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Reproductive strategies of *Cornus sanguinea* L. in three contrasting habitats

Fortpflanzungsstrategien von *Cornus sanguinea* L. an drei unterschiedlichen Standorten

by

Bertil O. KRÜSI and Max DEBUSSCHE

1. INTRODUCTION

It has often been observed that vigour and abundance of flowering of a species differ frequently from one habitat to another (e.g. BRAUN-BLANQUET 1964, TAMM 1972, KRÜSI 1981, LEUTERT 1983, KNAPP 1984). However, save for STEPHENSON (1984b), little quantitative work has hitherto been undertaken comparing the fate of flowers for individuals of a given species growing under contrasting environmental conditions.
It was, therefore, thought interesting to quantify these relationships for Cornus sanguinea L. The objective of the present study was twofold.

First, to evaluate in which of three contrasting habitats, viz. (i) an abandoned orchard, (ii) the edge and (iii) the interior of a deciduous forest, Cornus sanguinea thrives best in terms of cover, abundance of flowering and amounts of seed produced. Second, to determine whether the fate of flowers differs among the three habitats studied, i.e. whether there are differences in (i) the percentage of flowers that initiate the formation of fruits and (ii) the percentage that develops mature fruits. The experimental set-up permitted, in addition, to test whether abundance of flowering is a reliable predictor for the extent of fruiting. This is of particular interest with regard to the hypothesis put forward by KRÜSI (1981) that changes in the intensity of flowering may be used as an early indicator of future changes in species compositions.

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2. STUDY SITE AND METHODS

Site. The field site was located in southern France, approximately 45 km north-north-west of Montpellier, near the village of St.-Jean-de-Buèges (3^{o} 37' E, 43^{o} 49' N) at 230 m a.s.l., in a humid mediterranean climate with cold winters (mean annual precipitation about 1200 mm, mean daily minimum temperature during the coldest month 1^{o}C, mean daily maximum temperature during the warmest month 29^{o}C). The three contrasting habitats studied were (i) an abandoned orchard of olive trees, (ii) the edge and (iii) the interior of an adjacent forest with Quercus pubescens Willd. as dominating tree. They were located on a west-facing hillside with a slope of approximately 18^{o}. The substratum consisted of hard Jurassic limestone.

Species. Cornus sanguinea (Cornaceae) is an up to 4 m tall deciduous shrub. It grows in the sublayer of forests, in hedges but also on abandoned land. In southern France, C. sanguinea flowers from mid May to mid June and fruits ripen in early August. The fleshy, dark blue drupes are dispersed by birds almost throughout Europe. C. sanguinea is also capable of vigorous clonal growth.

Cover, abundance of flowering and fruiting. Percent cover of Cornus sanguinea was calculated by measuring the greatest and smallest diameter of each clone within the reference areas and using the formula for the surface of an ellipse. Intensity of flowering was calculated by counting the number of inflorescences of C. sanguinea on the area of reference in a given habitat multiplying it by the mean number of flowers per inflorescence. Intensity of fruiting was estimated by multiplying for a given habitat the flowering intensity by the mean percentage of flowers that produced mature fruits in that habitat.

Fate of flowers. The fate of flowers of Cornus sanguinea was monitored on ten clones within each of the three habitats. The experimental design was that of a mixed two-level nested ANOVA (see SOKAL and ROHLF 1981). In spring 1984, ten clones were chosen in each of the habitats and on each of the clones four twigs were selected. Clones within habitats and twigs within clones were basically chosen at random, but only clones and twigs with a reasonable number of flower buds were kept for further study.

Statistical procedures. Differences between habitats were determined by analysis of variance. Percentages and counts were transformed prior to analysis using the arcsine and the square root transformation, respectively (see SOKAL and ROHLF 1981). Tests of significance were performed on transformed data but means are reported in the untransformed scale in which they were also calculated. Unplanned multiple comparisons among pairs of means were tested according to the T-, T'- or the GT2-method, depending on the sample sizes (see SOKAL and ROHLF 1981).

