Observations on fruiting and seed-set of *Stratiotes aloides* L. in The Netherlands

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Accepted 9 February 1995

Abstract

In order to obtain an impression of fruit and seed production in stands of *Stratiotes aloides* L., 48 stands of this species in seven areas in the Netherlands were studied in 1992 and 1993. In 35 of these stands fruits were found; most of these appeared to be parthenocarpic. In the area of Giethoorn (province of Overijssel), however, most of the stands had many fruits with ripe seeds.

Seed production in the female plants appears to be dependent on the presence of male plants in the direct surroundings. Even in the stands with high seed production vegetative recruitment from offsets and turions appears to be much more important for the maintenance of the stand.

Keywords: *Stratiotes aloides*; Parthenocarpy; Fruit production; Seed production

1. Introduction

In populations of the water soldier (*Stratiotes aloides* L.) seeds are generally considered to be rare. Cook and Urmi-König (1983) for instance, examined nearly 500 herbarium specimens from all over Europe and only in one specimen (from Russia) was seed found. The only recent reports of seed-set in nature are those of Baude (1956) who has found seeds in Berlin-Spandau, Serbanescu-Jitariu (1972) who found them in Poland, and Roelofs (in Cook and Urmi-König, 1983) who found one fruit with seven seeds in October 1981 in the Netherlands.

In the Netherlands, *Stratiotes aloides* is considered to be native because male and female plants often occur together in the same area (Van Dijk and Westhoff, 1955; De Geus-Kruyt and Segal, 1973; Cook and Urmi-König, 1983; Smolders et al., 1994). De Geus-Kruyt and Segal (1973) stated that fruits are “fairly common” although they gave no further data on

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the production of fruits or the occurrence of seeds. Weeda et al. (1991), however, state that *S. aloides* seldom produces fruits and seeds. The first documented account on the production of seeds of *S. aloides* in the Netherlands was given by Smolders et al. (1993, 1994).

In this paper we report on field work carried out in 1992 and 1993 concerning some aspects of the generative propagation of *S. aloides*.

2. Materials and methods

2.1. Field observations

In order to check the occurrence of fruits and seeds in populations of *S. aloides* in the Netherlands, several regions well known for the abundance of this species were surveyed in September 1992, June/July 1993 and September 1993.

In September 1992 and 1993, at each location 100 plants were randomly collected and carefully checked for the presence of fruits. Every fruit found was checked for the occurrence of seeds. Furthermore, in June/July 1993 stands were checked for the presence of male and female flowers and the presence of flower-visiting insects. For some stands patterns of the distribution of male and female plants in the population were mapped.

In September 1993, 100 female plants were collected from five stands in the neighbourhood of Giethoorn (De Bramen 1, 2, 3 and 3 shaded and De Auken) and a population in the neighbourhood of Gorredijk, in order to make a quantitative comparison. Part of the De Bramen 3 location was shaded by high helophyte vegetation growing along the water side; in this location a shaded as well as a non-shaded stand was sampled.

For these plants the numbers of healthy and rotten fruits per plant were determined. The length and width of 100 fruits were measured and the numbers of seeds counted. Furthermore, for the seeds collected in the Gorredijk population and for 100 seeds collected in the populations near Giethoorn, seed length and seed width were measured.

3. Results

3.1. Fruit morphology

Well developed fruits were barrel-shaped, with four to six sides and two to five ridges (Figs. 1a–1f). Two of the ridges were generally more pronounced than the others and bore spines. The mature fruits bend out of the toothed (remains of the) spathes in a very pronounced way. When mature, the inner part of the pericarp becomes pulpy and the leathery outer part bursts irregularly (Figs. 1f–1g). In some stands in the neighbourhood of Giethoorn, double and even triple fruited peduncles were found (Figs. 1h and 1i).

Poorly developed fruits without seeds were much more slender and usually bent out of the spathes to a lesser degree than well developed fruits (Figs. 1a–1b). These parthenocarpic fruits did not mature but ultimately rotted away.

