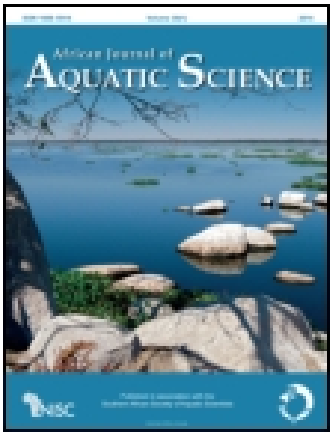

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Seed dynamics and control of Pistia stratiotes in two aquatic systems in Botswana

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Seed dynamics and control of *Pistia stratiotes* in two aquatic systems in Botswana

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The fruiting and seed dynamics of the alien invasive aquatic species *Pistia stratiotes* L. (water lettuce; Araceae) was investigated in the seasonally flooded Selinda Canal and Zibadianja Lake of the Kwando–Linyanti River system and in the perennial Chobe River, Botswana, in 1999–2003. The mean number of 30.3 seeds fruit^{-1} in the Selinda Canal is the highest ever recorded. An artificial earthen barrier or dyke was constructed on the Selinda Canal to allow manipulation of water levels downstream. By drying and subsequently reflooding a region of the stream, seed germination was stimulated, followed by the manual removal of water lettuce seedlings before their seeds reached maturity, which resulted in a decline in seed germination in surface sediment samples from 63.5% in 2002 to 31.7% in 2003. Manipulation of flooding, followed by the physical removal of *P. stratiotes* at regular intervals prior to anthesis and seed maturity, is considered the most viable strategy for arresting further additions to the seed bank, and could lead to its eradication in seasonally flooded areas where the biocontrol weevil *Neohydronomus affinis* has become locally extinct since its introduction in 1987.

Keywords: biocontrol, eradication, germination, seed bank, Selinda Canal

Introduction

Water lettuce *Pistia stratiotes* L., Araceae, is a flowering invasive aquatic floating weed of South American origin (Dray et al. 1993; Cordo and Sosa 2000). The plant consists of a rosette of velvety, light-green, hairy, ribbed leaves, with long feathery submersed roots hanging from a small rhizome. Flowers, clustered on a small fleshy stalk nearly hidden amongst the leaf axils, occur as a spathe with a single female flower below and a whorl of 4–9 male flowers above. The fruit is a many-seeded green berry (Buzgo 1994).

The species has a worldwide distribution in the tropics and subtropics (Parsons and Cuthbertson 2001), even growing in temperate areas in central Europe (Sajna et al. 2007). The weed is capable of developing dense infestations, impeding fishing and boat transport, adversely affecting dams and wetlands. Water lettuce responds very well to increased nitrogen and phosphorus in the water column, which enhances growth (Diop and Hill 2009). Control of *P. stratiotes* has been successfully achieved in many countries worldwide by using the host-specific biocontrol weevil *Neohydronomus affinis* Hustache (Neuenschwander et al. 2009), as well as in African countries such as Botswana (Forno 1987), Congo (Mbati and Neuenschwander 2005), Senegal (Diop and Hill 2009), South Africa (Cilliers et al. 1996, 2003) and Zimbabwe (Chikwenhere and Forno 1991; Chikwenhere 1994).

The main mode of propagation of *P. stratiotes* is via stolons (Lallana 1989), but seed formation seems the only way for it to survive periods of drought (Hollander et al. 1999). Seeds are released and scattered onto the root mass by the decay of the fruit wall and sink to the substrate where they are covered by decomposing roots and leaves (Buzgo 1994). Seeds can survive for at least two months at 4 °C and for several weeks at −5 °C (Neuenschwander et al. 2009). They do not germinate at temperatures <20 °C, but germinate readily in shallow warm waters >20 °C under high light intensities (Pieterse et al. 1981). It was originally thought that water lettuce did not produce viable seeds, but seed production has now been confirmed in Africa (Neuenschwander et al. 2009), India (Mitra 1966), South America (da Silva 1981), the USA (Dray and Center 1989), South-East Asia (Bua-ngam and Mercado 1975) and central Europe (Sajna et al. 2007). However, seed banks have not thus far been reported in southern Africa.

