

FRUIT SET, FRUIT REDUCTION, AND FRUITING STRATEGY IN *CORNUS SANGUINEA* (CORNACEAE)¹

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We studied various aspects of the fruiting biology of *Cornus sanguinea* (Cornaceae), a fleshy-fruit-producing deciduous shrub, in four populations in northwest Spain. One population was studied over a 5-yr period (1989–1994), and the remaining populations in 1994 only. Fruit-set level varied among years (range 11–18%) and among populations (range 8–22%), but was in all cases low. Within plants, fruit-set level did not vary significantly among inflorescences, indicating that inflorescence fruit set is independent of inflorescence position and inflorescence phenology. To investigate the function of surplus flowers, we carried out flower removal experiments. Inflorescence fruit-set level was unaffected by removal of up to ~75% of flowers. These results suggest that *Cornus sanguinea* regulates its fruit-set level via plasticity in the number of fruits aborted: if flower mortality has been high, fewer fruits will be aborted. Within the inflorescence, surplus flowers thus act as insurance against flower loss.

Key words: *Cornus sanguinea*; fruit set; reproductive resources; reserve ovary hypothesis.

Fruit production by higher plants has been the object of considerable interest over the past decade, largely as a result of increasing awareness of the evolutionary importance of this aspect of plant biology. The recent literature contains numerous studies that describe the fruit-set patterns of different species, investigate the factors that may affect these patterns, and postulate the evolutionary consequences of different strategies (for reviews, see Stephenson, 1981, 1992; Sutherland, 1986a; Primack, 1987; Lee, 1988).

Such studies have shown that most outcrossing hermaphrodites produce more flowers than fruits (Stephenson, 1981; Sutherland and Delph, 1984; Sutherland, 1986a, b). It has been reported for numerous species that the probability that a given flower will set fruit is affected by its spatial position within the inflorescence or on the plant, and/or by its temporal position within the inflorescence or plant, and/or by the number of seeds initiated (Stephenson, 1981, 1992; Stephenson and Winsor, 1986; Winsor, Davis, and Stephenson, 1987; Solomon, 1988; Stephenson, Devlin, and Horton, 1988; Byrne and Mazer, 1990; Ho, 1992; Vaughton, 1993; Vaughton and Carthew, 1993; Ehrlen, 1993; Harris and Whelan, 1993; Gutián, 1994). A number of hypotheses have been put forward to explain the production of "surplus" flowers, and a variety of experimental designs have been used to test the different hypotheses (Holtsford, 1985; Stephenson and Winsor, 1986; Winsor, Davis, and Stephenson, 1987; Sutherland, 1987; more recently Campbell, 1989; Ehrlen, 1991, 1993; Gutián, 1993). Likewise, considerable atten-

tion has been paid to whether observed low fruit-set levels are due to extrinsic factors, such as pollen limitation and flower predation, or intrinsic factors, such as genotype and stored resource content (see, for example, Stephenson, 1980, 1981, 1992; Wiens et al., 1987). Some authors have attempted to relate the proportion of surplus flowers to the cost of fruit production, estimated as the ratio of fruit dry mass to ovary dry mass (Primack, 1987) or of flower dry mass to fruit dry mass (Ehrlen, 1991; Ramírez, 1993). These authors have suggested that plants that produce fleshy (and thus probably energetically expensive) fruits can be expected to have low fruit set.

One plausible explanation for the production of surplus flowers is the reserve ovary hypothesis (Ehrlen, 1991), which postulates that surplus flowers constitute a stock of spare ovaries in the event of "unpredictable" flower mortality. Ehrlen's hypothesis can be viewed as a null alternative to the adaptive hypotheses that have been generated for high flower to fruit ratios. Here, we describe various aspects of flower and fruit production by *Cornus sanguinea* (Cornaceae), a shrub with fleshy fruits, and evaluate the extent to which the pattern of fruit production coincides with that predicted by the reserve ovary model. To this end, fruit-set levels were monitored (a) in a single population for 5 yr, and (b) in four populations (including that monitored for 5 yr) for 1 yr. This design allowed us to account for the possible effects of both among-year and among-population variability. We aimed to answer the following specific questions. (a) Do inflorescences function as autonomous units as regards allocation of resources for fruit production? (b) Are resource allocation patterns determined before or after fertilization? (c) What is the function of the surplus flowers of *Cornus sanguinea*?