Fig. 1. Fruits of *S. aloides* collected in a population near Giethoorn in the province of Overijssel (the Netherlands) in September 1992 and 1993. A, B, parthenocarpic fruits; C, D, fruits bearing seeds; E, double fruited peduncle; F, triple fruited peduncle; G, H, ripe, irregularly bursting fruits prior to seed release; I, remains of fruit after seed release. Bar represents ± 7 mm.

3.2. Occurrence of fruits and seeds

Fig. 2 shows the geographical positions of the locations in the Netherlands visited in 1992 and 1993. Stands with many seed bearing fruits were only found in the neighbourhood of the village of Giethoorn in the northwestern part of the province of Overijssel. In this region, 13 of the 19 investigated stands contained many fruits with seeds. These stands all consisted of female as well as male plants (mixed stands). The male and female plants, however, were not randomly distributed within the vegetation but showed a clustered pattern as shown in Fig. 3.

In 13 of the 48 stands investigated, fruits appeared to be absent. Five of them, all located in the Tienhoven region consisted of totally submerged stands. Although Kornatowski (1985) stated that submerged plants do not flower, in two of the five submerged stands, some partly submerged, female plants were found that were growing flowers. These flowers, however, appeared to rot away soon after opening. Inspection of the flowers of the other stands in which no fruits were found, showed that the plants of these stands were all male. In the remaining 22 stands all plants appeared to be female and bore many, mostly parthenocarpic, fruits. In 15 of these stands, some fruits with seeds were found, although in most cases less than five fruits with (few) seeds were found per 100 plants. In the remaining stands only parthenocarpic fruits were found. In entirely female stands, seeds were only found when male plants were present within a range of maximally 1 km. In one entirely female stand, located in the De Meije/Kockengen region (Fig. 2), more than half of the

Fig. 2. Geographical position of the areas and locations in the Netherlands visited in 1992 and 1993. In the locations Glimmen, Gorredijk, Breugel and Helenaveen, one stand was sampled. In the regions Giethoorn, Tienhoven and Meije/Kockengen, 19, 11 and 14 stands were sampled, respectively.

Fig. 3. Mosaic patterns of male and female plants in three mixed stands of *S. aloides* in the neighbourhood of the village of Giethoorn. Patterns were recorded in June 1993.

Table 1

Some characteristics of fruits and seeds in six *Stratiotes aloides* stands in the Netherlands, in September 1993. A, 'De Auken' near Giethoorn (entirely female stand); B, Gorredijk (entirely female stand); C, 'De Bramen 1'; D, 'De Bramen 2'; E, 'De Bramen 3'; F, 'De Bramen 3 (shaded)'. C, D, E and F are mixed stands located near Giethoorn. For all stands the parameters are determined for 100 plants collected in a zone where only female plants were encountered in June 1993

Parameter	Stand					
	A	B	C	D	E	F
% plants with fruits	40	61	54	61	58	58
No. of fruit stalks per fruit bearing plant	1.81	1.55	2.57	2.59	2.53	2.48
% rotten fruits	54	53	2	4	3	33
% fruits with 1 fruit per fruit stalk	100	100	74	82	97	99
% fruits with 2 fruits per fruit stalk	0	0	23	18	3	1
% fruits with 3 fruits per fruit stalk	0	0	3	0	0	0
Fruit length (mm)	15.7	11.8	22.1	20.8	20.0	16.4
Fruit width (mm)	7.3	6.2	13.0	13.6	11.8	11.1
% of fruits with seeds	0	13	90	89	85	40
No. of seeds per seed bearing plant	–	1.5	11.8	9.8	11.6	9.3
Seed length (mm)	–	8.56	8.64	8.61	8.50	n.m.
Seed width (mm)	–	2.64	2.60	2.68	2.58	n.m.
No. of seeds per 100 plants	0	9	1863	1558	1432	359

Fig. 4. The number of fruits per plant (A), the number of seeds per fruit (B), fruit length (C), fruit width (D) in two entirely female (De Auken and Gorredijk) and four mixed (De Bramen 1, 2, 3 and 3 shaded) stands of *S. aloides* in the Netherlands in September 1993. For all stands the parameters are determined for 100 plants collected in a zone where only female plants were encountered in June 1993.

fruits bore seeds. This stand, however, was located only 20 m from a ditch with an entirely male stand.