3. RESULTS

3.1. COVER AND ABUNDANCE OF FLOWERING AND FRUITING (Table)

The results obtained illustrate clearly to which extent Cornus sanguinea behaved differently in the three habitats studied. As far as the percent cover is concerned, C. sanguinea played the most important role at the edge of the forest where it covered with 37.5% of the reference area 3.1 times more than in the interior of the forest with 12.1% and 9.9 times more than in the abandoned orchard with 3.8%. In terms of the number of flowers and ripe fruits produced per unit of the area covered by C. sanguinea as well as per unit of the reference area, by contrast, C. sanguinea was much more vigorous in the orchard than both at the edge and in the interior of the forest.

The number of flowers produced per square meter covered by C. sanguinea was on the abandoned orchard 3.5 times higher than at the edge of the forest (2624 vs. 758 flowers/m^2, $P<0.001$) and as much as 468 times higher than in the interior of the forest (2624 vs.5.6 flowers/m^2, $P<0.001$), the difference between the edge and the interior of the forest being also highly significant ($P<0.001$). Even when expressed per unit of the area considered, and not per unit of the area covered by C. sanguinea, flowering of C. sanguinea was in the abandoned orchard (98.9 flowers/m^2) still 1.8 and 143.2 times more abundant than at the edge (54.5 flowers/m^2) or in the interior of the forest (0.69 flowers/m^2), respectively. The number of flowers per inflorescence, on the other hand, did not significantly vary between habitats, but significant differences were found between individuals within the habitats ($P<0.001$).

As to the intensity of fruiting, the differences between the abandoned orchard on the one hand and the edge and the interior of the forest on the other were even more pronounced. In the abandoned orchard, the number of ripe Cornus sanguinea fruits produced per square meter covered by C. sanguinea was 1.2 times greater than at the edge of the forest (211.0 vs. 18.9 fruits/m^2) and 680.7 times greater than in the interior of the forest (211.0 vs. 0.31 fruits/m^2). Expressed per unit of the reference area, fruiting was in the abandoned orchard (8.0 fruits/m^2) 5.7 times and 100.0 times more abundant than at the edge (1.4 fruits/m^2) and in the interior (0.04 fruits/m^2) of the forest, respectively. The three

habitats differed also significantly in the size of the ripe fruits produced ($P<0.01$). In contrast to the abundance of fruiting, however, the diameter of ripe fruits was significantly larger in the interior of the forest than both at the edge (6.73 vs. 6.11 mm, $P<0.05$) and on the abandoned orchard (6.73 vs. 5.85 mm, $O<0.01$). In addition to the differences among habitats, there were also significant differences in the size of ripe fruits among individuals within habitats.

Table Cover and intensity of flowering and fruiting of Cornus sanguinea in three contrasting habitats.
Two means in one line followed by the same letter in parentheses are not significantly different at $P<0.05$.

Tab. Deckungsgrad und Intensität des Blühens und Fruchtens von Cornus sanguinea an drei unterschiedlichen Standorten.
Zwei Mittelwerte innerhalb einer Zeile, die vom gleichen Buchstaben gefolgt sind, unterscheiden sich nicht signifikant auf dem 5% Niveau.
* Data from a comparable site nearby
Werte eines vergleichbaren Standortes in der Nähe

