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Suppression of germination and establishment of native annual rice by introduced para grass on an Australian monsoonal floodplain

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Summary

The native annual wild rice (*Oryza meridionalis*) underpins the vertebrate food chain on the monsoonal floodplains of northern Australia. It is being displaced by the exotic perennial para grass (*Urochloa mutica*). This study reports on a field experiment, where wild rice seed was sown into 1 m² quadrats of established para grass. Para grass cover was manipulated above the wild rice seed bed, including clipping and herbicide application. The behaviour of wild rice seed under para grass cover in this study was then compared to its behaviour under wild rice cover in a previous study.

***Oryza meridionalis* plants did not establish under para grass treatments, including herbicide treatments that successfully killed para grass. Retrieval of buried bags of wild rice seeds revealed that germination was suppressed. Although 40% of seeds remained viable in the soil for more than 2.5 years, suppressed germination prevented establishment of *O. meridionalis* populations. Under wild rice cover most seed germinated by this time.**

High biomass and complex architecture of para grass cover may modify the seedbed, preventing wild rice seeds receiving dormancy-breaking or germination cues. Simply spraying established para grass with herbicide may not allow re-establishment of wild rice. Additional site treatments may be required for re-establishment by *O. meridionalis* in wetlands managed for biodiversity.

Keywords: *Oryza meridionalis*, biomass, seed-bank, germination, dormancy, invasive grass, monsoonal wetlands.

Introduction

There is a pressing need for information on the ecology of floodplain species and their use in the management and rehabilitation of areas affected by exotic species. Given the limited resources to manage the extensive monsoonal floodplains in northern Australia, it is critical to focus resources on effective management actions that will promote native species with high conservation value (Byers *et al.* 2001).

Oryza meridionalis Ng (wild rice) is an ecologically important annual native wetland grass on the monsoonal floodplains of northern Australia. *O. meridionalis* seed production underpins the vertebrate food-chain at a critical time during the annual floodplain wetting and drying cycle. Magpie geese (*Anseranas semipalmata*) rely on the abundant *O. meridionalis* seed in the mid to late wet season when young accompany their parents in the move across the floodplains to permanent water (Frith and Davies 1961, Bayliss and Yeomans 1990, Whitehead and Tshirner 1990, Wurm 1998a, Whitehead and Dawson 2000). Dusky plains rats (*Rattus collettii*), themselves an important food resource for predators such as the water python (*Liasis fuscus*), also exploit *O. meridionalis* seed in the mid to late wet season as the water levels recede (Redhead 1979, Wurm 1998b, Madsen *et al.* 2006).

Abundant *O. meridionalis* seed is produced in the mid to late wet season, when the floodplain soils are still inundated or moist. The epidermal hooks on the awn and husk around its seeds assist their movement after dispersal through extant vegetation cover and into the inundated or wet soil. Dormancy ensures that they do not germinate in response to this initial moisture, and *O. meridionalis* populations persist only in the soil seed bank during the dry season. Eventually seed dormancy is broken and germination occurs during early wet season rains in subsequent years (Wurm 1998a).

The introduced perennial para grass (*Urochloa mutica* (Forrsk.) Nguyen) is displacing *O. meridionalis* in the Northern Territory (Wilson *et al*. 1990, Ferdinands *et al*. 2001). Para grass was introduced to the monsoonal floodplains of the Northern Territory for cattle pasture in the early 1890s (Miller and Redfern 1982, Cameron 1991, Cameron and Lemke 2002), but is now dispersed beyond grazed landscapes (Wilson *et al*. 1990, Cowie and Werner 1993, Clarkson 1995). Furthermore, the area covered by para grass is increasing. On the Magela Floodplain in the World Heritage-listed Kakadu National Park, its distribution tripled in size to cover an area of over 420 ha in the five years between 1991 and 1996, in areas which previously supported wild rice populations (Knerr 1996). Ferdinands *et al.* (2001) predicted that it will become even more widespread on the adjacent, nationally significant Mary River floodplain. This expansion is most likely to occur into floodplain habitat occupied by wild rice (Wilson *et al.* 1990, Ferdinands *et al.* 2001).