The first occurrence of *P. stratiotes* in Botswana was recorded in the Chobe River, and in Zibadianja Lake and Selinda Canal on the Kwando River, in 1986 (Forno 1987; Kurugundla 2000). As a response, the Botswana Department of Water Affairs imported 437 individuals of the biological control weevil *N. affinis* in 1987 from the Commonwealth Scientific Industrial Research Organisation (CSIRO), Australia (Forno 1987). Upon their arrival, the weevils were mass-reared in artificial pools and released on *P. stratiotes* infestations in the Selinda Canal in November 1987, and three months later in Zibadianja Lake and the Chobe River. However, no post-release evaluation has been carried out.

The objective of this study was to determine the presence and viability of *P. stratiotes* seeds in these two aquatic systems, and to develop a long-term control strategy for this weed in Botswana.

Materials and methods

Study sites

The study was conducted in the seasonally flooded Selinda Canal (18°32'03.5'' S, 23°3'47.8'' E) and Zibadianja Lake (18°34'39.4'' S, 23°32'27.3'' E) in the Kwando River, and at a site (17°58'14.6'' S, 24°27'23.5'' E) on the perennial Chobe River (Figure 1a). The region normally receives its rain between the months of November and March.

Selinda Canal

Between February and July from 1990 to 1998 the weed infestation was sporadic because of low-flood events in the Kwando River (Kurugundla et al. 2010). The weed increased to a thick infestation covering the Selinda Canal for a distance of 2.7 km (0.230 km^2) in 1999 and 0.248 km^2 in 2000 (Figure 1b), as a result of above-average rainfall at Selinda (554 mm in 1999, 656 mm in 2000) and higher flows in the Kwando River (Kurugundla et al. 2010) reaching the weed-infested areas out of Dumatau Lake (Figure 1a). The width of the canal along its infested section was c. 10–20 m, and the depth ranged from 1.0 to 1.7 m in the flood season.

Manipulation of downstream water levels

In September 1999 an artificial earthen barrier or dyke was constructed across the Selinda Canal well upstream of the point of infestation using earth-filled plastic bags (Figure 1b). This provided an opportunity to dry out the canal and to regulate the water flowing downstream as and when required between 1999 and 2003. The seedlings that germinated in the canal downstream of the barrier were physically removed between 1999 and 2003.

Zibadianja Lake

The area of Zibadianja Lake is 1.857 km^2. Survey records in the Department of Water Affairs showed that *P. stratiotes* had been sporadic in occurrence since the 1990s in the western part of the lake in low-flood events of the Kwando River. The above-average rainfall in 1999 and 2000, with high discharge in the Kwando River (Kurugundla et al. 2010), favoured weed re-infestation from the seed bank in the western part of the lake in November 1999, resulting in a 0.065 km^2 mat of water lettuce (Figure 1b). Between November 1999 and March 2000 the weed was removed manually, dried and burnt. The water did not reach the site in 2001 and 2002, and therefore the weed was not observed. The lake was completely dry by June 2003, and refilled in December 2003 after the clearance of vegetation blockages in the lake's supplier streams (Kurugundla et al. 2010). Seeds of *P. stratiotes* in the sediment on the bed of the lake germinated and the weed spread, forming a 0.48 km-long by 5–7 m-wide (0.003 km^2) mat in January 2004 (Figure 1b). The weed was manually removed between January and March 2004, prior to its seed maturation.

Chobe River

The Chobe River, which forms the border between Botswana and Namibia (Figure 1a), connects to the Kwando–Linyanti

