Studies on the seed biology of arum lily (*Zantedeschia aethiopica* (L.) Spreng.)

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Summary

Seeds of arum lily (Zantedeschia aethiopica (L.) Spreng.) have a low temperature optimum for germination and are unaffected by exposure to light. Experimental removal of the outer layer of the testa caused the majority of seeds to die before germination could occur. Viability loss was rapid during dry storage in the laboratory. In the field, no viable seeds were recovered from the soil under dense infestations when sampling was conducted several months before shedding of the seed crop.

Seed production can be prevented completely if plants are sprayed with chlorsulfuron before the infructescence begins to expand. The effectiveness of single spot-spray applications of chlorsulfuron, coupled with the lack of a persistent seed bank, account for the relative ease of obtaining local eradication of this weed.

Introduction

Arum lily (Zantedeschia aethiopica (L.) Spreng.: Araceae), native to Natal and the Cape Province of South Africa, is naturalized locally through much of Australia, but is a problem weed only in the wetter areas of south-western Western Australia. Here it invades native vegetation and can achieve dominance in swampy pastures, which otherwise would provide forage during the dry summer months (Parsons and Cuthbertson, in press). Arum lily has been held responsible for cattle deaths, presumably due to the high content of calcium oxalate in its leaves (Everist 1974). In addition, a nitrogenous base of an alkaloidal nature has been isolated from the inflorescence, spathe and flower stem (Watt and Breyer-Brandwijk 1962).

Over much of its range, property owners are required to eradicate this weed. Until recently, infestations of arum lily were treated with either ester or amine formulations of 2,4-D. Because it was necessary to spray for a minimum period of three years in order to exhaust the rhizomes (Parsons and Cuthbertson, in press), this approach achieved little acceptance on the part of land holders. However, single spot-spray applications of chlorsulfuron now generally eradicate the vegetative population (R. Madin, unpublished results).

Seeds are the major means of spread, although local spread also occurs through the proliferation of a rhizome network. Seeds are produced by cross-pollination, since plants are protandrous (Marloth 1915), and are presented in succulent orange berries (Fig. 1). They are at least occasionally dispersed by birds, as evidenced by the appearance of seedlings along fence lines, under roosts and in the forks of trees. Because nothing has been reported about the seed biology of this species, a series of studies was undertaken to investigate aspects of seed production, germination requirements and seed longevity.

Materials and methods

Seed production

Collections of ripe infructescences were made from arum lily populations at Wonnerup (33°38'S, 115°26'E), Margaret River (33°57'S, 115°00'E) and Denmark (34°57'S, 117°21'E) on 13-14 January 1986. From each collection, 15 infructescences encompassing the range of available sizes were selected. Counts were obtained of the number of developed and undeveloped berries per infructescence and the number of seeds per developed berry.

In order to assess the effects of timing of chlorsulfuron application upon seed production, an experiment was conducted at locations near Margaret River and Dunsborough (33°36'S, 115°06'E) on 5-6 November 1986. Four stages of flowering/fruit development were recognized: Stage 1 = anthesis; Stage 2 = immediately post-anthesis; Stage 3 = infructescence 33-50% final size; Stage 4 = infructescence fully expanded, yet still green. Five plants from each stage were marked and sprayed to run-off with a mixture of .02 g L^{-1} chlorsulfuron with 1:500 wetting agent. At each location the experiment was conducted at both a 'wet' (depression) and a 'dry' (hillside) site. Infructescences were collected when fully mature and counts were obtained of the numbers of seeds per infructescence. Seed viability was determined by staining with a 1% solution of tetrazolium chloride.

Germination requirements

Using the seeds collected from Wonnerup, Margaret River and Denmark, the effects upon germination of temperature, light, and partial removal of the testa were investigated. The experiment was a 5 x 2 x 2 factorial, comprising combinations of temperature regimes, light availability and presence of the outer portion of the testa. When seeds were removed from the berries they were enclosed by a delicate testa, approximately 0.5 mm thick. Since this

layer did not appear to survive passage through the digestive tracts of birds (Panetta, personal observations), removal of its outer portion was effected by gentle abrasion, leaving the tegmen intact (see Fig. 1).