Once established, para grass forms dense stands in which other plant species are uncommon (Ferdinands *et al*. 2001), and produces much higher above-ground biomass than many native floodplain species (Finlayson 1991, Baruch 1994, Bunn *et al*. 1998, Tomar *et al.* 2003, Douglas and O'Connor 2004). In the Northern Territory para grass is free from pests and diseases (Cameron and Lemke 2002) and maintains green growth through much of the year (Miller and Redfern 1982, Cameron 1991). Its capacity to produce a dense mono-specific cover (Miller and Redfern 1982, Bunn *et al*. 1998, Ferdinands *et al.* 2001, Chamberlain 1983) is a risk to biodiversity in wetlands (Whitehead *et al*. 1990, Humphries *et al.* 1991, Clarkson 1995, Knerr 1996, Groves and Willis 1999, Whitehead and Dawson 2000, Ferdinands *et al*. 2001).

Previous studies around the world have shown that the presence of above ground biomass (cover and litter) significantly effects vegetation biodiversity (Fynn *et al*. 2004), and cover and litter have been shown to effect germination and/or emergence from the soil seed bank (Harper 1977, Fowler 1988, van der Valk and Pedersen 1989, Xiong and Nilsson 1999, Vranjic *et al.* 2000, Jutila and Grace 2002, Clark and Davison 2004). The nature and magnitude of the effect varies with the type, depth and mass of litter present (Xiong and Nilsson 1999). The mechanism for this effect may be through altered soil properties such as temperature (Thompson *et al*. 1977, Abrecht and Bristow 1990, Koto *et al*. 1992), moisture, through prevention of light cues for germination reaching seed in or on the soil (Grime 1979 p. 92 ff, Insausti *et al.* 1995, Grace *et al*. 2000), or as a physical barrier to seedling emergence (Grime 1979, van der Valk 1986).

Control of native plants by invasive species at the population level is predicted and hypothesized, but has rarely been measured (Gordon 1998). This study approaches the displacement of an important native grass from a population perspective by investigating the seed bank behaviour of the annual *O. meridionalis* under para grass cover, and comparing this with its behaviour under wild rice cover. It has an explicit management focus for areas of conservation value where para grass has already established. If the mechanism for the suppression and displacement of wild rice is via cover, then it may be possible to ameliorate this by the timely manipulation of para grass cover, for example with herbicide, and the re-introduction of native species by seed-sowing. However, if the mechanism for suppression and displacement is more complex, or if the effects of the type, depth and mass of litter under para grass cover on the seed bed itself are significant, additional or alternative management strategies will have to be employed.

The specific question to be addressed in this study is: Does disturbing the cover of para grass allow germination and establishment of *O. meridionalis*? The study compares germination and establishment of *O. meridionalis* in undisturbed wild rice populations, obtained from a previous study, with that under a treated cover of para grass. Thus the study investigates the impact of a typical management strategy (herbicide treatment), albeit at a small scale, while recording the population-level behaviour of a native annual in the presence of this treatment strategy.

Methods

The study was undertaken on floodplains in the wet-dry tropics of northern Australia. The average rainfall is approximately 1485 mm, most of which falls between December and March (the wet season) each year, followed by a period of almost no rain (the dry season). The mean maximum and minimum temperatures are 34°C and 22°C respectively (Figures for Jabiru township; Australian Bureau of Meteorology 2005). At the study areas, floodplains are inundated from approximately January to June/August each year, although the exact periods of inundation vary among years (Taylor and Tulloch 1985). The floodplains are underlain by vertisols of heavy, black, cracking clays.

Para grass sites used to test effects of disturbing cover on Oryza meridionalis germination and establishment

Para grass sites were located approximately 75 km east of Darwin, Northern Territory, located in the Mary River Conservation Reserve, on the Mary River floodplain in the wet-dry tropics of northern Australia (12°19'S, 131°34'E). These para grass stands have been established for approximately 20 years (Robert Townsend personal communication 2003).

Two para grass sites, approximately 2 km apart, were selected in the northern catchment of the Mary River. Selection criteria for sites were: (a) an established cover of para grass, (b) the potential for the site to support *O. meridionalis*, as indicated by water depth at the time of survey and the occurrence of wild rice nearby, and (c) accessibility for researchers during the wet and dry seasons. Although surrounded by pastoral leases, and conditionally made available for grazing, the sites were not heavily grazed, due to the distance from water in the dry season. Some feral pigs were present in the area, and damaged some replicate quadrats during the course of the study.

At each para grass site, fifteen (15) permanent 1 m × 1 m quadrats were randomly selected and marked.