Parameter	Habitat		
	Abandoned orchard	Edge of the forest	Interior of the forest
	Area considered		
	1536.0 m^2	280.0 m^2	10496.0 m^2
Cover:			
- cover percentage of C. sanguinea	3.8%	37.5%	12.1%
- mean area covered by one clone of C. sanguinea	3.2 m^2 (a) (n=18)	4.0m^2 (a) (n=26)	9.6 m^2 (a) (n=132)
Flowers produced:			
- per 1 m^2 covered by C. sanguinea	2624.4 (a) (n=10)	757.8 (b) (n=26)	5.6 (c) (n=132)
- per 1m^2 of the area considered	98.8	54.5	0.7
- per inflorescence	35.5 (a) (n=175)	27.8 (a) (n=147)	26.6 (a) (n=119)
Mature fruits produced:			
- per 1 m^2 covered by C. sanguinea	211.0 (a) (n=10)	18.9 (b) (n=26)	0.31 (c) (n=132)
- per 1 m^2 of the area considered	8.0	1.4	0.04
- per 100 flowers (n=40)	8.0 (a)	2.5 (a)	5.5 (a)
- diameter (mm)* (n=100)	5.85 (a)	6.11 (a)	6.73 (b)

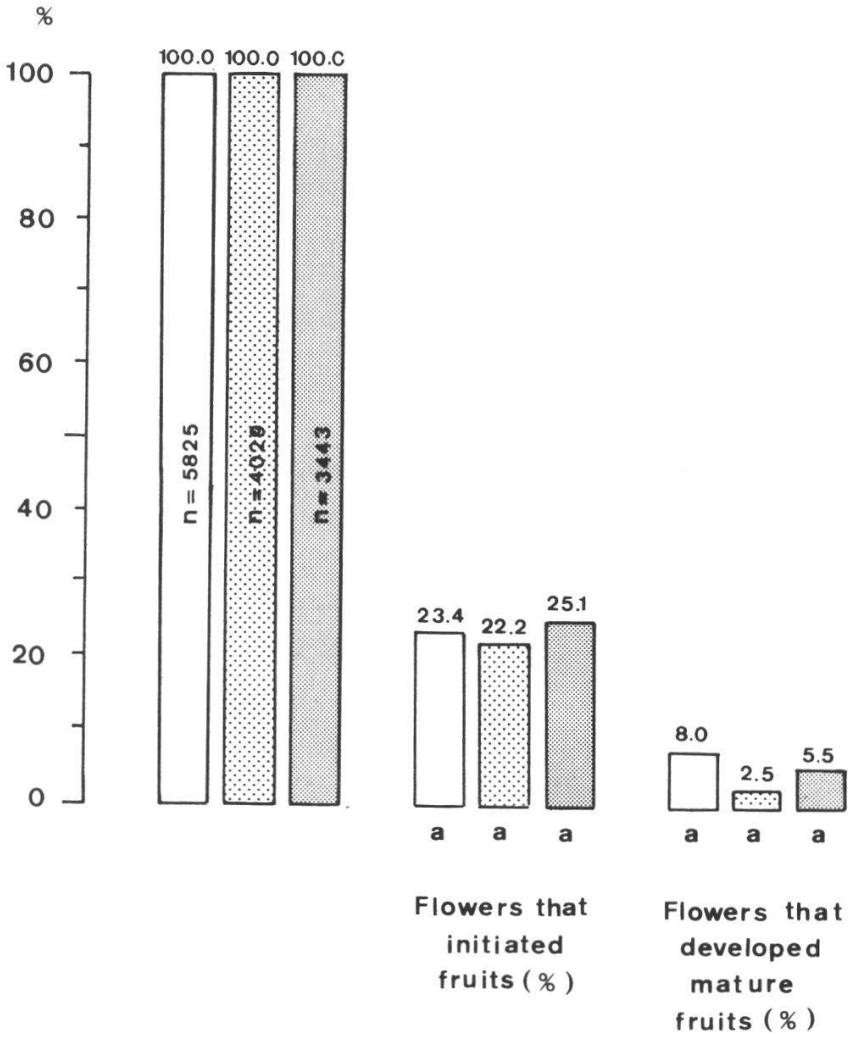

Fig. Fate of the flowers of Cornus sanguinea in three contrasting habitats.
Values are means of the respective percentages observed on the individual samples. Within each group of columns, two habitat means sharing the same letter are not significantly different at $P<0.05$

Abb. Schicksal der Blüten von Cornus sanguinea an drei unterschiedlichen Standorten.
Bei den angegebenen Zahlen handelt es sich um Mittelwerte der jeweiligen an den einzelnen Proben beobachteten Prozentsätze. Zwei Mittelwerte innerhalb einer Säulengruppe, die den gleichen Buchstaben gemeinsam haben, unterscheiden sich nicht signifikant auf dem 5% Niveau.

