixis in the angiosperms with special reference to *Calamagrostis* and *Poa*. In: Hawkes JG (ed) *Reproductive biology and taxonomy of vascular plants*. Pergamon, London, pp 131–140
- Ornduff R (1969) Reproductive biology in relation to systematics. *Taxon* 18:121–124
- Prest VK (1970) Quarternary geology in Canada. In: Douglas RJW (ed) *Geology and economic minerals of Canada*, vol 1. Geological Survey of Canada, Ottawa, pp 676–764
- Pridgeon AM, Cribb PM, Chase MW, Rasmussen FN (2003) *Genera Orchidaceum*, vol 3. Orchidoideae (part 2), Vanilloideae. Oxford University Press, New York
- Primack RB, Hall P (1990) Costs of reproduction in the pink lady’s slipper orchid: a four-year experimental study. *Am Nat* 136:638–656
- Primack RB, Miao SL, Becker KR (1994) Costs of reproduction in the pink lady’s-slipper orchid (*Cypripedium acaule*): defoliation, increased fruit production, and fire. *Am J Bot* 81: 1083–1090
- Pyke GH (1978) Optimal foraging: movement patterns of bumblebees between inflorescences. *Theor Popul Biol* 13:72–98
- Rathcke B (1983) Competition and facilitation among plants for pollination. In: Real L (ed) *Pollination biology*. Academic, New York, pp 305–329
- Ridley HN (1888) Notes on self-fertilization and cleistogamy in orchids. *J Linn Soc Bot* 24:389–395
- Robertson C (1893) Flowers and insects. *Bot Gazette* 18:47–54
- Robertson C (1929) *Flowers and insects*. Science, Carlinville, IL
- Roland AE, Smith EC (1962–1969) *The flora of Nova Scotia*, Parts 1–4. *Proc Nova Scotia Inst Sci* 26:1–745



- Schmid-Hempel P, Speiser B (1988) Effects of inflorescence size on pollination in *Epilobium angustifolium*. *Oikos* 53:98–104
- Schmidt JM (1987) Reproduction and Life History Characteristics of a North American Prairie Orchid *Spiranthes cernua* (Linneaus) L. C. Richard. M.A. thesis, University of Nebraska, Omaha, Nebraska, USA
- Schmidt JM, Antlfinger AE (1992) The levels of agamospermy in a Nebraska population of *Spiranthes cernua* (Orchidaceae). *Am J Bot* 79:501–507
- Schnarf K (1929) *Embryologie der Angiospermum*. Borntraeger, Berlin
- Sheviak CJ (1973) A new *Spiranthes* from the grasslands of central North America. *Bot Mus Leaflet Harv Univ* 23:285–297
- Sheviak CJ (1974) An introduction to the ecology of the Illinois orchidaceae. Illinois State Museum Scientific Papers XIV, Springfield, Illinois
- Sheviak CJ (1976) Biosystematic Study of the *Spiranthes cernua* Complex with Emphasis on the Prairies. Ph.D. thesis, Harvard University, Cambridge, MA
- Sheviak CJ (1982) Biosystematic study of *Spiranthes cernua* complex. Bulletin No. 448. New York State Museum, Albany, NY
- Sheviak CJ (1984) *Spiranthes diluvialis* (Orchidaceae), a new species from the western United States. *Brittonia* 36:8–14
- Sheviak CJ (1989) A new *Spiranthes* (Orchidaceae) from Ash Meadows, Nevada, USA. *Rhodora* 91:225–234
- Sheviak CJ, Brown PM (2002) *Spiranthes*. In: Flora of North America Editorial Committee (ed) Flora of North America North of Mexico, vol 26. University of Oxford Press, New York, pp 530–544
- Sheviak CJ, Catling PM (1980) The identity and status of *S. ochroleuca* (Rydberg) Rydberg. *Rhodora* 82:525–562
- Simpson RC, Catling PM (1978) *Spiranthes lacera* var. *lacera* X *romanzoffiana*, a new natural hybrid orchid from Ontario. *Can Field Nat* 92:350–358
- Sipes SD (1995) Reproduction of the rare, riparian orchid *Spiranthes diluvialis*: pollination ecology, variations in reproductive success, and implications for conservation. Masters thesis, Utah State University, Logan, UT
- Sipes SD, Tepedino VJ (1995) Reproductive biology of the rare orchid, *Spiranthes diluvialis*: breeding system, pollination, and implications for conservation. *Conserv Biol* 9:929–938
- Sipes SD, Tepedino VJ, Bowlin WR (1993) The pollination and reproductive ecology of *Spiranthes diluvialis* Sheviak (Orchidaceae). In: Sivinski R, Lightfoot K (eds) Proceedings of the Southwestern rare and endangered plant conference. Santa Fe, New Mexico, pp 320–333
- Snow AA, Whigham DF (1989) Costs of flower and fruit production in *Tipularia discolor* (Orchidaceae). *Ecology* 70:1286–1293
- Solbrig OT (1976) On the relative advantages of cross- and self-fertilization. *Ann MO Bot Gard* 63:262–276
- Stebbins GL Jr (1941) Apomixis in the angiosperms. *Bot Rev* 7:507–542
- Stevenson JC (1973) Evolutionary strategies and ecology of *Goodyera* and *Spiranthes* species (Orchidaceae). Ph.D. thesis, University North Carolina, Chapel Hill, NC
- Stoutamire WP (1974) Terrestrial orchid seedlings. In: Withner CL (ed) The Orchids scientific studies. Wiley, New York, pp 101–128
- Summerhayes VS (1951) Wild orchids of Britain. Collins, London
- Sun M (1996) The allopolyploid origin of *Spiranthes hongkongensis* (Orchidaceae). *Am J Bot* 83:252–260
- Swamy BGL (1948) Agamospermy in *Spiranthes arnua*. *Lloydia* 11:149–162
- Szlachetko DL (1993) *Schiedeella romeroana* (Orchidaceae, Spiranthinae), a new and interesting species from Mexico. *Rhodora* 95:1–5
- Tamm CO (1972) Survival and flowering of some perennial herbs II. The behavior of some orchids on permanent plots. *Oikos* 23:23–28
- Uphof JCT (1938) Cleistogamic flowers. *Bot Rev* 4:21–49

- Weller SG, Ornduff R (1977) Cryptic self-incompatibility in *Amsinckia grandiflora*. *Evolution* 31:47–51
- Wells TCE (1967) Changes in a population of *Spiranthes spiralis* Chevall. at Knocking Hoc National Nature Preserve, Bedfordshire, 1962–65. *J Ecol* 55:83–99
- Wells TCE (1981) Population ecology of terrestrial orchids. In: Syngé H (ed) *The biological aspects of rare plant conservation*. Wiley, London, pp 281–295
- Whigham DF (1984) Biomass and nutrient allocation of *Tipularia discolor* (Orchidaceae). *Oikos* 42:303–313
- Willems JH, Dorland E (2000) Flowering frequency and plant performance and their relation to age in the perennial orchid *Spiranthes spiralis* (Linnaeus) Chevall. *Plant Biol* 2:344–349
- Willems JH, Lahtinen ML (1997) Impact of pollination and resource limitation on seed production in a border population of *Spiranthes spiralis* (Orchidaceae). *Acta Bot Neerl* 46:365–375
- World Checklist of Monocotyledons (2008) The Board of Trustees of the Royal Botanic Gardens, Kew. <http://www.kew.org/wcsp/monocots/>. Accessed Oct 2008
- Zimmerman M (1982) Optimal foraging: random movement by pollen collecting bumblebees. *Oecologia* 53:394–398

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