Assessment of Oryza meridionalis seed viability

Oryza meridionalis seed was collected in April 2002, just prior to being used in the para grass study quadrats. Germinability of this fresh seed was first assessed in the laboratory. It is known that seeds are dormant when shed, and that this dormancy is controlled by the husks (Wurm 1998a). Thus to assess seed germinability, husks were removed from eight batches of 25 randomly chosen seeds, which were then incubated in Petri dishes on flooded filter paper at a constant temperature of 32°C and a 12 hour light and 12 hour dark cycle for two weeks. The seed was found to be viable, with 96.3 ± 4.7% germinating in the laboratory.

Addition of Oryza meridionalis seed to para grass sites

In April 2002, after the completion of the laboratory assessment of seed germinability described above, batches of 2000 seeds were broadcast into each quadrat. This seed density is based on the seed bank size previously measured in the field (Wurm 1998a). At this time the para grass quadrats were inundated with approximately 50 cm of still water and supported emergent para grass cover.

At the same time as seeds were broadcast into quadrats, two mesh bags of twenty-five seeds were buried in each quadrat. The 10 cm × 10 cm bags were buried at approximately 3 cm below the soil surface, the depth within which most *O. meridionalis* seeds normally occur in the soil seed bank (Wurm 1998a). The heavy, plastic nature of the clay soil and dense vegetation cover made it difficult to control the exact depth of burial, however.

Para grass cover treatments

Cover treatments were implemented when para grass quadrats were again exposed in December 2002 (late dry season) and then re-implemented in October 2003 (mid-late dry season). Treatments were implemented within each quadrat and 50 cm outside the perimeter to account for edge effects.

Cover treatments (n = 2 sites, fixed; n = 3 replicates of each treatment, random) were:

1. Remove existing para grass cover and do not replace.
2. Remove existing para grass cover and replace all para grass litter.
3. Remove existing para grass cover and replace as thin para grass litter.
4. Leave existing para grass cover, and spray with herbicide (2% glyphosate; non-selective systemic herbicide; sold as RoundUp Biactive®).

5. Leave existing para grass cover untouched (control).

In order to characterize the para grass cover present in the treatments, the wet weights of total para grass cover were measured in those quadrats from which cover was removed (in December 2002 and October 2003). Wet weights were measured in the field using a hand-held spring balance. A sub-set of wet samples were then returned to the laboratory and dried to a constant weight at 65°C. These dry weights were then correlated with field wet weights to estimate field dry weights (t ha^{-1}) for all samples. Visual descriptions of the architecture of para grass cover were also made in the field.

Oryza meridionalis germination and establishment under para grass cover

Para grass quadrats were later inspected for established *O. meridionalis* plants in each of the two years after the seeds were sown, and the percentage projected cover of all species present was recorded. The first inspection was conducted during the dry season in October 2003. Any *O. meridionalis* plants that had established in the preceding wet season would have died by this time, but should still be identifiable in the grass canopy. For logistic reasons, it was not possible to return in the 2002/3 wet season. A second inspection for established plants was undertaken during the wet season in March 2004, when established wild rice plants are easily visible. Small emergents or plants that did not subsequently establish as mature plants would have been missed during both inspection times.

At the time that the percentage cover was assessed after the first and second wet season after burial, one bag from each quadrat was also retrieved. Retrieved bags were inspected for germinants, rotted seed/empty husks and ungerminated seed. Any retrieved ungerminated seed was then incubated in the laboratory to test for germinability, as described previously.

Wild rice sites used for information on Oryza meridionalis germination under undisturbed wild rice cover

This component of the study was undertaken previously as part of a larger study (Wurm 1998a), and a summary of the results are used here as a control for the study of *O. meridionalis* seed behaviour under para grass cover.

Wild rice sites were located in undisturbed native vegetation in Kakadu National Park, on the South Alligator River floodplain, approximately 250 km east of Darwin (12°28’S, 132°21’E), Northern Territory (Wurm 1998a). The two rice sites were approximately 30 km apart, in the mid-catchment of the South Alligator River, and supported an established, continuous, wet season cover of *O. meridionalis* throughout the study. Like the Mary River sites, these sites were underlain by heavy, black cracking-clay vertisol soils.