MATERIALS AND METHODS

Study area and study species—The experiments were carried out in four populations (Covas, Chana, Valiña, and Cancela) in northwest Spain (El Bierzo, León). The four populations fall within a circle of 10 km radius and are at similar altitude (500–600 m above sea level). All four populations form part of thornshrub communities fringing *Quercus*

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rotundifolia woodland. Such communities are a typical component of the vegetation at the Eurosiberian/Mediterranean Region transition in the northwest Iberian Peninsula.

Cornus sanguinea L. (Cornaceae) is a deciduous shrub of up to 4 m in height, found in woodland fringes and clearings throughout most of temperate Europe. It has white hermaphrodite flowers arranged in umbels. Each umbel is composed of four subumbels. The fruit is a black single-seeded drupe of 6–7 mm in diameter, commonly eaten by frugivorous birds (particularly the robin *Erithacus rubecula* and members of the genera *Turdus* and *Sylvia*; J. M. Guitián, unpublished observations).

Experimental design.—In 1989 we marked 15 plants in the Covas population with plastic tags, and over this and the subsequent 4 yr (i.e., 1989–1994) recorded number of flowers and number of fruits produced on each plant. In total 9455 flowers were monitored. This provided the basis for estimation of among-year variation in fruit-set level. In 1994 we marked ten plants in each of the four populations, and again recorded the number of flowers and number of fruits produced on each plant (total = 8136 flowers). Comparison of the 1994 data for the four populations provided the basis for estimation of among-population variation in fruit-set level.

In 1990 and 1991 we monitored the flowering and fruiting phenology of ten plants in the Covas population; plants were visited every 3–15 d before fruit ripening with recording of the number of flower buds, flowers, initiated fruits ("Ifruits") and ripe fruits ("Rfruits") at each visit. This allowed calculation, for each plant, of the percentage loss, with respect to original number of buds, at each transition (bud-to-flower, flower-to-Ifruit, Ifruit-to-Rfruit); note that the sum of these three percentages plus fruit-set level is 100%. Note also that, in 1991, flowers and initiated fruits were considered as a single stage. Losses due to evident external causes (insect damage, predation by birds, inclement weather, etc.) were classified as due to extrinsic causes; otherwise, losses were classified as due to intrinsic causes (see Stephenson, 1981).

In 1994, to investigate whether there was significant within-plant between-inflorescence variation in fruit set, we marked all umbels on four plants in the Valiña population with numbered tags ($N = 70$ umbels). Number of flowers and number of fruits produced were recorded for each umbel. To investigate patterns of resource allocation, we carried out bud/flower removal experiments with ten plants in the Covas population in 1994. On each plant four umbels (A–D) were marked; umbel A was left untouched, while one subumbel was removed from umbel B, two subumbels from umbel C, and three subumbels from umbel D. This experiment was carried out at the prefertilization (i.e., bud) phase on five plants, and at the postfertilization (i.e., Ifruits) phase on the remaining five plants. Fruit-set levels (with respect to both pre- and postremoval number of flowers) were determined in all cases. This series of experiments allowed evaluation of whether umbels act as autonomous units as regards allocation of resources to fruit production, and was also a means of testing the validity of the "reserve ovary" hypothesis.

Fruit-set level can be defined as "the proportion of buds that survive the period of competition" ("final fruit set;" Goldwin, 1992). Note that ripe fruits may remain on the plant for ≈ 2 mo; losses occurring over this period were not monitored.