Replicates of seed (n = 20) were held in Petri dishes. The seeds sat upon watchglasses, covered with filter paper, which drew water from an excess located in the bases of the dishes. The temperature regimes, established in cabinets, were 5/15, 10/20, 15/25, 20/30 and 27/35°C, with a 12 hour thermoperiod and a photoperiod of similar duration which coincided with the period of higher temperature. Darkness was maintained by enclosing dishes in three layers of aluminium foil.

Each treatment was replicated three times and the experiment commenced on 19 February 1986 (seed age = 5 weeks). With the exception of the treatments which were maintained in darkness, replicates were checked several times a week, at which times newly germinated seeds were removed. At the end of eight weeks, germinated seeds in the dark treatments were counted and all ungerminated seeds from all treatments were tested for viability as before.

Effects of seed storage

At the time of commencement of the previous experiment, seed lots from each of the three populations were divided in half and stored subsequently in paper bags in cabinets, maintained in darkness either at 25°C or at alternating 15/40°C, with a 12 hour thermoperiod. Following storage for 15 weeks, replicates (3 x 20) of seeds with intact testae were set to germinate under a 12 hour photoperiod at either 5/15, 10/20 or 15/25°C. This experiment ran for 8 weeks, after which the viability of ungerminated seeds was assessed as before.

Seed longevity

During 25-26 November 1985, prior to the maturation of the current season's seed crop at Wonnerup, Margaret River and Denmark, soil samples (20 x 20 x 15 cm) were taken within dense populations of arum lily. The soil types at the three sites were a loam, coarse sand and sandy loam, respectively, all with a high content of organic matter. A total of 15 samples was taken per site. Samples were returned to the laboratory where they were washed and/or sieved and the residual organic matter examined for seeds.

Statistical analysis

Except for the results from the seed longevity study, the significance of all main effects and their interactions was determined through analysis of variance, following data transformation when necessary.

Results

Seed production

Only small differences were apparent between populations in the parameters of seed production (Table 1). The consistently high proportions of developed berries indicated that successful pollination was associated with low levels of fruit abortion.

Significant effects of location ($P < 0.05$), site type ($P < 0.001$) and developmental stage ($P < 0.001$) upon the seed numbers of sprayed plants were observed (Table 2a). No plants produced seeds when sprayed during anthesis, although low numbers were produced when plants were treated just after anthesis (Stage 2). Sprayed plants from the dry site generally produced fewer seeds than those at the wet site, regardless of location or stage of development. Seed numbers of plants sprayed when infructescences were fully expanded (Stage 4) did not differ significantly from those of unsprayed controls.

Seed viability was markedly reduced by chlorsulfuron at every developmental stage (Table 2b). The viability of seeds from unsprayed controls was 100% at both of the Dunsborough sites and at Margaret River was 78.3% and 96.7% at the wet and dry sites, respectively. A significant ($P < 0.05$) interaction was observed between the effects of developmental stage and location upon the viability of seeds produced by sprayed plants. When the seed viability of unsprayed plants was compared with that of sprayed Stage 4 plants, all first order interactions (involving location, site type and herbicide treatment) were significant ($P < 0.05$).

Germination requirements

Highest germination of fresh seeds was obtained at the lowest test temperatures (Fig. 2). Levels of germination decreased rapidly at mean

temperatures in excess of 20°C, and germination was minimal at 27/35°C. The availability of light did not have a significant effect upon seed germination (Fig. 2). Low rates of germination were observed for all collections at all temperatures. Generally, no germination occurred until seeds had been imbibed for three weeks and cumulative germination then increased gradually over the next several weeks (Fig. 3).

The majority of seeds for which the outer layer of the testa had been removed rotted, regardless of the temperature regime (results not presented).

Effects of seed storage

Except for seeds collected at Wonnerup, marked decreases in dormancy and viability occurred over the course of 15 weeks storage (Table 3). The effect of neither storage temperature nor test temperature was significant. While small changes in cumulative germination were observed for stored seeds, germination rates were comparable to those of fresh seeds (results not presented).

Seed longevity

No viable seeds or recognizable seed parts were recovered from soil samples taken from any location.