Greater access to these *O. meridionalis* sites was possible and allowed more time to implement field treatments and thus a greater number of replicates were used. Two 300 m transects were established down a gentle depth gradient in pure stands of *O. meridionalis* at both sites. At three points along each transect, fifteen bags of twenty five seeds were buried. Five bags were retrieved from each point after both the first and second wet season after burial. The seed in these bags was assessed as described above.

Analysis of data from para grass sites

Data from para grass sites were analysed using multi-factor ANOVA (Statsoft 2002). Factors in the study design were site (n = 2, fixed), date (n = 2, fixed) and treatment (n = 5, fixed). Samples comprised three replicate quadrats. For the seed bag retrieval study it was not possible to locate seed bags in some quadrats in the second year. Consequently, data from the two para grass sites for October 2003 only was used in a 2-factor ANOVA, in order test for an effect of treatment on retrieved seed behaviour, and data for Site 1 only was used in a 2-factor ANOVA to compare seed status between dates, to accommodate missing cells. Germination data were transformed by calculating the arcsine of the square root of proportional data. Prior to ANOVA, transformed data were inspected for normality by inspecting plots of residuals, and tested for heteroscedasity using Cochran’s test. Tukey’s test for unequal values of n was used for post hoc comparisons of means.

Results

***Oryza meridionalis* germination in undisturbed wild rice populations** *Oryza meridionalis* germination under wild rice cover is high, with relatively little seed death occurring. By the end of the first wet season after burial, an average of 46.4 ± 2.9% of seed had germinated, 36.8 ± 3.3% remained ungerminated and 16.8 ± 1.3% died. After two wet seasons only 5.0 ± 0% remained ungerminated (but viable), and no further seed death was detected. Further, as a result of this germination, a continuous cover of wild rice established in both wet seasons of the study (Wurm 1998a).

Field establishment of *Oryza meridionalis* under para grass cover *Oryza meridionalis* plants did not establish in any para grass quadrats during this study, regardless of the cover treatment (Table 1).

***Oryza meridionalis* seed germination, longevity and viability under para grass cover** Very little germination was detected under para grass cover in any treatments, despite the measured germinability of seed in the laboratory (96.3 ± 4.7%). Under para grass cover 50–85% (69.1 ± 16.5% for pooled data) of seeds remained ungerminated after one wet season and 20–55% (56.5 ± 23.3% for pooled data) remained ungerminated after the second wet season (Table 2). Cover treatment had no significant effect on the number of seeds remaining ungerminated (or dying) (Table 2). The significant decline in the number of ungerminated seeds between 2003 and 2004 ($F_{1,18}$ = 26.4, P = 0.000) was due to seeds rotting (Table 2).

Most of the retrieved ungerminated seed was still germinable in the laboratory (Table 3). For seeds retrieved in October 2003, 93.4 ± 7.3% germinated and of those retrieved in October 2004, 86.7 ± 28.9% germinated in the laboratory. (The larger error for October 2004 seeds is due to the patchy but higher loss of seeds to fungus for some samples during the laboratory germination trials.)

Rice seed under herbicide-treated para grass showed no difference to other cover treatments in germination or death (Table 2), despite herbicide killing the para grass cover (Table 1).

Characterization of para grass cover biomass and architecture Cover mass recorded for para grass was high. Para grass cover mass (t ha^{-1}, dry weight) at Site 1 ranged from 16.3 ± 2.7 (December 2002) to 22.5 ± 2.1 (October 2003), and at Site 2 from 11.6 ± 1.3 (December 2002) to 11.1 ± 2.1 (October 2003).

There was a significant effect of treatment on para grass cover ($F_{4,37}$ = 63.00, P = 0.000), and a significant interaction between site and treatment ($F_{4,37}$ = 4.96, P = 0.003). Para grass cover was successfully killed by the herbicide treatment, although spray treatment in December 2002 in two quadrats at Site 1 drifted outside the quadrat, and was not as successful as it was in the other site or times. For the clipping treatments, para grass cover had almost completely recovered by the time the sites were revisited for monitoring (Table 1).

The para grass canopy was generally tall (1.0–1.5 m) and had a complex architecture (as recorded during the dry season), comprising (a) a layer of fine roots and trapped organic particles (litter) that formed a ~10 cm mat on the soil surface, over which lay (b) a layer of loosely packed dead recumbent stems, and (c) an open canopy of green shoots that emerged from the layers below (Table 4). The litter layer integrated with the soil surface.