Data analysis.—Among-year and among-population variations in fruit-set level were investigated by chi-squared analysis. Among-plant variation was investigated by analysis of variance following an arcsine transformation of the data. The effects of subumbel removal ("level") and of time of subumbel removal (pre- or postfertilization) ("treatment") on the probability of fruitset by the remaining flowers in that umbel were investigated by maximum likelihood logistic regression (subroutine CATMOD in the SAS package; SAS, 1988). This technique, like other logistic regression methods, constructs a log-linear model allowing prediction of the probability of a given outcome (from among

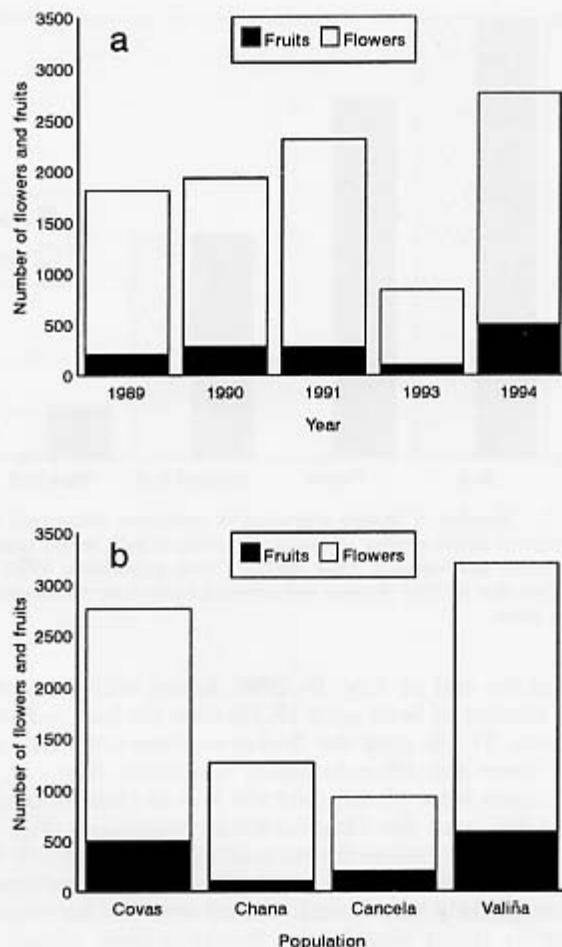


Fig. 1. Number of flowers and fruits produced by the *Cornus sanguinea* plants (a) studied over 5 yr in the Covas population and (b) studied in 1994 in the Covas, Chana, Cancela, and Valiña populations.

two or more possible outcomes) given the values of one or more independent variables; subsequent analysis of variance allows estimation of the statistical significance of the effect of each independent variable and of the likelihood ratio (a measure of the goodness of fit of the model). In the present case, each flower was treated as an event with two possible outcomes ("set fruit" or "not set fruit"), and the independent variables were "number of subumbels removed from that flower's umbel" (zero, one, two, or three) and "time of removal of subumbels from that flower's umbel" (pre- or postfertilization).

RESULTS

Among-year and among-population variation in fruit set.—Fruit-set level was low ($<25\%$) in all years and in all populations studied. Over the period 1989–1994, fruit-set level in the Covas population ranged from 11.2% to 18.0%; thus, in this population, between 5.6 and 8.9 flowers were produced for every fruit (Fig. 1a). Fruit-set level varied significantly among years ($\chi^2 = 45.7$, $df = 4$, $P < 0.0001$). In 1994, fruit-set level in the four populations ranged from 7.8% to 21.6% (Fig. 1b); among-population variation was significant ($\chi^2 = 71.7$, $df = 3$, $P < 0.0001$).

