CHAPTER 2

PHENOLOGY AND SURVIVORSHIP OF *Eucharis caucana* Meerow (AMARYLLIDACEAE), AN AMAZON LILY ENDEMIC TO THE CAUCA VALLEY, COLOMBIA

Eucharis caucana Meerow (Amaryllidaceae) is known only from four small remnant patches of forest in the nearly deforested Cauca Valley and adjacent piedmont in western Colombia. It was unknown to science until 1987, when the author and colleagues discovered it at the Hacienda El Medio; this new species was described by Meerow (1989).

At the time of its discovery, nothing was known about the life history of *E. caucana*, and little was known about the life history of the genus *Eucharis*. Most ecological studies of Amaryllidaceae have been carried out on Old World species (e.g., Howell & Prakash, 1990; Ruiters et al., 1993; Budnikov & Kricsfalusy, 1994; Johnson & Bond, 1994; Arroyo & Dafni, 1995; Snijman & Linder, 1996). The purpose of this study was to investigate the relationship between the phenological behavior of a neotropical species of Amaryllidaceae, *Eucharis caucana*, and the bimodal rainfall pattern of the tropical dry forest ecosystem that it inhabits.

The Hacienda El Medio is a large ranch in the Cauca Valley, between the Western and Central Cordilleras of the Andes. The Cauca Valley formerly was covered by marshes and forests, but now is dominated by sugar cane plantations; only a few small patches of secondary forest remain. One of the most diverse of these is located in the western part of the Hacienda El Medio, between the towns of La Paila and Zarzal, at 4º20'07"N, 76º04'52"W. The elevation is 950 m, with a mean annual temperature of about 23º C and mean annual precipitation of 1316 mm. It lies in Holdridge's (1967) Tropical Dry Forest zone, with two dry seasons (December to February and

June to August) and two rainy seasons (March to May and September to November). The driest month is January, and the wettest month is October. This 12.5 ha secondary forest is the last remnant of a large cacao grove that was abandoned in the 1930's; it is dominated by trees of *Anacardium excelsum* (Kunth) Skeels (Anacardiaceae) that attain 40 m height and 2 m dbh.

Field observations were made at El Medio from 1989 to 1998; from 31 October 1992 to 24 February 1996, visits were made every two weeks. Leaf phenology of 115 plants at El Medio was studied from 7 March 1993 to 13 August 1994. Phenology of flowering and fruiting of 179 adults of the wild population at El Medio was studied for five full years, from 1991 through 1995. Plants were considered adult if they flowered at least once during the study. Plants, flowers, fruits, and leaves were labeled. For calculating leaf life-span, new leaves were considered to have been produced on the day when first seen and dead leaves to have died on the day when found dead. Rainfall records are from rain gauge 592-17 at the Hacienda El Medio.

To study survival under field conditions, a cohort of 100 seeds from wild plants of *E. caucana* was planted on 16 June 1991 at 50 cm intervals at the type locality, within the forest of El Medio, behind the phenology study area; the positions of the seeds were marked by plastic labels. No care was given to these plants. Counts of survivors were made after 1 mo, 2.5 mo, 6 mo, and every 6 mo thereafter for the next 6 yr.

Eucharis caucana is found only in forest; it is a terrestrial, perennial, bulbiferous herb (geophyte). It lacks an aerial stem. The number of leaves present per wild plant at a given time varies from none to four, but usually is one or two.

Only one new leaf is produced at a time. Production of new leaves occurs simultaneously among many individuals and is concentrated at the beginning of each rainy season (Fig. 2.1a). A small number of new leaves is produced at other times, but their growth in the dry seasons is very slow.

Some leaf loss occurs throughout the year, but peak losses occur in the dry seasons (Fig. 2.1b). The number of individuals without leaves also reaches maximum levels in the dry seasons (Fig. 2.2). Leaves are lost one at a time; many individuals lose all their leaves, but total leaf loss never occurs in the entire population simultaneously. Of the 115 individuals included in the leaf phenology study, there were only 33 individuals (28.7%) without leaves simultaneously even at the peak period of leaflessness. Fifty-nine plants (51.3%) were totally leafless at least once during the study period, and 11 of these (9.6%) lost all their leaves twice during one year. Thus *E. caucana* is facultatively deciduous. The behavior of cultivated individuals of this species also shows that total leaf loss is facultative; when watered three times a week, they never are leafless.

The number of days that an individual was leafless ranged from 27 to 209 (mean = 81.5 d = 2.7 mo, n = 23 plants). Life-span of marked leaves was 29-533 d (mean = 284 d = 9.5 mo, n = 78 leaves).

Although cultivated plants of *E. caucana*, watered three times a week, can flower at the age of 1.5 yr, wild plants in the forest of El Medio, subjected to seasonal drought, reach reproductive maturity much later (surviving individuals of a cohort planted in the forest had not yet flowered 6.5 yr after germination).

At the beginning of each flowering season, the plants produce a single erect peduncle 21-79 cm tall. Two to six flowers are produced per plant. The perianth is white and 6.5-8 cm long. Flowers open in succession; no more than two flowers are open simultaneously on the same plant. Each flower remains open continuously for 5-6 d.

The population of *E. caucana* at El Medio flowers twice a year. The time of initiation of new inflorescences is not known. Emergence of the first new inflorescences occurred in the middle or end of the dry seasons. In the study period, peak anthesis (number of plants with at least one open flower) coincided with peak rainfall, except in one season, in which it slightly preceded peak rainfall (Fig. 2.3a).

The proportion of adults participating in each flowering never exceeded one-third. There is no consistent relationship between fluctuations in numbers of flowering plants and fluctuations in current and previous rainfall (Table 2.1).