Abandoned orchard (flowers monitored n=5825)
Brachliegender Olivenhain (Zahl der beobachteten Blüten n=5825)
Edge of the forest (n=4029)
Waldrand (n=4029)
Interior of the forest (n=3443)
Waldesinnere (n=3443)

3.2. FATE OF FLOWERS (Table, Figure)

Global evaluation of the data with no regard to different habitats showed that of the 13297 Cornus sanguinea flowers monitored 76.9% (10219) aborted, 23.1% (3078) initiated fruits and 5.6% (750) developed mature fruits. In contrast to the marked differences in the amount of flowers and fruits produced per unit area, the fate of the flowers did not differ significantly among the three habitats. There was, however, a higly significant ($P<0.001$) added variance between individual C. sanguinea clones within habitats. The variation among clones represented 30.6% and 55.2% of the overall variation among and within clones for the proportion of flowers that (i) initiated the formation of fruits and (ii) produced mature fruits, respectively.

4. DISCUSSION

The present data suggest that the reproductive strategy of Cornus sanguinea changes with environmental conditions. In an open environment, C. sanguinea reproduces abundantly by seed, increasing the population size locally and colonizing new areas through dispersal of fruits by birds (e.g. McDONNELL and STILES 1983, DEBUSSCHE et al. 1985). In a closed environment, on the other hand, C. sanguinea expands or persists predominantly by clonal growth, unless environmental conditions are changed by disturbance.

This change in strategy according to environmental conditions is consistent with the view that several regenerative strategies may be exhibited by the same species and that populations of the same species in neighbouring habitats may depend on different reproductive strategies (e.g. GRIME 1979). It can obviously not be excluded that genetic differences among populations may be involved in this phenomenon (e.g. ANTONOVICS 1978, TURKINGTON and HARPER 1979, URBANSKA-WORYTKIEWICZ 1980, DICKENMANN 1980). However, the findings of the present study suggest that genetic variation was more important within populations than between them.

In contrast to the marked differences in cover and abundance of flowering and fruiting, the fate of the flowers was basically the same in the

three contrasting habitats. The same has been reported by STEPHENSON (1984b) for Lotus corniculatus grown under resource-enriched and resource-deprived conditions. These findings suggest that fruit production is merely a function of flower number and that the flower-to-fruit ratio has been selected for reasons other than uncertainties in resource availability. Of the hypotheses proposed to explain the adaptive significance of producing surplus flowers (see STEPHENSON 1984b, SUTHERLAND and DELPH 1984, and references therein), the one stating that "excess" flowers in hermaphroditic flowering plants increase male fitness by pollen donation, corresponds best to our data. In the present study, 77% of the flowers of Cornus sanguinea aborted, 23% initiated fruits and 6% developed mature fruits. These proportions are well within the ranges reported by other authors for a variety of species with different life histories, breeding systems and life forms (e.g. STEPHENSON 1981, SUTHERLAND and DELPH 1984).

Production of fruit may be limited by extrinsic factors such as (i) resource availability, (ii) pollination, (iii) predation on flowers, fruits and leaves (defoliation) and (iv) weather conditions as well as by intrinsic factors such as (i) age or size, (ii) genetic conditions and (iii) maternal control (see e.g. STEPHENSON 1981, 1984b and references therein). In response to varying environmental conditions and resource availability, the plant has the possibility to regulate the maternal investment (i) by altering the number of flowers, (ii) by aborting immature fruits, (iii) by changing the number of seeds per fruit or (iv) by altering the seed mass (see e.g. STEPHENSON 1981, 1984a,b, LEE and BAZZAZ 1982).