Phenology and loss of reproductive structures.—The first flower buds appeared in mid-April, and the first ripe

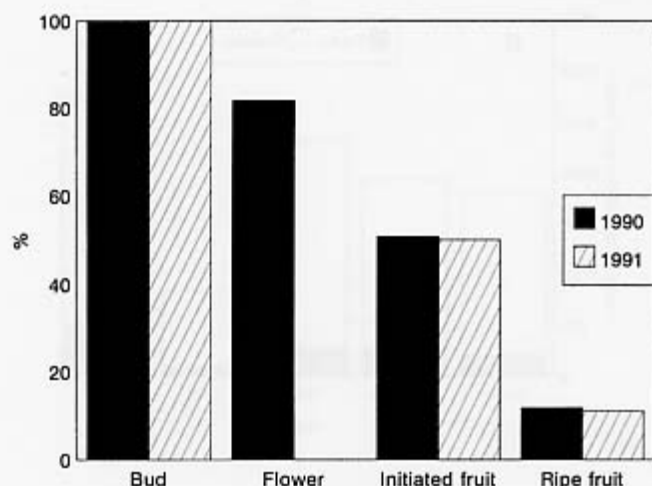


Fig. 2. Number of female reproductive structures (expressed as a percentage of initial number of buds) remaining at each major stage of predispersal development. Data for the Covas population, 1990 and 1991. Note that in 1991 flowers and initiated fruits were considered as a single stage.

fruits at the end of July. In 1990, losses with respect to initial number of buds were 18.3% over the bud-to-flower transition, 31.6% over the flower-to-fruit transition and 39.0% over the Ifruit-to-Rfruit transition (Fig. 2). In 1991, losses were 53.4% over the bud-to-Ifruit transition and 41.3% over the Ifruit-to-Rfruit transition (Fig. 2). Losses over the bud-to-flower transition were largely due to extrinsic causes such as herbivory and inclement weather (mainly late frosts). Losses over the subsequent transitions (most notably the flower-to-Ifruit transition) were largely due to intrinsic factors.

Umbel characteristics and fruit set—The mean number of flowers per umbel was 46.3 ± 20.8 ($\bar{X} \pm SD$) ($N = 54$), and there were 10.1 ± 5.1 fruits produced per umbel. Within each plant, fruit-set level did not vary significantly among umbels, indicating that umbel fruit-set level is independent of umbel position and umbel phenology (Table 1). Umbel fruit-set level did, however, vary significantly among plants ($F = 37.1$, $P < 0.0001$).

Effects of subumbel removal—The results of maximum likelihood logistic regression (Table 2) indicate that both treatment (pre- or postfertilization subumbel removal) and level (zero, one, two, or three subumbels removed) had significant effects on the probability of fruit set by the remaining flowers in the treated umbel. The interaction treatment \times level was also significant, indicating that the effect of level differed among treatments. As can be seen from Fig. 3, prefertilization removal of

TABLE 2. Analysis of variance table (maximum likelihood logistic regression, subroutine CATMOD in the SAS package) to investigate the effect of the factors Treatment (pre- or post fertilization) and Level (number of subumbels removed) on the probability that a *Cornus sanguinea* flower will give rise to a mature fruit.

Source	df	χ^2	P
Treatment	1	16.25	0.0001
Level	3	8.59	0.0353
Treatment \times Level	3	37.50	0.0001
Likelihood ratio	0	0.00	1.0000

three subumbels led to increased fruit-set levels with respect to the number of flowers remaining after subumbel removal. Postfertilization subumbel removal did not affect fruit-set level with respect to number of fruits remaining, but led to a significant reduction in fruit-set level with respect to initial number of flowers (see Fig. 4).

More detailed analysis of the results of the prefertilization subumbel removal experiments indicate that removal of one or two subumbels had no significant effect on fruit-set with respect to the number of flowers remaining ($\chi^2 = 0.12$, $df = 2$, $P = 0.94$), whereas removal of three subumbels had a significant effect ($\chi^2 = 8.17$, $df = 1$, $P = 0.004$). However, fruit-set level with respect to initial number of flowers was not significantly affected by prefertilization subumbel removal ($\chi^2 = 4.8$, $df = 3$, $P = 0.18$).

