PROJECT REPORT

Physical and biological factors determining the distribution and abundance of the wild rice *Oryza meridionalis* Ng in the Northern Territory.

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Inundation, morphology, growth and fecundity of *Oryza meridionalis* Ng

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Summary

Wild rice *Oryza meridionalis* Ng (formerly *Oryza rufiopogon* Griff.) is a widespread and abundant annual floodplain grass, endemic to northern Australia. Its seeds provide an important annual food resource for floodplain fauna, particularly the Dusky Plains Rat *Rattus colletti* and the Magpie Goose *Anseranas semipalmata*.

Floodplains of the monsoonal wet-dry tropics are a hydrologically dynamic habitat. During the annual wet season, the underlying clay soils are flooded by 10 to 200 cm of water, while during the dry season they are dry and deeply cracked. The annual wetting and drying cycle is a reliable occurrence, but the timing of wet season onset, and the extent and duration of inundation are not.

This study investigated the significance of inundation regime to growth and fecundity of *O. meridionalis* in a tank experiment, growing potted plants in four inundation treatments.

The growth habit, vegetative productivity, fecundity and mortality of *O. meridionalis* plants were significantly affected by inundation regime, with plants grown in the two intermediate inundation regimes (with maximum depths of 15 and 74 cm) being the most vegetatively productive. The two intermediate inundation treatments also resulted in the greatest number of spikelets per plant (a mean range of 1,900 and 2,300 spikelets per plant). Both the exposed and deepest treatments (0 cm and 120 cm respectively) resulted in significantly fewer spikelets per plant.

Although inundation regime had a significant effect on growth and fecundity, reproductive output was still > 700 spikelets per plant in all treatments, illustrating the plasticity of growth of *O. meridionalis* in response to inundation. The 700 spikelets per plant in this study equates with 30,100 spikelets m^{-2} in the field.

The preference of *O. meridionalis* in the field for areas of intermediate depth is unlikely to be explained only by inundation alone. Although spikelet production for *O.*

meridionalis, was significantly decreased by the driest and wettest inundation treatments, it was still high (>700) under a 120 cm range of inundation regimes. In the field inter-specific competition and density-dependent effects, may also interact with these edaphic factors to limit spikelet production and *O. meridionalis* population size. Ability to tolerate abiotic "stress" is frequently inversely related to competitive ability, and this high reproductive effort under a range of inundation regimes may at the expense of the competitive ability of *O. meridionalis*. However if habitat variability, such as inundation regime, limits the growth and reproduction of perennial species, then *O. meridionalis* would be well placed to occupy any vacated space.

In the field, significant differences in growth and fecundity were also detected between years of different inundation period. For example, the 1992 wet season commenced 6 weeks later than it did in 1994. This additional time for vegetative accumulation prior to the initiation of inflorescences also may have contributed to higher spikelet production in the field populations.

Introduction

Wild rice *Oryza meridionalis* Ng is a widespread and abundant annual floodplain grass, endemic to northern Australia (Cowie et al. 2000), see plate below. Its seeds also provide an important annual food resource for floodplain fauna, particularly the Dusky Plains Rat *Rattus colletti* (Redhead 1979; Friend et al. 1988; Williams 1991; Madsen & Shine 1996) and the Magpie Goose *Anseranas semipalmata* (Frith & Davies 1961; Bayliss & Yeomans 1990; Tulloch et al. 1988; Whitehead & Tschirner 1990). Juvenile recruitment of both these abundant fauna species coincides with *O. meridionalis* seed shed in the late wet to early dry season.

Seeds of *Oryza meridionalis*, from which the husk has been removed. The reddish brown colour is variable.
Photo: Penny Wurm

Mature *Oryza meridionalis* plants in flower, prior to seed set. Water Recorder Point, South Alligator River floodplain, February 2004.
Photo: Penny Wurm

A stand of wild rice towards the end of the growing season, which has been partially trampled by browsing magpie geese. Although recumbent stems can produce new inflorescences, at this time of year (April) the water levels are receding, and plants are beginning to senesce. Water Recorder Point, South Alligator River floodplain, April 2004.
Photo: Penny Wurm

The researcher collecting fortnightly growth data for the *Oryza meridionalis* inundation experiment, Charles Darwin University Campus (then Northern Territory University Campus), February 1995.
Photo: P.A.S. Wurm

Floodplains of the monsoonal wet-dry tropics are a hydrologically dynamic habitat. During the annual wet season, the underlying clay soils are flooded by 10 to 200 cm of water, while during the dry season they are dry and deeply cracked. Rainfall occurs predominantly from November to April, and almost no rain falls between June and August (McAlpine 1976). Although the concomitant annual wetting and drying cycle is itself a reliable occurrence , the timing of wet season onset, and the extent and duration of inundation are not, and rainfall in the months of transition from the dry season to the wet season is extremely variable (Taylor & Tulloch 1985; Cook & Heerdegen 2001).