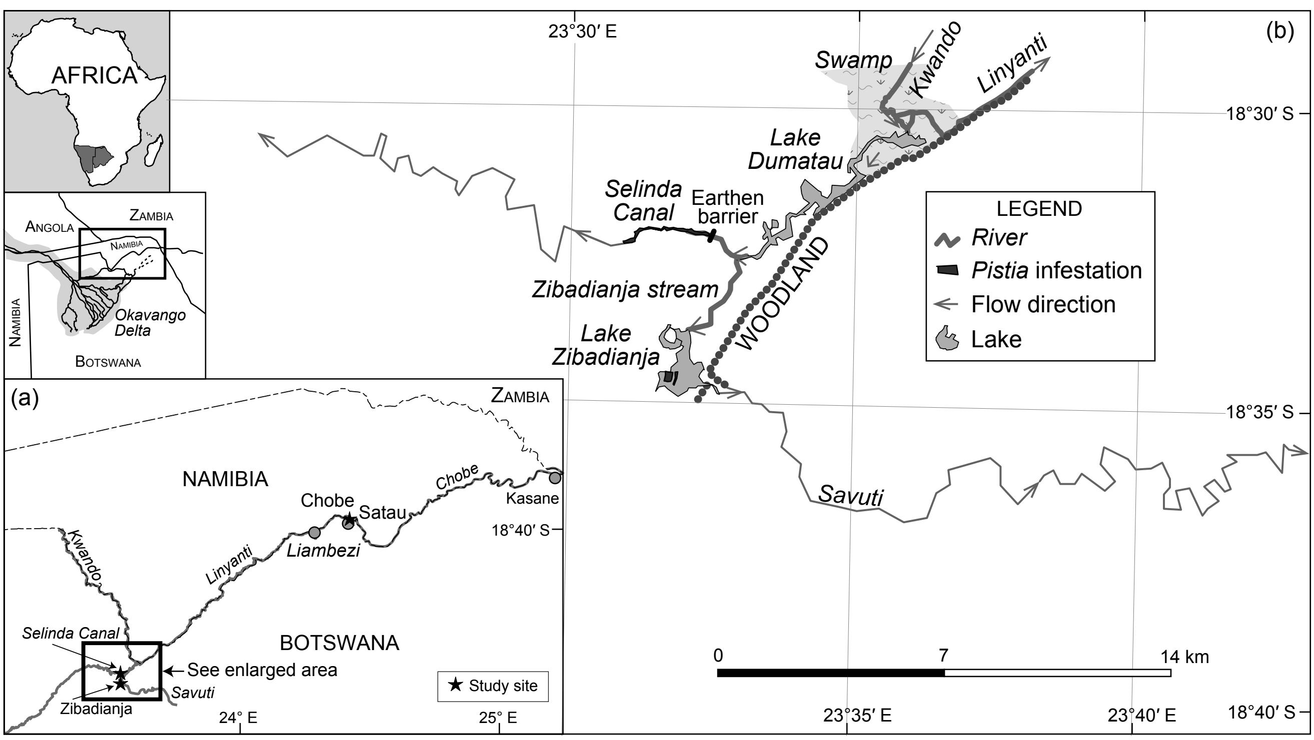

Figure 1: (a) Sites of *Pistia stratiotes* infestation in Selinda Canal and Zibadianja Lake on the Kwando River and at the Chobe site on the Chobe River; (b) details of location of *P. stratiotes* infestation in Selinda Canal and Zibadianja Lake between 1999 and 2004

River system via Lake Liambezi in Namibia. The hydrology of the system depends on the relative flood levels in the Zambezi River. *Pistia stratiotes* was first recorded in the Chobe River in 1986. In 2000, isolated patches of *P. stratiotes* with its biological control weevil were observed in a 3.4 km-long infestation in Chobe River close to Satau village (Figure 1a). The release of the weevil *N. affinis* at this site in 1987 has kept the weed under control since that time. Seeds of *P. stratiotes* were observed on drying river banks during flood recessions.

Seed collection and germination

Seeds were collected on the plants and in the soil sediment for germination to determine the difference in percentage seed viability between the seeds on plants and seeds in canal bed. In general, the seeds were observed mostly on the surface of the soil bed, associated with the decomposing *P. stratiotes* leaves.

Soil germination

One soil sample of up to 10 cm depth was collected from the soil surface in each 0.5 m × 0.5 m quadrat at 12 random sites in the infested area of Zibadianja Lake on 4 November 2000. Soil samples were also collected at 16 sites along the infested Selinda Canal on 19 December 2002 to determine the rate of seed germination. The soil of each sample was mixed well and a subsample of 1 kg was taken.

Seed germination experiments were carried out in a greenhouse, using plastic containers of 50 cm diameter and 20 cm depth. The 1 kg soil samples were placed in the plastic containers and filled with water to 6 cm below the container rim. The soil-water contents were stirred until the dry seeds floated. The floating seeds were counted and placed back into their respective containers to determine the germination rate.