Although the population flowers twice a year, individuals rarely do so (Table 2.2). Only 11% of 155 sequential flowerings, involving only 15 of 179 adults, occurred in two flowering seasons in a row. Only one plant flowered three seasons in a row. After flowering, most plants paused from one to seven seasons before flowering again. The most common behavioral pattern (39.3% of sequential flowerings) was pausing one season. In more than half of all sequential flowerings (56.1%), plants paused one or two seasons.

In cultivated plants, the period from pollination of a flower to dehiscence of the fruit derived from that flower is 75-99 d (mean = 86 d, $n = 73$ flowers). In six wild plants, this period was 93-108 d ($n = 7$ flowers).

The number of plants with only immature undehisced fruits peaked at the height of the rainy seasons. Fruit dehiscence (as measured by the number of plants with at least one seed-bearing open fruit on a standing peduncle) began in the latter part of the rainy seasons and peaked in the dry seasons (Fig. 2.3b).

There are five to six ovules per locule; a theoretical maximum of 18 seeds thus could be produced in the three-loculed fruit, but the maximum number of seeds per fruit found in wild plants was 14. Seeds lack a dormant period, and if not dispersed, they sometimes germinate within the open fruits. Reproductive success of the wild population at El Medio was relatively high (Table 2.3). Of a cohort of 100 seeds planted by hand within the forest of the Hacienda El Medio, 98% germinated. Most mortality occurred in the first 1.5 yr; after 6.5 yr, 12% of the original cohort still survived (Fig. 2.4).

Fig. 2.4 shows heavy mortality in the initial period of life. This is a Deevey Type III survivorship curve (Silvertown, 1982). In *E. caucana*, as in most plants, the seedling stage is the most vulnerable period. Herbivore damage to seedlings was not observed.

Causes of mortality may be chiefly desiccation during dry seasons and burial by leaf litter and fallen branches (seedlings lack bulb reserves needed to grow through a substantial overlying layer of litter). Scariot (2000) reported that litterfall can be an important cause of seedling mortality in the tropics (14-38% of cohorts).

Maximum life-span in *E. caucana* is unknown. The first wild adult individual marked in this study still survived after nine years. An individual cultivated by the author is still alive after 12 years. In another geophytic species of Amaryllidaceae, *Haemanthus pubescens* L., maximum life-span is at least 24 years (Ruiters et al., 1993).

Eucharis caucana is a facultatively deciduous geophyte. Its leaf phenology is the result of selection for avoidance of dehydration in a tropical dry forest climate. Dafni et al. (1981) noted that in geophytes, storage organs may be renewed annually or may be perennial, and leaves may be hysteranthous (present only when plants are not in flower) or synanthous (present simultaneously with the flowers); they also noted that leaf phenology may follow a "rapid route" (rapid leaf production and short-lived leaves adapted to a brief photosynthetic period) or a "slow route" (slow leaf production and relatively long-lived leaves adapted to a longer photosynthetic period). In *Eucharis caucana*, storage organs are perennial, leaves usually are synanthous, and leaf phenology follows a "slow route."

The environmental stimulus that triggers initiation and subsequent emergence of inflorescences is not known. Since the first inflorescences emerge in mid or late dry season, the stimulus is not rain itself, although changes in cloud cover, relative humidity, and temperature associated with the impending rainy season may play a role. It is also possible that the timing of the beginning of flowering has been selected to allow initiation of fruit dehiscence at a favorable season.

Fruit dehiscence begins in the latter part of the rainy seasons, and the number of plants with at least one open fruit peaks in the dry seasons. This strategy seems maladapted, since the apparent outcome would be dispersal of most of the seeds at the season least favorable for germination and seedling growth. Note, however, that the intact ecosystem, including its faunal component, to which *E. caucana* originally belonged no longer exists. Under original conditions, seeds displayed in open fruits would have been dispersed soon after fruit dehiscence. But *E. caucana* in the forest fragment at El Medio may have lost its dispersers (evidence supporting this hypothesis is presented in Chapter 4 of this book). Thus after fruit dehiscence its seeds remain attached to the open fruits for an average of 3 wk (until the

peduncle dies and falls), and the number of plants with open seed-bearing fruits reaches a peak in the dry season. Under original conditions, many seeds would have been dispersed and, perhaps, their seedlings established, before cessation of the rains.

The number of plants participating in each flowering season was not uniform (Table 2.1). The percentage of adult plants that flowers each season probably depends on the number of plants with sufficient reserves in their bulbs. In synanthous-leaved geophytes with perennial bulbs, first flowering occurs only after accumulation of surplus reserves; Daphni et al. (1981) called these reserves the "shortage fund," which they defined as the reserves in excess of the amount needed for maintenance for one year. They suggested that if the "shortage fund" is large enough, after its first flowering an adult will flower almost every year. This is the most common phenological pattern in *Eucharis caucana*. The population flowers twice a year, but individual plants usually flower once a year. They usually do not flower in two consecutive seasons because they must pause, to replenish their "shortage fund," at least one (and sometimes more) seasons before their next reproductive effort (Table 2.2). Of the 17 sequential flowerings (only 11% of total sequential flowerings) that did take place in two consecutive seasons, four involved plants that had flowered but had not produced fruits in the first season and thus had not depleted their reserves. After several heavy flowering seasons, there will be a decrease in the number of plants flowering, until reserves can be augmented. Ruiters et al. (1993) noted similar behavior in a South African amaryllidaceous geophyte.

Eucharis caucana is in serious danger of extinction in the wild; it should be placed in the category CR (critically endangered), according to IUCN Red List criteria (IUCN, 2001).