Discussion

Although arum lily plants produce large numbers of viable seed, these appear to be short-lived. The relatively low temperature optimum for germination (Fig. 2) should restrict germination to the autumn and winter months immediately following the period of seed production. For seed collections from Margaret River and Denmark, viability loss occurred so quickly during dry storage (Table 3), that a significant proportion of one year's seed production could lose viability prior to the onset of the winter rains. The depletion of seed pools due to germination, loss of viability and, possibly, seed predation would account for the failure to detect viable seeds in the soil several months (November) before the ripening of new fruits (January). Because seeds do not survive between years, if adult plants are killed before they produce viable seed, a site should remain free of arum lily until it is recolonized. This is in accordance with observations made following spot-spray applications of chlorsulfuron in the Busselton/Margaret River region (M. Sparrow, pers. comm.).

In order to prevent the production of viable seeds, arum lily populations should be treated before the infructescenses of the most advanced plants have developed to any extent. The time of spraying is not as critical in relatively dry sites, where chlorsulfuron appears to be more effective (Table 2). This type of site may be regarded as marginal for the species, however. Since all plants at a location were sprayed on the same day, it was not possible to test for the interaction between chemical treatment, stage of development and time of year. However, it is doubtful whether the reproductive fates of plants would be greatly affected by such an interaction, provided they were sprayed during the flowering or early fruiting stages.

The high frequency of seed death following removal of the outer layer of the testa was surprising. I suspect that this result is an artefact of the experimental conditions (i.e. incubation within Petri dishes). However, in order to define the roles of animals in the spread of arum lily, further work is necessary to determine:

a) what proportion of a seed crop is consumed by birds and other animals, and

b) how many seeds survive ingestion.

Acknowledgments

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References

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Table 1 Seed production characteristics of unsprayed arum lily plants

Location	No. of berries infructescence^{-1}	No. of seeds berry^{-1}	No. of seeds infructescence^{-1}	Percentage of developed berries infructescence^{-1}
Wonnerup	40.9	4.4	181	88.8
Margaret River	53.6	4.0	217	73.5
Denmark	50.6	3.4	176	83.5
LSD (P = 0.05)	9.1	0.8	NS	11.0

Table 2 Seed production of arum lily plants sprayed with chlorsulfuron at different stages of flowering or fruit development

Location	Wet Site Stage				Dry Site Stage			
	1	2	3	4	1	2	3	4
a) Seeds infructescence^{-1}								
Margaret River	0.0(0.0)	37.2(1.00)[A]	76.6(1.87)	355(2.47)	0.0(0.0)	1.0(0.16)	53.6(1.65)	56.8(1.73)
Dunsborough	0.0(0.0)	45.0(1.11)	83.6(1.87)	470(2.66)	0.0(0.0)	13.6(0.82)	67.8(1.79)	119 (2.28)
LSD (P = 0.05)								
Location main effect	(0.24)							
Site type main effect	(0.24)							
Stage main effect	(0.29)							
b) Seed viability (%)								
Margaret River	-	5.0(10.4)[B]	40.0(39.1)	60.0(51.0)	-	0.0(0.0)	6.7(11.9)	36.7(36.9)
Dunsborough	-	5.0(10.4)	8.3(13.2)	28.3(31.3)	-	0.0(0.0)	1.7(4.3)	1.7 (4.3)
LSD (P = 0.05)								
Location main effect	(5.9)							
Site type main effect	(5.9)							
Stage main effect	(7.2)							
Location x stage interaction	(10.3)							

A Values in parentheses are log (x + 1) transformations.

B Values in parentheses are arcsin transformations.

Table 3 Changes in status of arum lily seeds following storage for 15 weeks at 15/40°C

Source	Fresh	Stored
a) Dormant seeds (%)[A]		
Wonnerup	5.0 (10.4)[B]	6.7 (14.8)
Margaret River	41.7 (40.1)	3.3 (8.6)
Denmark	38.3 (37.6)	1.7 (4.3)
LSD (P = 0.05)		
Location main effect		NS
Seed age main effect		(9.0)
Location X seed age interaction		(15.6)
b) Inviable seeds (%)		
Wonnerup	8.3 (16.6)	18.3 (25.3)
Margaret River	8.3 (16.6)	81.7 (64.8)
Denmark	28.3 (30.1)	73.3 (59.2)
LSD (P = 0.05)		
Location main effect		(12.4)
Seed age main effect		(10.1)
Location X seed age interaction		(17.5)

A Dormant seeds failed to germinate during incubation for 8 weeks at 5/15°C.