Laboratory studies

The numbers of fruits per plant on 25 random plants and seeds per fruit in 25 randomly collected fruits were determined in Selinda Canal in March 2000 and at the Chobe River site in October 2001. However, the seed germination rates under laboratory conditions were conducted only for Selinda seeds.

Seeds on fruits were initially collected in Selinda Canal in April, May and June 2002 for germination studies. In most cases, the seeds of *P. stratiotes* were found scattered on the roots as a result of the decay of the fruit wall. About 430 such seeds were collected from roots in the Selinda Canal on 22 August 2002, dried in sunlight for a day and then germinated under laboratory conditions. After opening the earthen barrier in late August 2003, floodwater occupied the downstream Selinda Canal. About 350 floating seeds were collected in the canal on 4 September 2003, dried in sunlight and germinated under laboratory conditions. In the germination experiments, 50 seeds were spread onto filter paper in a Petri dish and covered with 1 cm of water. The seeds in Petri dishes ($n = 6$ for each study site) were exposed to intermittent sunlight for 6 h a day in the laboratory and they were watered periodically during the germination period of 15 days.

Plant biomass and Neohydronomus affinis

The prevalence of *N. affinis* on weeds, at 15 random sites each in the Selinda Canal (March 2000), at Zibadianja Lake (November 1999), and at Chobe River (October 2001), was determined using Berlese funnels (Boland and Room 1983). The plant rosette density (no. m^{-2}) and sun-dried biomass (kg m^{-2}) were recorded at the same time, as well as the number of stolons plant^{-1} in the Selinda Canal and at the Chobe site.

Data analysis

Student's *t*-test was used to determine the significance of differences in fruits plant^{-1}, seeds fruit^{-1}, plant density and dry biomass between the Selinda Canal and Chobe River infestations (Snedecor and Cochran 1989). Arc Map 10 was used to prepare maps and determine the area infested by the weed in km^2.

Results

The time taken for the emergence of the first leaf in the germinating seedlings was 13–15 days in the field as well as in the laboratory experiments. Mean soil seed bank germination rates in Zibadianja Lake and Selinda Canal were very similar (Table 1). However, the rate of germination of the

Table 1: Mean number (± standard error) of fruits plant^{-1} and seeds fruit^{-1} in Selinda Canal and Chobe River, viability of seeds collected from the beds of Zibadianja Lake and Selinda Canal, and germination percentages of seeds obtained from plants and floating seeds from Selinda Canal

	Seed and fruit production		
	Selinda Canal[x] ($n = 25$)	Chobe River ($n = 25$)	Significance level
No. fruits plant^{-1} (range)	5.4 ± 0.2 (3–7)	4.3 ± 0.3 (2–6)	$p < 0.005$
No. seeds fruit^{-1} (range)	30.3 ± 1.4 (18–42)	19.9 ± 2.2 (4–37)	$p < 0.001$
	Germination success rate		
Soil-germination studies	Zibadianja Lake ($n = 12$)	Selinda Canal[x] ($n = 16$)	
	Nov. 2000	Dec. 2002	
	62.6% ± 4.5%	63.5% ± 5.5%	
Laboratory studies ($n = 6$)	Zibadianja Lake	Selinda Canal[x]	Selinda Canal[x]
	2001–2003	Aug. 2002	Sep. 2003
	Dry	88.8% ± 3.5%	31.7% ± 2.9%

[x] *N. affinis* absent

Table 2: Area of *Pistia stratiotes* infestation, mean ± SE plant number, dry biomass, stolons plant^{-1} and weevil density in Selinda Canal, Zibadianja Lake and Chobe River, Botswana

Site	Year	Area of infestation (km^2)	Plant no. (m^{-2})	Dry biomass (kg m^{-2})	Stolons (plant^{-1})	Weevil no. (kg^{-1})
Selinda Canal	1999	0.230	–	–	–	Absent
	2000	0.248	72.6 ± 2.4	0.49 ± 0.09	5.2 ± 0.3	Absent
Zibadianja Lake	1999	0.065	74.1 ± 3.2	0.61 ± 0.05	–	Absent
	2004	0.003	–	–	–	Absent
Chobe River	2001	–	*34.6 ± 1.0	*0.31 ± 0.01	*2.4 ± 0.2	8.2 ± 2.2

* Significant difference between the Selinda Canal and Chobe River ($p < 0.001$)

floating seeds collected in September 2003 in Selinda Canal in the new flood was 31.7% ± 2.9% (Table 1). Similar studies on *P. stratiotes* were not conducted in Zibadianja Lake after April 2000, as the lake remained dry until 2003.

