Chapter 4

POSSIBLE DISPERSAL STRATEGIES, AND DISPERSER LOSS, IN THE GENERA *Eucharis* AND *Plagiolirion* (AMARYLLIDACEAE) IN SOUTHWESTERN COLOMBIA

In the departments of Valle del Cauca and Risaralda in southwestern Colombia, there are at least ten wild species of plants of the family Amaryllidaceae. From 1989 to 2008, the author carried out studies of four of these species: *Eucharis bonplandii* (Kunth) Traub, *E. caucana* Meerow, *E. sanderi* Baker, and *Plagiolirion horsmannii* Baker. During a phenological study of *E. caucana*, the author noted the lack of dispersal of the seeds, and this led to observations on the dispersal strategy of the four species included in this study.

The study site of the wild population of *Eucharis caucana* was a secondary forest of 12.5 ha in the sector called “La Flora” of the western part of the hacienda El Medio (4°20’07”N, 76°04’52”W), west of the Panamerican highway, north of the town of La Paila, in the municipality of Zarzal, department of Valle del Cauca, Colombia. This forest is the only remnant of a large cacao grove that existed here before 1960 (Iván Cadavid, pers. comm.).

The author carried out a phenological study of *Eucharis caucana* in this forest from 1989 to 1996. All adult plants were marked with plastic labels. The wild population was visited every two weeks during 3.5 years, from October, 1992, to February, 1996. Observations were made on leaf production and loss, flowering, fruit production and maturation, and presence and duration of seeds in open fruits. In 1990, a blind made of green cloth was placed in the forest adjacent to a group of plants of *E. caucana* that had open fruits. The individuals with open fruits were observed from the blind, in daylight hours, during 54 hours on eight different days, to ascertain which animals dispersed the seeds.

Between 1995 and 2008, observations were made in Cali on the morphology of fruits and seeds and phenology of cultivated individuals of *Eucharis bonplandii*, *E. sanderi*, and *Plagiolirion horsmannii.* These individuals were cultivated from seeds taken from wild populations of these species (*E. bonplandii*: hacienda Vera Cruz, municipality of Cartago, Valle del Cauca; *E. sanderi*: Pacific coast near Buenaventura, municipality of Buenaventura, Valle del Cauca; *P. horsmannii*: hacienda Alejandría, municipality of Pereira, Risaralda).

Eucharis sanderi

Professor Robert Tulio González-Mina, of the Universidad del Pacífico in Buenaventura, has studied wild populations of *Eucharis sanderi* in their natural habitat in the Pacific coastal region of the department of Valle del Cauca. He observed that these plants grow along the shores of small streams (*quebradas*). Before fruit maturity, the peduncle curves downward, and the fruits touch the soil. When the fruits dehisce, the seeds remain attached to the fruits for about one week, and then fall (Robert Tulio González-Mina, pers. comm.).

I cultivated *E. sanderi* from seeds supplied by R. T. González-Mina. This species is self-compatible; plants self-pollinated by hand produced fruits. Usually only two flowers and fruits are produced (Fig. 4.1b). Before fruit maturity, the peduncle curves downward in an arc. By 27-38 days after the beginning of anthesis, peduncles of fruiting plants had curved downward so far that their fruits reached ground level (Fig. 4.2). This occurred well before fruit maturity (final fruit color change occurred about 95-98 days after pollination). Fruit color was very pale dull orange to very pale brown. By the time fruit color changed to pale brown, the texture of the pericarp became chartaceous (papery).

The black seeds have a loose, wrinkled, dull coat (unlike the turgid, smooth, shiny coat of the three other species studied). They have a thick, spongy, subsurface layer and float in water. They are much larger than the seeds of the three other species (12-21 mm long, versus 8-12 mm long, Fig. 4.3).

The streamside habitat, downward curving of the peduncle before fruit maturity, dull fruit and seed color, and thick, spongy, subsurface layer of the seeds suggest that hydrochory is the seed dispersal mechanism. The position of the wild plants observed by Professor González-Mina suggests that the fruits may drop the seeds directly into a stream, or so close that overflow during rainy periods could carry the seeds downstream.

Plagiolirion horsmannii

Plagiolirion horsmannii differs from the other three species studied in its much more numerous and smaller, zygomorphic flowers; usually all six tepals are borne on the upper side of the flower (Fig. 1.2a). The flowers are borne on an erect peduncle. As in the three other species studied, the flowers are protandrous and self-compatible. Several hours after the beginning of anthesis, the anthers dehisce, but the style is declinate. The style gradually rises, reaching a horizontal position by the third day of anthesis. By the fifth or sixth day, the tepals wither, but they never close.

The fruits are much smaller than in the other three species (Table 1.1). They are pale yellowish or yellow-green. Usually, two carpels abort, leaving only one fertile carpel, which opens in two valves 60-71 days after pollination of the flower. The two valves wither by the second day after dehiscence, leaving the solitary seed upright and completely exposed. The seed is subglobose, 8-11 mm long x 6-9 mm wide, turgid, smooth, black, and shiny.

Thus there is a notable difference in dispersal strategy between *P. horsmannii* and the other three species studied. Only one seed per carpel is produced, and usually only one of the three carpels produces a seed. In contrast, *Eucharis caucana* has no more than six flowers in an inflorescence (versus 15-26 or rarely more in *P. horsmannii*), and all three carpels are fertile, producing up to six seeds per carpel.

The difference in seed production per fruit may be related to the mode of dispersal. The solitary seed of *Plagiolirion horsmannii*, visually, is a perfect berry mimic (Fig. 4.1a). It offers no reward. It could be swallowed whole and pass out of the digestive tract unharmed at another place, thus effecting dispersal. Small frugivorous birds might be the dispersers.