Discussion

Wild rice seed is dormant at seed shed. Under wild rice cover, the dormancy of

Table 1. Percentage cover (mean ± S.E.) for para grass cover treatments, in October 2003 (when quadrats were exposed) and March 2004 (when quadrats were inundated). Treatments were implemented in December 2002 and October 2003. In March 2004 the sites were inundated and so only the cover of emergent vegetation could be recorded. Cover values that are not significantly different (P >0.05) are indicated by having the same letter code. (n = 3 except where indicated with * which indicates n = 2.) *O. meridionalis* was not detected in the cover of any quadrat.

Period	Site	Treatment	Para grass	*Leersia hexandra*	*Eleocharis dulcis*	Cyperaceae sp.	*Hygrochloa aquatica*
December 2002	1	Control	100.0 ± 0 [A]	0.2 ± 0.2	0	0	0
		Clip and remove all	100.0 ± 0 [A]	0.2 ± 0.2	0	0	0
		Clip and replace all	100.0 ± 0 [A]	0.6 ± 0.2	6.7 ± 6.7	0	0
		Clip and replace thin	100.0 ± 0 [A]	0.3 ± 0.2	0	0	0
		Herbicide	76.7 ± 20.9 [AC]	0.8 ± 0.6	8.3 ± 8.3	0	0
	2	Control	100.0 ± 0 [A]	0.2 ± 0.2	1.7 ± 1.7	0	0
		Clip and remove all	100.0 ± 0 [A]	0.2 ± 0.2	0	0	0
		Clip and replace all	100.0 ± 0 [A]	0.4 ± 0.3	0	0	0
		Clip and replace thin	100.0 ± 0 [A]	0	0	0	0
		Herbicide	3.0 ± 1.0 [B]	1.0 ± 0.6	1.7 ± 1.7	0	0
October 2003	1	Control	70.0 ± 10.4 [C]	0.3 ± 0.2	0	0	0
		Clip and remove all	66.7 ± 4.4 [C]	0	0	0	0
		Clip and replace all	51.7 ± 14.5 [C]	0.3 ± 0.2	1.8 ± 1.6	0	0
		Clip and replace thin*	55.0 ± 5.0 [C]	0	0	0	0
		Herbicide	0.3 ± 0.2 [B]	0.2 ± 0.2	1.8 ± 1.6	0.3 ± 0.3	0.2 ± 0.2
	2	Control *	50.0 ± 10.0 [C]	0	0.3 ± 0.3	0	0
		Clip and remove all	45.0 ± 10.4 [C]	0	0	0	0
		Clip and replace all*	55.0 ± 20.0 [C]	12.5 ± 12.5	0	0	0
		Clip and replace thin	56.7± 12.0 [C]	0.2 ± 0.2	0	0	0
		Herbicide	0.3 ± 0.2 [B]	0	5.2 ± 4.9	0	0

almost all *O. meridionalis* seed is broken and most germination has occurred within two wet seasons after seed enters the soil seed bank (Wurm 1998). Thus, under wild rice cover the *O. meridionalis* seed bank was largely depleted by germination within this time frame.

Under para grass cover, 20–55% of seeds entering the seed bank remained dormant and germinable in the soil after three dry seasons, and were not depleted by germination. The time between usual germination (early wet seasons) and retrieval (subsequent dry season) in this study meant that evidence of germination may not have been detected in all cases, as some germinated seed may have been included in the count of rotted seeds. However, even if this was the case, there was still a substantially higher proportion of seed remaining ungerminated under para grass cover. Thus, if germination continued to be suppressed, the seed bank may eventually be depleted by seed death.

The failure of *O. meridionalis* plants to establish under any of the cover treatments, including herbicide treatment, was a surprising result, as it was predicted that the removal or death of cover would create a canopy gap that would allow the establishment of *O. meridionalis* plants (Connell 1978, Douglas *et al.* 2001, Jutila and Grace 2002, Petraitis *et al.* 1989).

The principal reasons that buried seeds do not germinate in soil are (a) seed dormancy, an innate trait of the seed which requires exposure to a dormancy breaking process for germination to occur, and (b) seed quiescence (in non-dormant seeds) for which there is a cueing requirement for germination to occur (Baskin 2004). These processes and cues detected in other studies include light (Baskin and Baskin 1989), temperature (Mott 1978, Baskin and Spooner 1989, Lonsdale 1993, Baskin, Baskin and Chester 1999), flooding and anaerobic conditions, and possibly the presence of fungus (e.g. Keeley 1988). Soil moisture and temperature may interact to prolong or break seed dormancy (Bewley and Black 1982). Temperature fluctuations can be significant in breaking dormancy and enabling germination (e.g. Dillon and Forcella 1985).