Seeds in fruits collected in the Selinda Canal in April, May and June 2002 did not germinate, whereas the seeds collected in August 2002 germinated and showed 88.8% ± 3.5% germination under laboratory conditions (Table 1).

A significant difference ($p < 0.005$) was observed in the mean number of fruits plant^{-1} between the Selinda Canal (5.4; SE 0.2) and Chobe River (4.3; SE 0.3) (Table 1). The average number of seeds fruit^{-1} in the Selinda Canal (30.3; SE 1.4) was significantly higher ($p < 0.001$) than in the Chobe River (19.9; SE 2.2) (Table 1).

The biocontrol weevil was absent from the Selinda Canal and Zibadianja Lake in all sample years, whilst an average of 8.2 (SE 2.2) weevils kg^{-1} fresh weight of the weed were recorded in the Chobe River in 2001 (Table 2). The plant rosettes were dense in the Selinda Canal and the mean number of plants (72.6 m^{-2}; SE 2.4) was significantly higher ($p < 0.001$) than in the Chobe River (34.6 m^{-2}; SE 1.0). Correspondingly, the dry biomass of the plant material was also high in the Selinda Canal (0.49 kg m^{-2}; SE 0.09) compared to that in the Chobe River (0.31 kg m^{-2}; 0.01). The plant number and biomass values in Lake Zibadianja were comparable with those of Selinda Canal (Table 2). There was a significant difference ($p < 0.001$) between the average number of stolons plant^{-1} in the Selinda Canal and the Chobe River (Table 2).

Discussion

Seed production

Depending on the conditions, seed production has been observed in *P. stratiotes* in both South and North America, Asia and Africa (Neuenschwander et al. 2009) and in temperate central Europe (Sajna et al. 2007). The presence of a persistent seed bank at the infested sites has not been reported in southern Africa, but was observed in this study at the infested areas of the Selinda Canal, Zibadianja Lake and Chobe River. The seeds remain dormant for months in dry sediments (Bua-ngam and Mercado 1975; Dray and Center 1989), can withstand both freezing and drought (Pieterse et al. 1981; Kan and Song 2008) and readily germinate when rehydrated during rains and wet periods (Neuenschwander et al. 2009). The high rainfall in the Selinda Canal area in 1999 and 2000, coupled with above-average discharge outflows of the Kwando River (Kurugundla et al. 2010), induced the germination of seeds from the seed bank in the Selinda Canal. The plant surface cover of 0.065 km^2 in Zibadianja Lake was physically removed and burnt between November 1999 and April 2000, whereas in the Selinda Canal the removal of the plants occurred from 1999 until 2003.

Pistia stratiotes produces flowers throughout the year in perennial waterbodies, and seeds were recorded in summer in South Africa (Neuenschwander et al. 2009). As observed from 1999 to 2002, flowering was induced from March to June depending on the arrival of flood, completing the weed's growth cycle with the production of a higher number of mature seeds fruit^{-1} in the Selinda Canal than in the perennial Chobe River. The number of seeds per fruit at these two sites (range of 18–42 in the Selinda Canal and 4–37 in the Chobe River) is the highest on record. In South Africa, one fruit has been recorded plant^{-1} with 4–6 seeds fruit^{-1} (MP Hill, Rhodes University, pers. comm., 2010), while 4–11 seeds fruit^{-1} have been reported in Australia (Harley 1990), 4–9 seeds fruit^{-1} in Brazil (da Silva 1981), 6–10 seeds fruit^{-1} in India (Mitra 1966) and 2 fruits in a rosette with a range of 1–17 seeds fruit^{-1}, averaging 4 seeds fruit^{-1}, in the USA (Dray and Center 1989). The greater number of fruits plant^{-1} and high production of seeds fruit^{-1} in densely crowded rosettes in the Selinda Canal, compared to those in the Chobe River, show the weed's greater potential for seed production in seasonally flooded areas in Botswana compared to those in other countries. *Pistia stratiotes* plants produce a high number of reproductive structures under densely crowded conditions (Coelho et al. 2005) and rapid seed production has been observed under high-salinity conditions associated with drought in the Senegal River (Hollander et al. 1999).