Eucharis caucana and *Eucharis bonplandii*

Both *Eucharis caucana* and *E. bonplandii* have conspicuous, orange, three-lobed capsular fruits. When the fruits open, they reveal the shiny, black seeds within. As Meerow (1989) noted, the shiny, black color of the seeds contrasts sharply with the orange pericarp (cover photo and Fig. 4.4a, 4.4b). Fruits dehisce successively (not simultaneously). The peduncles remain erect for several weeks after the beginning of fruit dehiscence. Most seeds remain firmly attached to the open fruits.

The author observed fruiting plants of *Eucharis caucana* from a blind at the forest of El Medio. During 54 hours of diurnal observation on eight days, no seed dispersal was observed. Squirrels (*Sciurus granatensis* Humboldt) and Little Tinamous (*Crypturellus soui* Hermann) passed immediately adjacent to fruiting plants of *E. caucana*, but showed no interest in them.

Week after week, I observed the same number of attached seeds in the same fruits. Some seeds became detached and fell directly beneath the peduncle, but most seeds remained attached to dehisced fruits until the senescent peduncle collapsed. Thus dispersal distance was no more than the length of the peduncle.

Seeds of *E. caucana* in the forest of El Medio rarely are dispersed at present. In the past, however, they were dispersed; the species is found at four localities in the Cauca Valley and adjacent piedmont, and within the forest at El Medio plants of this species are aggregated in seven major clumps, which are separated by several meters from each other.

What was the dispersal agent of *Eucharis caucana*? It is unlikely that seeds were dispersed by ants. Ant-dispersed seeds usually bear a nutrient-rich elaiosome (Pijl, 1982); seeds of the Old World amaryllidaceous genus *Sternbergia*, which are dispersed by ants, have elaiosomes (Dafni & Werker, 1982). Elaiosomes are lacking in the seeds of *E. caucana* (and in the seeds of the three other species included in this study). A dispersing ant would have little incentive to carry off such a seed. In seven years of field observation, I never saw ants approach these seeds.

The seeds of all four amaryllidaceous species studied float in water. It is possible that hydrochory was a subsidiary dispersal mechanism (some forests of the Cauca Valley formerly were subject to seasonal flooding), but (unlike *E. sanderi*) the thin subsurface layer of the seeds, erect peduncle, conspicuous orange fruits, and striking color contrast between pericarp and seeds of *E. caucana* and *E. bonplandii* suggest a different principal dispersal agent.

The fruit-seed display exhibits five of the nine characteristics that Pijl (1982) included in his syndrome of bird diaspores: signalling colors when mature, lack of odor, permanent attachment of seeds, no closed hard rind, and exposed seeds. Birds perceive colors (Walls, 1942; Goldsmith, 2006) and probably use color to find suitable fruits (Wheelwright & Janson, 1985); colorful fruit displays probably evolved for the attraction of avian dispersal agents (Willson & Thompson, 1982). Under certain experimental conditions, frugivorous birds remove fruits more rapidly from bicolored displays than from single-colored displays (Morden-Moore & Willson, 1982; Willson & Melampy, 1983). In two neotropical forests, 71.8% of plant species with black ripe fruits have associated contrasting colors (Wheelwright & Janson, 1985). Bicolored fruit displays may increase the probability of seed dispersal when avian frugivores are scarce (Willson & Thompson, 1982).

I believe that the striking fruit-seed display of *Eucharis caucana* and *E. bonplandii* is a case of mimetic ornithochory (McKey, 1980; Pijl, 1982), not with seeds alone, but with contrasting colors of fruit and seeds. This is a strategy of deceit. The plant itself offers no reward for an avian disperser. Bicolored or tricolored models that do offer a reward (edible arils) abound in the forest of El Medio, e.g., *Drymonia serrulata* (Jacq.) Mart. (Gesneriaceae), *Guarea guidonia* (L.) Sleumer (Meliaceae), *Cupania latifolia* Kunth (Sapindaceae), and *Paullinia fraxinifolia* Triana & Planch. (Sapindaceae).

It is not surprising that dispersers of *E. caucana* may no longer exist at El Medio, given the near-total destruction of habitat and associated fauna that has occurred in the Cauca Valley. The forest of El Medio is a tiny remnant immersed in a sea of sugar cane.

Former dispersers of *E. caucana* and *E. bonplandii* may have been small frugivorous or partly frugivorous birds, such as Pipridae, Thraupidae, and Tyrannidae. One of the best candidates for a former disperser is the Golden-collared Manakin, *Manacus vitellinus* (Gould), a piprid formerly resident in the Cauca Valley (Hilty & Brown, 1986). It still is present at 1100 m in the lower piedmont of the Western Cordillera at La Buitrera (adjacent to Cali). It forages at low levels within forest, is a frugivorous “gulper” (not a “masher”), and although small, has a large mouth (gape over 1 cm) and thus could easily swallow the 7-8 mm-wide seeds of *E. caucana* and *E. bonplandii* (Humberto Álvarez, pers. comm.). Seeds of other plant families pass through the digestive tract of manakins in viable condition (Levey et al., 1994).

Eucharis caucana is a plant that apparently has lost its dispersers. Terborgh & Winter (1980) and Ortiz-Quijano (1992) noted that frugivorous animals sometimes disappear from small fragments of habitat, because these fragments lack sufficient nutrient resources to maintain frugivores throughout the year. Loss of frugivorous animals significantly reduces seed dispersal (Cramer et al., 2007). Unfortunately, disperser loss probably will become common in the tropics and may cause extinction of many species of plants that now persist in small fragments of habitat (Redford, 1992). These doomed species have been aptly called the “living dead” (Janzen, 1986, 1988 ; Raven, 1999).