In Fig. 4 and Table 1, some characteristics are given for the six more thoroughly studied stands. The entirely female De Auken and Gorredijk stands differed considerably from the mixed De Bramen stands in the numbers of fruit stalks and percentage of rotten fruits. Furthermore, the entirely female stands contained more smaller fruits with only few or no seeds at all, whereas most of the fruits in the mixed stands contained seeds. In the shaded part of the mixed De Bramen 3 stand only, less than half of the fruits contained seeds. The mean number of seeds per seed-containing fruit was 1.5 in the Gorredijk stand, whereas the seed-bearing fruits in the mixed stands contained 9.3–11.8 seeds per fruit. Also, the calculated number of seeds varied considerably between the mixed and entirely female stands (Table 1). Furthermore, in the mixed stands, clear differences were observed in the amount of fruits per peduncle (one, two or three fruits per peduncle) (Table 1).

4. Discussion

In general, fruiting does not seem to be rare in (partly) female populations of *S. aloides* in the Netherlands. Although many of the plants did not have ripe seeds, in almost all regions we visited fruits were present. Although the production of seedless fruits in *S. aloides* stands is seldom mentioned in recent literature, Beguinot (1929) and Negodi (1929) described the occurrence of parthenocarpic fruits from Italian *S. aloides* stands. Their descriptions of the parthenocarpic fruits being half the size of the normal fruits are in accordance with our findings. As only developing seeds can lead to full fruit development (McLean and Ivimey-Cook, 1955), parthenocarpic fruits often remain small and rot early. Not all entirely female stands, however, produced the same amount of parthenocarpic fruits. In their review, Cook and Urmi-König (1983) reported that female spathes bear one or, occasionally, two flowers. In one of the stands near Giethoorn, however, triple fruiting peduncles were found. The distribution of plants, with one, two or three fruits per peduncle differs between the stands studied in detail (Table 1).

Although in the Netherlands the production of parthenocarpic fruits is fairly common in female *S. aloides* plants, seed setting is rather rare as only a minority of the fruits outside the Giethoorn region bore seeds. The observations prove that the female plants have to be located very near to a male stand in order to be successfully pollinated. Kernick (1961) gives data for the isolation requirements of different crop plant species. The isolation requirement for a population is the minimal distance to other populations of the same species needed to prevent cross pollination. For insect-pollinated species Kernick's isolation requirements differ between 30–60 m for *Lactuca sativa* L. and 800–3000 m for *Camellia sinensis* L. Our observations indicate that for *S. aloides* the isolation requirement is about 1 km. In general, only female plants that are closely located to male plants will bear seeds.

The clustered patterns of the mixed stands in the region of Giethoorn indicate that clonal vegetative propagation, by means of offsets and turions, is the dominant mode of propagation, even in *Stratiotes* stands producing more than 1500 seeds per 100 female plants. In 39–46% of the female plants in mixed populations no fruits were found. This relatively high number can be explained by the vegetative growth of the species. Offsets that have

been produced in July and August do not flower but have been counted in September as separate plants. Furthermore, experiments of Cook and Urmi-König (1983) and Smolders et al. (1995) show that *Stratiotes* seeds do not germinate very well. We also observed that seedlings introduced in artificial peat ponds in a greenhouse were eaten almost completely by snails of the species *Planorbarius corneus* (L.) (Planorbidae) within a few days. Another reason for the poor recruitment of *Stratiotes* from seed could be the adverse conditions in anaerobic sediments. In some stands sulphide and other phytotoxins accumulate in the sediment owing to the inlet of sulphate-rich alkaline river water. Furthermore, in these sediments, gas production weakens the sediment (Smolders and Roelofs, 1993). Germinating seeds and seedlings will suffocate because they are easily covered by sediment particles, resulting in decreased light levels and increased exposure to phytotoxins.