Soil seed bank

In *P. stratiotes*, the time of 13–15 days taken for seed germination to the first-leaf seedling stage in the Selinda Canal and in laboratory studies is in contrast to that of water hyacinth seeds, which germinate in 3–4 days (Perez et al. 2011). Dray and Center (1989) reported 80% seed germination in *P. stratiotes* in Florida, USA. The higher rate of germination of the seeds found on the root masses in the Selinda Canal in August 2002 (88.8% ± 3.5%) compared to that of the soil germination studies (63.5% ± 5.5%) is possibly due to the fact that during dormancy in the field some of the seeds might be damaged by a combination of biotic and abiotic factors. Small insects, snails and other organisms generally feed on the seeds of wetland plants (Lallana 1989). Cook (1996) reported that small animals eat the seeds of *P. stratiotes*. Furthermore, Datta and Biswas (1970) observed that low O_2 and high CO_2 levels in the bottom mud prevented the germination of aquatic plant seeds. The seeds in the channel bed generally dehydrate slowly, because the wet canal dries slowly. Kan and Song (2008) reported that seeds subjected to slow dehydration resulted in 62.5% germination, showing that seeds of *P. stratiotes* could tolerate dehydration. This strongly suggests that the seed bank is an important factor in the dynamics of *P. stratiotes* populations in the seasonally flooded areas. Similar results have been reported in the USA (Dray and Center 1989), while Sajna et al. (2007) proved the viability of seeds collected from the seed bank, but did not find seedlings occurring under natural conditions in Slovenia, central Europe.

Control of Pistia stratiotes

During the study period, between 1999 and 2003, incoming floods were regulated twice a year at the artificial earthen barrier in the Selinda Canal from February to August to allow the seeds on the channel bed to germinate from the seed bank. The ability to control the water flow at the artificial earthen barrier in the Selinda Canal facilitated seed germination so that the manual removal of seedlings following germination depleted the seed bank. The similar rates of soil germination in Selinda Canal and Zibadianja Lake indicated that the seed bank had been present over a period of time in these two seasonal waterbodies. The dramatic decline in the germination rate in September 2003 (31.7%) in the Selinda Canal was mainly caused by the reduced production of viable seeds due to the continuous physical removal of the weed prior to seed maturity, preventing further additions to the seed bank. Physical removal continued until 2005 and no plants were observed after 2006. Provided that this practice can be continued long enough, and that the site is monitored, the desired outcome of driving the species to local extinction is likely. As an additional measure, an approximately 300 m wide band of *Phragmites australis* (Cav.) Steud beds was uprooted, dried and burnt, in order to inactivate any hidden seed bank.

The weevil became locally extinct in the seasonally flooded areas of the Selinda Canal and Zibadianja Lake, as it lost its food source due to the cycle of wet and dry regimes. Cilliers et al. (1996) reported that the weevil had a limited impact in seasonally flooded areas infested with *Pistia*, and suggested that the weed should be controlled either by herbicides or by reintroducing the weevil. In the Chobe River, the low density of plants m^{-2}, and a lower number of fruits $plant^{-1}$, seeds $fruit^{-1}$ and stolons $plant^{-1}$, may be attributed to the occurrence of weevils on the *P. stratiotes* plants there.

During the study period, when water in the seasonal wetland was drawn down artificially and seedling germination took place, baboons uprooted the plants and fed selectively on the rhizomes of *P. stratiotes*, resulting in the death of the seedlings. Thus, the possible role of baboons in assisting in the control of *P. stratiotes* requires further investigation.

Conclusion

The survival of seeds examined in this study in Selinda Canal and Zibadianja Lake demonstrated the regeneration capacity of the weed in seasonal waterbodies. After this study, only about 80 plants were removed in the 2004 growing season, only four plants were removed in 2005 and none were noticed afterwards in the Selinda Canal and Zibadianja Lake. We conclude that the manipulation of water levels plus the physical removal of the weed at regular intervals prior to anthesis is an effective way to control or eradicate *P. stratiotes* in seasonal waterbodies.

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