B Values in parentheses are arcsin transformations.

Figure captions

Figure 1 Drawings of (a) infructescence and (b) longitudinally sectioned seed of arum lily (from Engler (1915)).

Figure 2 Temperature responses of arum lily seeds collected from (○ , ●) Margaret River, (□ , ■) Wonnerup and (△ , ▲) Denmark and either (○ , □ , △) exposed to light or (● , ■ , ▲) maintained in continuous darkness.

Figure 3 Time course of germination of arum lily seeds collected from (○) Margaret River, (□) Wonnerup and (△) Denmark and maintained under a 12 hour photoperiod at 5/15°C.

Fig. 1

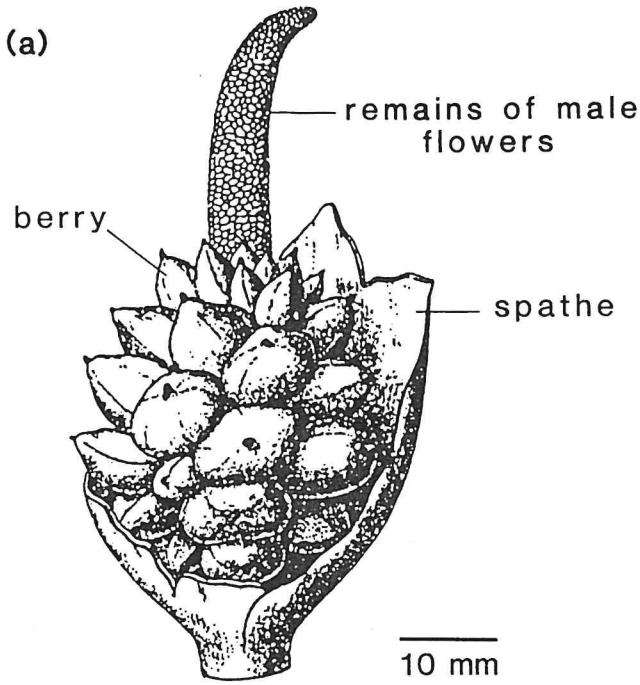
(a)
remains of male flowers
berry
spathe
10 mm
(b)
outer testa
tegmen
embryo
1 mm

Fig. 2

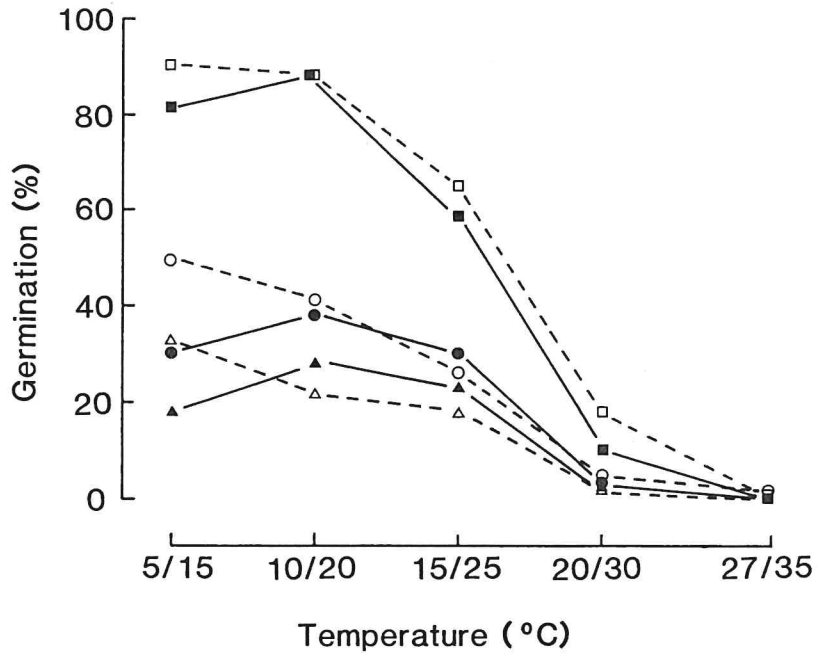
100
80
60
40
20
0
Germination (%)
5/15
10/20
15/25
20/30
27/35
Temperature (°C)

Fig. 3