DISCUSSION

Fruit-set levels for *Cornus sanguinea* in the study area were consistently low (8–22%) in all population/year combinations studied; this is in accordance with the hypothesis that plants with “expensive” fruits will tend to have low fruit-set levels (Stephenson, 1981; Sutherland and Delph, 1984; Ehrlén, 1991; Ramírez, 1993). In a study of this species in southeastern France (Krusi and Debussche, 1988), fruit-set level did not vary significantly among habitats; on average, $\approx 23\%$ of flowers

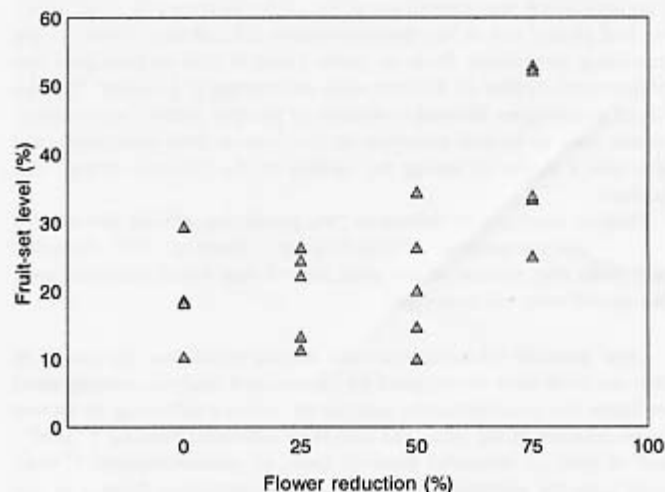


Fig. 3. Percentage fruit set (with respect to number of flowers remaining after reduction) for treated umbels of plants on which zero, one, two, or three subumbels have been removed before fertilization; each point corresponds to one plant.

TABLE 1. Values of χ^2 for among-inflorescence heterogeneity in fruit-set level, for four *Cornus sanguinea* plants in the Covas population.

Plant number	df	χ^2	P
1	8	4.7	0.79
2	18	16.4	0.57
3	9	7.9	0.54
4	16	11.6	0.77

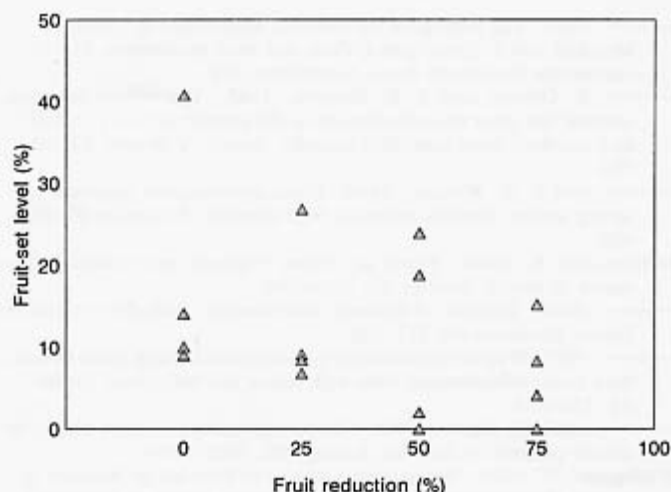


Fig. 4. Percentage fruit set (with respect to initial number of flowers) for treated umbels of plants on which zero, one, two, or three subumbels have been removed after fertilization; each point corresponds to one plant.

reached the "immature fruit" stage and $\approx 6\%$ produced ripe fruits. These data are not directly comparable with our data for a number of reasons; in general terms, however, they suggest a similar pattern of fruit-set to that observed in our region, with a high proportion of surplus flowers.