In the present study, the available resources represented the decisive extrinsic factor. It has been observed with several species that often resources rather than pollination limit seed and fruit production (e.g. STEPHENSON 1981, 1984b, McDADE and DAVIDAR 1984). However, the relative importance of these factors has been debated (BIERZYCHUDEK 1981, STEPHENSON 1981) and has been shown to vary between species (GROSS and WERNER 1983). As to the maternal investment, Cornus sanguinea regulated its seed crop primarily by limiting the number of flowers produced. This finding is consistent with the opinion that resource availability may play a major role in determining the number of flowers produced (LEE and BAZZAZ 1982, STEPHENSON 1984b). The significant differences in fruit/flower ratio observed among clones within habitats suggest that also

genetic differences among individual clones may be of importance, and that fruit yield cannot be described as simply resource or pollen limited (McDADE and DAVIDAR 1984).

As far as the indicator value of flowering intensity is concerned (KRÜSI 1981), the data show that on the population level the quantity of the seed crop can reliably be inferred from the intensity of flowering. This conclusion is supported by the findings of STEPHENSON (1984b) with Lotus corniculatus grown under controlled conditions. Due to genetic differences among clones, predictions for individual clones are less reliable.

In addition to the quantity, also the quality of the seed crop is of major ecological significance, the crucial factor being the proportion of germinable seeds. It has been shown that the percentage of germinating seeds is closely correlated to fruit and seed size (e.g. POLLOCK and ROOS 1972, STEPHENSON 1984a, and references therein). In the present study, the fruits produced in the interior of the forest were significantly larger than those produced in the two other habitats. It is, therefore, argued that the seeds produced in the interior of the forest were most certainly, not poorer in quality than those produced at the forest edge or on the abandoned orchard.

In conclusion, Cornus sanguinea responded to the different environmental conditions in the three habitats studied by a marked shift in the relative significance of reproduction by seed and clonal growth. In contrast, the proportion of flowers developing into mature fruits did not differ significantly between the three contrasting habitats. The findings suggest, therefore, that flowering intensity is a good predictor of the amount of fruits and seeds produced.

SUMMARY

In the Mediterranean region of France, cover, abundance of flowering and fruiting and the fate of flowers of Cornus sanguinea was studied in three contrasting habitats viz. (i) an abandoned orchard of olive trees, (ii) the edge and (iii) the interior of a deciduous forest dominated by Quercus pubescens.

Percent cover and abundance of flowering and fruiting of C. sanguinea differed widely between the three habitats. Percent cover was highest at the edge of the forest (38%) followed by the interior of the forest (12%) and the abandoned orchard (4%). Expressed per square meter covered by C. sanguinea, the number of flowers was in the abandoned orchard 3.5 and 486 times higher than at the edge and in the interior of the forest, respectively (2624 vs. 758 and 5.6 flowers/m^2).

The fate of the flowers, on the other hand, did not significantly differ between habitats: all three habitats combined, 77% of the flowers aborted, 23% initiated fruits and 6% developed mature fruits. There were, however, significant differences between individual clones within a given habitat.
It is concluded that the reproductive strategy of Cornus sanguinea, i.e. the relative importance of reproduction by seed and clonal growth, changes according to habitat conditions. It seems that C. sanguinea regulates the quantity of its seed crop primarily by limiting the number of flowers. The number of flowers is apparently controlled for the most part by resource availability and genetic factors. Intensity of flowering appears to be a reliable indicator of the amount of ripe fruits produced, the fruit/ flower ratio remaining constant over a wide range of environmental conditions.