Field monitoring of the phenology of *O. meridionalis* populations has shown significant spatial and temporal variation in spikelet and seed production (Wurm 1998). This is likely to result from interactions between a number of inter-specific, intra-specific and abiotic factors. The results of field monitoring point to both the timing of wet season onset and the subsequent inundation regime as having a role. Field studies also show that, although seedlings are able to survive complete inundation, rapid flooding early in the growing season can significantly increase seedling mortality (Wurm 1998). This study focuses on the next stage of the life-cycle of *O. meridionalis*, by measuring the response of established plants to different inundation regimes. Because of the logistic obstacles inherent in the unpredictable monsoonal floodplain environment, this study was carried out in a tank experiment.

Although the occurrence of an annual wet season is reliable (Humphrey et al. 1990), the timing, duration and quantity of rainfall varies greatly between years (Taylor & Tulloch 1985; Cook & Heerdegen 2001). This variability is then reflected in the inundation regime on the floodplains. After analysing 113 years of rainfall data, Taylor and Tulloch (1985) concluded that "rainfall extremes are at least as important as the means in the stability or otherwise of plant and animal populations". Field studies confirmed that the floodplain inundation regime also varies spatially within a given wet season (Wurm 1998), due to the effects of local soils, topography and rainfall, and thereby run-off and drainage. Thus *O. meridionalis* populations must survive a range of inundation regimes within and among years at the one site.

In a large scale vegetation survey of floodplain wetlands in the Northern Territory, Wilson et al. (1991) found that water depth (and salinity) were significantly correlated with the distribution of species and assemblages. In that study, *O. meridionalis* was found to occur at sites of intermediate depth (approximately 50 cm in the year of the survey), such as extensive low-lying depressions and plains, the fringes of deeper swamps and margins of paleochannels and billabongs. Mechanisms determining wetland vegetation patterns and species distributions are probably a complex interaction between biological and hydrological factors, with inundation regime playing a significant role (e.g. Gopal 1986; Brock 1986; Walker et al. 1986; Neill 1993; Rea & Ganf 1994a). For perennial emergent species, inundation has been shown to affect the overall allocation to vegetative and/or reproductive structures (Brock 1986; Grace 1989;

Rea & Ganf 1994a,b), the relative contribution of sexual versus vegetative propagation (Rea & Ganf 1994c; Lieffers & Shay 1981), and the relative distribution of species (van der valk & Davis 1980; Walker et al. 1986; Greening & Gerritsen 1987; Botts & Cowell 1988; Grace 1989; Rea & Ganf 1994c). Reproduction in annual emergent species reproduction also can be affected by inundation (Stevenson & Lee 1987). For *O. meridionalis* reproductive output is also likely to be affected by inundation regime.

Emergent perennial and annual plants respond to inundation with either increased elongation of shoots to match changes in water level or toleration of increased water level and submergence through a pause in growth until water levels recede (Rea 1992; HilleRisLambers & Seshu1982; Blom et al. 1990; Weisner et al. 1993). Perennial species may also respond to inundation over a range of time scales (Rea & Ganf 1994a). Although they may tolerate short periods of complete submergence (e.g. at the seedling stage during the flood events observed in the field during this study; Mazaredo & Vergara 1982), emergent annuals must respond to the immediate water level in order to achieve the annual seed production. It has been argued that variability in the habitat of an annual aquatic plant constitutes a selection pressure towards plasticity in growth response (Counts & Lee 1988b). Thus, given the potential for annual variation in inundation regime on monsoonal floodplains, and that *O. meridionalis* is a widespread and abundant species across this habitat, it is likely that *O. meridionalis* plants have a capacity for plasticity in their response to different inundation regimes.

This study investigated the significance of inundation regime to growth and fecundity of *O. meridionalis* plants, thus testing some of the implications of field monitoring (Wurm 1998). The capacity for morphological plasticity, and variation of growth and fecundity in response to different inundation regimes was measured. These results, which focus on responses at the individual plant level, were used to make further interpretations of the results of field monitoring, which was focused at the population level. The likely impact of inundation on population maintenance is then discussed.

Materials and Methods

Tank conditions

The tank growth experiment commenced in January 1995, and finished 5 months later when the final harvest took place in May 1995. The timing of this experiment coincided with establishment, growth and flowering of plants in the field. Experimental plants were consequently exposed to the same air temperatures, degree of cloud cover, humidity and photoperiod as their field counterparts.