What factors limit the production of fruits by *Cornus sanguinea*? Our data indicate that significant losses of reproductive structures occurred during all three major stages of the reproductive period (bud-to-flower, flower-to-fruit, fruit-to-ripe). Proportional losses at each transition were very similar in the 2 yr of study. About 50% of flowers initiated fruit development; of the initiated fruits, only $\approx 25\%$ reached ripeness. Krusi and Debussche (1988) found that $\approx 23\%$ of flowers initiated fruit development; of these, only $\approx 17\text{--}35\%$ reached ripeness. Our data and those of Krusi and Debussche (1988) are thus similar as regards the time course of loss of reproductive structures, and suggest that there are significant losses due both to extrinsic causes (herbivory, frost, etc.) and intrinsic causes (Lloyd, 1980; Stephenson, 1981, 1992; Montalvo and Ackerman, 1987; Lee, 1988).

Our results also indicate that fruit-set, and thus abortion rate, do not vary significantly among inflorescences of the same plant. First, this suggests that inflorescence fruit-set level is independent (a) of number of flowers in the inflorescence, (b) of inflorescence phenology with respect to plant phenology, and (c) of inflorescence position. These results contrast with those of Wyatt (1982) who found that fruit-set level for *Asclepias tuberosa* was higher in inflorescences that were physically closer to the source of resources. Second, these results suggest that the low fruit-set levels were not due to insufficient pollination since, if pollination were limiting, between-inflorescence differences in fertilization rate would be expected. That fruit set is not limited by pollen/pollinator availability has since been confirmed by supplementary pollination experiments (L. Navarro, unpublished data). These results thus argue against the "attraction hypothesis" (i.e., that surplus flowers are produced in order to

increase attractiveness to pollinators; Willson and Rathcke, 1974; Stephenson, 1979; Sutherland and Delph, 1984; Sutherland, 1987).

The results of our subumbel removal experiments suggest that within-inflorescence redistribution of resources only occurs in response to prefertilization losses of reproductive structures. By contrast, postfertilization subumbel removals led to reductions in fruit set. In prefertilization subumbel removal experiments, inflorescence fruit-set level (with respect to initial number of flowers) was independent of number of subumbels removed (zero, one, two, or three); one of us has previously obtained similar results with another fleshy-fruit-producing species (*Prunus mahaleb*; Guitián, 1993). Bearing in mind that the various hypotheses that have been put forward to explain the production of surplus flowers are not mutually exclusive (Stephenson, 1981, 1984; more recently Guitián, 1993), these results are compatible with the "reserve ovary hypothesis," which postulates that surplus flowers constitute an ovary reserve in case of "unpredictable" mortality at the flower level: that is, inflorescences of *Cornus sanguinea* in which a proportion of flowers are lost due to extrinsic causes (e.g., herbivory, disease, frost) are able to maintain fruit-set levels by "allowing" the development of surplus flowers that would otherwise be aborted. These flowers thus act as an insurance policy, and the risk of flower loss is presumably sufficiently high to justify the cost of their production and maintenance (Ehrlén, 1991, 1993). That this insurance mechanism acts at the inflorescence level suggests that inflorescences behave as semiautonomous units (i.e., integrated physiological units sensu Watson and Casper, 1984) with respect to resource use.

Ehrlén (1991) has developed a numerical model based on the reserve ovary hypothesis, in which flower-to-fruit ratio is predicted on the basis of flower-to-fruit cost ratio and ovary mortality. However, the model is difficult to apply to species with inflorescences that may potentially produce many fruits such as *C. sanguinea* (J. Ehrlén, University of Stockholm, personal communication).

In conclusion, *Cornus sanguinea* appears to regulate its fruit-set level via plasticity in the number of fruits aborted: if flower mortality has been high, fewer fruits will be aborted. Within each inflorescence, the surplus flowers act as insurance against flower loss. This seems to be a common strategy among fleshy-fruit-producing plants.

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