ZUSAMMENFASSUNG

Im französischen Mittelmeergebiet wurden Deckungsgrad, Intensität des Blühens und Fruchtens sowie das Schicksal der Blüten von Cornus sanguinea an drei unterschiedlichen Standorten untersucht: (1) in einem aufgelassenen Olivenhain, (2) am Rande und (3) im Innern eines Flaumeichenwaldes.
Der Deckungsgrad sowie die Intensität des Blühens und Fruchtens von C. sanguinea unterschieden sich beträchtlich an den drei untersuchten Standorten. Der Deckungsgrad war am Waldrand mit 38% am höchsten, im Waldesinnern betrug er 12%, und im aufgelassenen Olivenhain war er am niedrigstens mit 4%. Die durchschnittliche Zahl der Blüten auf einem von C. sanguinea bedeckten Quadratmeter war im ehemaligen Olivenhain (2624 Blüten/m^2) 3.5 mal höher als am Waldrand (758 Blüten/m^2) und 468 mal höher als im Waldesinnern (5.6 Blüten/m^2).
Das Schicksal der Blüten war im Gegensatz dazu an allen Standorten sehr ähnlich: alle drei Standorte zusammengenommen, gingen 77% der Blüten zugrunde, 23% setzten Frucht an und 6% produzierten reife Früchte. Hingegen waren die Unterschiede zwischen den einzelnen Klonen zum Teil signifikant.
Zusammenfassend kann geschlossen werden, (1) dass sich die Fortpflanzungsstrategie von Cornus sanguinea, d.h. das Verhältnis von generativer zu vegetativer Vermehrung, in Anpassung an die Standortsbedingungen ändert; (2) dass C. sanguinea die Menge der produzierten Früchte und Samen hauptsächlich über die Zahl der Blüten reguliert; (3) dass die Menge der produzierten Blüten von den äusseren Gegebenheiten des Standorts sowie von genetischen Faktoren abhängt, und (4) dass die Blühintensität ein zuverlässiger Indikator für die Menge der produzierten reifen Früchte ist, da der Prozentsatz der Blüten, die reife Früchte hervorbringen, über einen weiten Bereich von Standortsbedingungen konstant bleibt.

RESUME

Le recouvrement, l'abondance de la floraison et de la fructification ainsi que le devenir des fleurs de Cornus sanguinea ont été suivis jusqu'à la maturité des fruits dans trois habitats contrastés et voisins situés en région méditerranéenne française: 1) une olivette abandonnée, 2) une lisière et 3) le sous-bois d'un peuplement de Quercus pubescens.
Le recouvrement et l'abondance de la floraison et de la fructification

diffèrent significativement dans les situations. Le recouvrement de Cornus sanguinea est le plus important en lisière du bois (38%), puis en sous-bois (12%), enfin dans l'olivette abandonnée (4%). Le nombre de fleurs est 3.5 fois plus élevé dans l'olivette abandonnée qu'en lisière et 486 fois plus élevé dans cette olivette qu'en sous-bois (2624 fleurs/ m^2 couvert par Cornus sanguinea vs 758 et 5.6, respectivement).
En revanche, le devenir des fleurs ne diffère pas significativement d'un habitat à l'autre: en moyenne 77% des fleurs avortent, 23% donnent des fruits et 6% donnent des fruits arrivant à maturité. Il y a cependant entre clônes des différences significatives pour un même habitat.
En conclusion, la part prise par la reproduction par graine et la part prise par la multiplication végétative changent en fonction des conditions de milieu. Il semble que Cornus sanguinea régule le nombre de graines produites en limitant en priorité le nombre de fleurs. Le nombre de fleurs serait contrôlé en majeure partie par le niveau des ressources disponibles et des facteurs génétiques. L'abondance de la floraison apparaît comme un bon indicateur du total des fruits arrivant à maturité, le rapport nombre de fruits/nombre de fleurs restant assez constant dans une large gamme de situations.

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