The experiment was conducted in a circular tank (1.5 m depth and 6.5 m diameter) situated on the campus of Charles Darwin University, Darwin. The tank was constructed of a sheet metal wall and a non-toxic, potable standard, vinyl tank liner, and was filled with water from the town supply.

Floodplain soils were used in the experiment to ensure that nutrition and soil chemistry were similar to field conditions. The heavy clay vertisols which underlie the floodplains may provide particular constraints to below-ground root development, such as resistance to penetration of roots, which an artificial potting mixture may not. The use of floodplain soils, however, precluded the measurement of underground biomass, because of the difficult handling properties of the clay and the subsequent error that would be generated in measurements. Soil for the experiment was excavated directly from the field at Middle Point Research Farm on the Adelaide River floodplain. As vertisols shrink and harden when dry and swell when wet, it was necessary to produce a manageable slurry by completely saturating the soil before transferring it to 30 cm x 30 cm black plastic pots, to ensure an equal volume of soil in each pot.

Plant establishment

The seed used in the experiment was collected from the field during the previous wet season, approximately 7 months prior to the experiment and stored in the laboratory. Approximately 4 weeks prior to the commencement of the inundation treatments, seed was germinated in a laboratory growth cabinet (at 32 $^{\circ}$C, with a 12 hour dark/light cycle). Germinants were then transplanted into the pots, placed in a small "nursery" tank, and flooded to the level of the soil surface. An excess of pots and germinants was prepared, such that seedlings of similar height and vigor could be selected to commence the experiment. Seedlings were removed from, or transplanted to, pots so that each pot

finally contained three seedlings. This represented a density of 43 seedlings m^{-2} (densities in the field may be up to hundreds of seedlings m^{-2}; Wurm 1998). Pots were left in the nursery tank for a four week establishment period, by which time seedlings were approximately 15 cm tall. Pots were then transferred to the larger experimental tank, and allowed to acclimatise for two days before experimental treatments were imposed.

Inundation treatments

Four inundation treatments were used in the experiment (Figure 1 a,b): *Exposed*, in which the soil surface was kept at 15 cm above the water surface; *Shallow* in which the soil surface was lowered to 15 cm below the water surface prior to flowering; *Intermediate* in which the soil surface was lowered to 75 cm below the water surface prior to flowering; *Deep* in which the soil surface was lowered to 120 cm below the water. Thus for the two deepest treatments pots were lowered approximately every 10 days until the final depth was reached. These depth increments were chosen so as not to completely submerge the plants at any stage. The final depths for all inundation treatments were reached prior to the emergence of the first inflorescences. Pots were positioned on top of stacks of concrete bricks, which were removed until the desired treatment depth had been reached. At the commencement of the experiment all pots were positioned such that the soil surface was level with the water surface. In this way, shallower depth treatments were reached and maintained earlier in the experiment then deeper treatments. This simulation is similar to those inundation regimes observed in the field, representing the pattern of inundation occurring within four different types of wet season, or at different sites within the one wet season. Because each inundation treatment was commenced and terminated on the same date, the length of growing season was the same for each treatment.
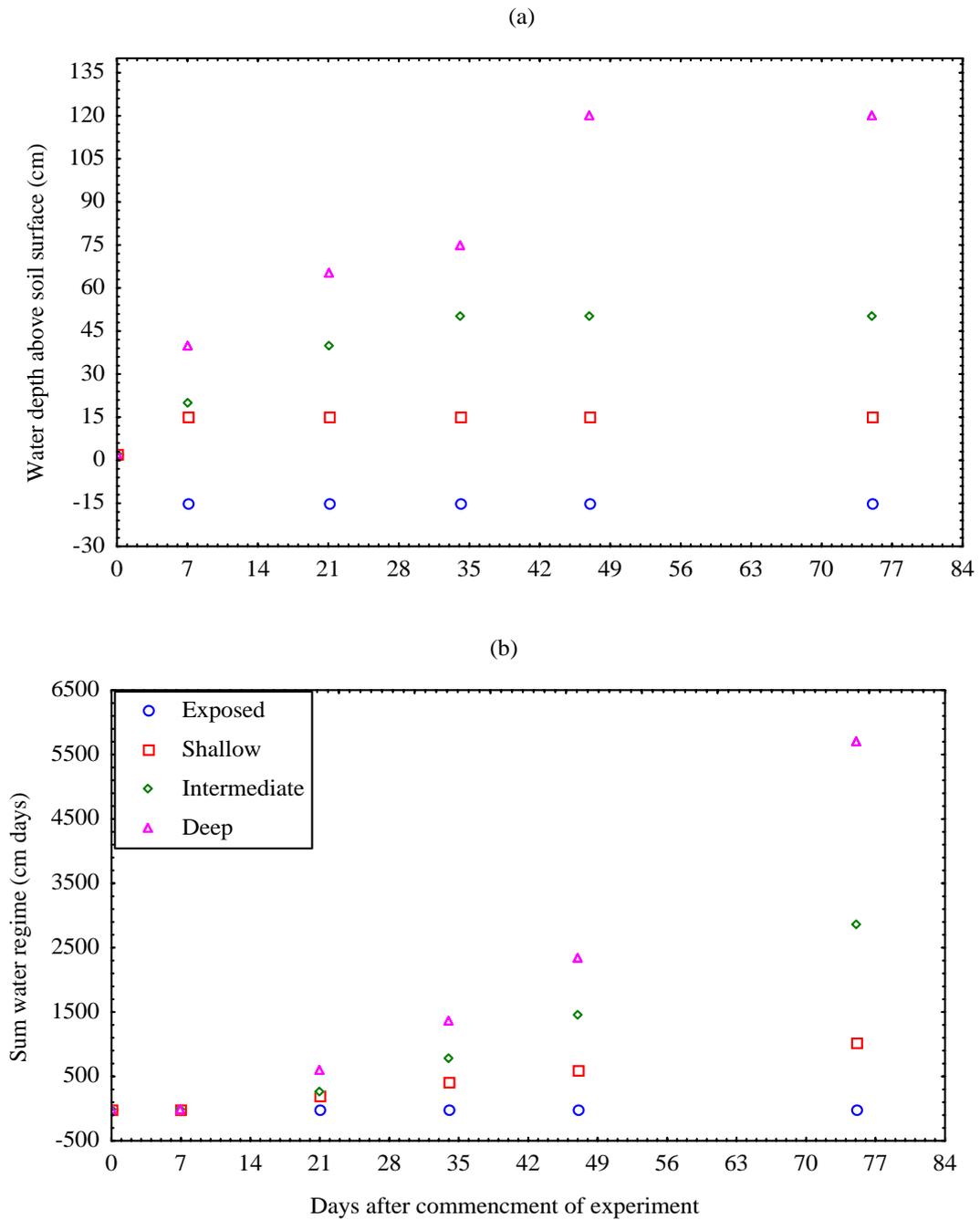
(a)