Soil temperatures of up to 60°C have been measured in the study area (Mott 1978, Lonsdale 1993, Wurm 1998a), with diurnal temperature fluctuations of up to 30°C. These may provide stimuli for germination, by signalling the presence of canopy gaps to the seeds in the soil (Insausti *et al.* 1995). However, mean soil temperature, and the amplitude of soil temperature fluctuations, decrease with both increasing soil moisture and the presence of surface litter (e.g. Abrecht and Bristow 1990, Koto *et al*. 1992). Additional studies currently underway indicate that allelopathy was not a factor in the suppression of germination and establishment of *O. meridionalis*.

Although the cover in clipping treatments had almost completely recovered by the time quadrats were re-assessed, herbicide treatment did successfully kill para grass. However, para grass cover has a complex structure, reflecting the growth of stolons in response to the annual wetting and drying cycle – namely adventitious roots produced on stolons during the wet season are added to the layer of fine roots and other litter at the soil surface; new, emergent green shoots produced during the wet season, become recumbent during the dry season, forming a mat above the soil surface through which new shoots arise (or seedlings of other species must penetrate).

Para grass cover may create a different seed-bed to that typically occurring in stands of native floodplain grasses such as *O. meridionalis*. Para grass produced a cover biomass that is 2–3 times greater (Douglas and O'Connor 2004) than that recorded for wild rice (Finlayson 1991). The higher total biomass and a complex architecture of para grass cover, including a thick litter layer integrating with the soil surface, may prevent dormancy breaking and

Table 2. Percentage of buried seed that were ungerminated, present as husks/rotted or germinated when retrieved, at the two sites for each five treatments, when retrieved in (a) 2003 dry season and (b) 2004 dry season. Seed bags were buried in April 2002. Although all raw data are presented below, several analyses were undertaken to account for the missing cells. These were (i) a 3-factor ANOVA (Site x Year x Treatment) was conducted without the treatment 'clip and replace all cover' (differences indicated by letters A and B), and (ii) a 2-factor ANOVA (Year × Treatment) for Site 1 data only, (differences indicated by the letters X and Y). Values that are not significantly different have the same letter code, and those with no letter code were not included in the analysis. A 2-factor ANOVA (Site × Treatment) for 2003 data only did not detect any significant affects of treatment.

(a) 2003

Treatment	Seed status	Site 1	Site 2
Control	% ungerminated	51.0 ± 6.8 (n = 3) AB XY	60.3 ± 31.8 (n = 3) AB
	% husk	41.7 ± 10.9	39.8 ± 31.8
	% germinated	7.3 ± 8.9	0
Clip and remove all cover	% ungerminated	67.5 ± 19.9 (n = 3) AB XY	68.5 ± 5.6 (n = 3) AB
	% husk	32.5 ± 19.9	28.7 ± 3.2
	% germinated	0	2.7 ± 2.4
Clip and replace all cover	% ungerminated	77.2 ± 8.3 (n = 3) Y	76.4 ± 15.8 (n = 2)
	% husk	22.8 ± 8.3	23.6 ± 15.8
	% germinated	0	0
Clip and replace thin cover	% ungerminated	85.5 ± 18.1 (n = 3) B Y	64.6 ± 7.2 (n = 3) AB
	% husk	14.5 ± 18.1	33.8 ± 4.8
	% germinated	0	1.6 ± 2.7
Herbicide treatment	% ungerminated	66.4 ± 12.6 (n = 3) AB XY	78.5 ± 10.5 (n = 3) B
	% husk	32.1 ± 11.5	19.9 ± 12.3
	% germinated	1.5 ± 2.6	0