In the shaded part of the De Bramen 3 stand, seed production was less than in the non-shaded parts. In the shaded zone plants were observed to flower later than in the non-shaded zone, in which all male plants were located. Differences in flowering time most probably explain the strongly decreased seed production in the shaded zone.

The biggest fruits we encountered were wider (17–20 mm) than those obtained by artificial pollination by Cook and Urmi-König (1983) who mention a maximum fruit width of 15 mm. The same is true for the number of seeds per fruit; Cook and Urmi-König (1983), who pollinated the flowers artificially, reported a maximum of 24 seeds per fruit, whereas we found a maximum of 30. Given the high numbers of fruits per plant in the mixed populations in the Netherlands, the natural pollination process must have been very successful in these stands. Counts and observations on insect pollinators visiting the flowers confirmed that pollinators were abundant in every stand visited (A.J.P. Smolders, unpublished data, 1993, 1994). Daumann (1931) and Weeda et al. (1991) also describe the abundance of pollinators in *Stratiotes* stands.

Cook and Urmi-König (1983) put forward the hypothesis that seeds are produced, but subsequently eaten by fruit and/or seed eating predators. This hypothesis is based on the observation that fossil seeds are often found in coproliths. As far as the investigated stands are concerned, there is no indication of the existence of fruit or seed eating predators. No signs of predatory activity on seeds were observed. Only the larvae of the chironomid *Endochironomus gr. dispar* were found in a few fruits. As the seeds of these fruits did not show any sign of damage, it is likely that these chironomid larvae fed on the pulpy content of the fruits.

Our results confirm the statement of De Geus-Kruyt and Segal (1973) that fruits are fairly common in the Netherlands. In our experience, however, the fruits are very easily overlooked as they are not very conspicuous. Plants have to be raised from the water in order to find the fruits that grow downwards and ripen under the water surface between the decaying older leaves (Smolders et al., 1993). Further, the formation of ripe fruits takes place very late in the season and many stands of *S. aloides* are difficult to reach owing to their location.

It is not clear why the mixed stands were only found in the Giethoorn area. The conditions for the development of seedlings are relatively good as the hydrology of the region is more or less intact and the inlet of hard river water is minimal. The intensity and time of dredging which is carried out to maintain the ditches, can determine the amount of seeds left on the bottom. In most areas, *Stratiotes* ditches are dredged yearly to prevent water management

problems. When the ditches are cleaned before fruits have entirely ripened and lost their seeds, chances of recruitment of plants from seeds are limited.

In conclusion, in *S. aloides* the presence of both sexes appears to determine the availability of seeds. In many *Stratiotes* stands, however, one of the sexes is thought to be absent (Cook and Urmi König, 1983; Weeda et al., 1991). The resulting lack of generative propagation is also mentioned as a possible cause for the general decline of *S. aloides* (Weeda et al., 1991). In general, generative propagation increases genetic variability within populations (Levin, 1986) and enhances the chances of survival of a population when environmental conditions change (Hutchings, 1986). In this respect it is important to note that in the area where mixed populations of *S. aloides* were found, *Stratiotes* stands are well developed and the species is abundant in many ditches.

Acknowledgement

The authors thank A.H.N. van Duynhoven, J.B. Muntendam, L.H.T. Vergeer, R. Nijboer and Y.C.M. de Wit for assistance in the field and Prof dr. G. van der Velde and Dr. H. Moller-Pillot for identification of the chironomid larvae.

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