(b) 2004

Treatment	Seed status	Site 1	Site 2
Control	% ungerminated	19.1 ± 15.0 (n = 3) A X	52.2 (n = 1) AB
	% husk	79.3 ± 12.7	47.8
	% germinated	1.7 ± 2.9	0
Clip and remove all cover	% ungerminated	48.0 ± 17.0 (n = 2) AB XY	37.1 ± 25.9 (n = 2) AB
	% husk	52.5 ± 17.0	62.9 ± 25.3
	% germinated	0	0
Clip and replace all cover	% ungerminated	42.5 ± 25.6 (n = 3) XY	No samples located
	% husk	58.8 ± 27.5	
	% germinated	1.4 ± 2.4	
Clip and replace thin cover	% ungerminated	31.9 ± 11.4 (n = 2) AB XY	55.6 ± 23.2 (n = 2) AB
	% husk	64.8 ± 16.1	44.4 ± 23.2
	% germinated	3.3 ± 4.7	0
Herbicide treatment	% ungerminated	30.0 ± 25.4 (n = 2) A XY	30.9 ± 11.6 (n = 2) A
	% husk	70.0 ± 25.5	69.1 ± 11.6
	% germinated	0	0

germination cues reaching seed, particularly in well established stands such as those used in this study. Visual inspection of the seedbed made during this study indicates a much higher litter and organic matter content and increased root-structuring in the soil under para grass cover, than occurs under *O. meridionalis* cover. These features have the potential to increase shade and humidity at the soil surface, and soil moisture content, during the dry season. These effects are likely to reduce soil temperature and dampen diurnal soil temperature fluctuations. These features may alter the conditions experienced by seed, which could prevent dormancy-breaking and germination cues from reaching the soil seed bank.

Wild rice can establish after para grass has been treated with herbicide (Douglas *et al*. 2001). However, in this study spraying para grass with herbicide or clipping the cover was not sufficient to allow germination of *O. meridionalis* seeds. The para grass stand in which this study was undertaken was long established, and the modifications to the seed bed may have been more significant than those in more recently established stands of para grass. The time frame over which habitat modifications significantly impact on the soil seed bank, and subsequently *O. meridionalis* populations persistence, have not yet been determined. Similarly, the specific dormancy breaking and germination cues for *O. meridionalis* have not yet been determined. These two issues require further investigation, if para grass stands are to be successfully managed and native species established on these monsoonal floodplains, while using limited weed control resources efficiently.

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Table 3. Percentage (mean ± S.D.) of retrieved ungerminated seed that germinated subsequently in the laboratory. Seeds were retrieved in (a) 2003 dry season and (b) 2004 dry season. Although all raw data is presented below, only treatments without missing cells were include in a 2-factor ANOVA. Thus, due to missing cells, analyses undertaken were Treatment × Site for 2003 data only, and Treatment × Year for Site 1 data only. No significant difference was detected among seeds retrieved from the various periods, sites or treatments.

Treatment	Site 1	Site 2
(a) 2003		
Control	90.7 ± 8.2 (n = 3)	89.0 ± 15.3 (n = 3)
Clip and remove all cover	96.3 ± 6.4 (n = 3)	97.8 ± 3.8 (n = 3)
Clip and replace all cover	89.8 ± 2.2 (n = 3)	97.6 ± 3.4 (n = 2)
Clip and replace thin cover	96.5 ± 3.2 (n = 3)	93.9 ± 10.5 (n = 3)
Herbicide treatment	93.0 ± 6.7 (n = 3)	96.5 ± 6.1 (n = 3)
Pooled across treatments	93.3 ± 5.7 (n = 15)	94.8 ± 8.6 (n = 14)
(b) 2004		
Treatment	Site 1	Site 2
Control	100 ± 0 (n = 3)	Germination trials aborted
Clip and remove all cover	96.7 ± 4.7 (n = 2)	100 (n = 1)
Clip and replace all cover	100 ± 0 (n = 2)	Germination trials aborted
Clip and replace thin cover	100 ± 0 (n = 2)	94.4 ± 7.8 (n = 2)
Herbicide treatment	95.8 ± 5.9 (n = 2)	100 ± 0 (n = 2)
Pooled across treatments	98.6 ± 3.1 (n = 15)	97.8 ± 8.0 (n = 5)

Table 4. Mean (and the range) of layer thicknesses in the para grass cover architecture, in control quadrats on the Mary River floodplain, during the 2003 dry season.

	Root mat layer (m)	Recumbent stems layer (m)	Total canopy height (m)
Site 1 (n = 3)	0.13 (0.11 – 0.14)	0.15 (0.12 – 0.21)	1.03 (0.81 – 1.41)
Site 2 (n = 3)	0.08 (0.06 – 0.11)	0.12 (0.10 – 0.13)	0.79 (0.54 – 0.89)

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