(b)

Figure 1: Inundation regime for each of the four experimental treatments, expressed as (a) water depth (cm), and (b) Sum Water Regime (cm days; Rea, 1994a). For Exposed treatment the soil surface was 15 cm above the water surface, and for Shallow, Intermediate and Deep treatments the soil surface reached a maximum of 15 cm, 75 cm and 120 cm below the water surface, respectively.

Experimental design

The experiment used a completely randomised block design, with 9 blocks. Each block contained 4 randomly chosen pots, each of which was randomly allocated to one of the four treatments. Blocks were arranged in the centre of the tank in a 3 x 3 grid. Each block was separated by approximately 1 m to minimise the effect of shading between blocks. This design removed block position within the grid as a factor from the experiment. A preliminary analysis of variance confirmed that block had no effect on growth and fecundity parameters.

It is unlikely that the growth and fecundity of plants grown a tank will be the exact numerical equivalent of those in the field (Stevenson & Lee 1987; Counts & Lee 1988a). The study will, however, provide an indication of the direction and magnitude of plant responses to flooding. The results of this tank study are discussed with those constraints in mind.

Data collection

Plant height was measured 0, 34 and 75 days after the experiment began. Plants were finally harvested in May, after 5 months of growth. By that time plants had begun to senesce and most seeds had been shed. The parameters recorded for each of the three plants in each pot were: *plant height* (cm); number of *basal stems* per plant; above-ground *dry weight* of plant (g); total number of *inflorescences* per plant; number of *incipient inflorescences* (defined as those that had not emerged from the leaf sheath at the time of harvest), number of *spikelets per inflorescence* (on a sub-sample of 5 inflorescences per plant). To determine total above ground dry weight, each plant was oven dried at 80 $^{\circ}$C to a constant weight. Mean values for each parameters (n = 3 plants/pot) were used in analyses.

Analysis of data

A one-factor ANOVA was used to test for a significant effect of the four inundation treatments on the measured growth and fecundity parameters, using "Statistica for Windows", release 5.0 (StatSoft Inc., 1996). Plots of residuals were inspected for normality of the data prior to analyses. Cochran's test was used to test for homogeneity of variances for all parameters prior to ANOVA. Data were transformed where necessary, as described in the ANOVA tables. Tukey's test was used for *post hoc* comparison of means. Results for mortality were inspected without further analysis.

Results

Overall, inundation had a significant effect on all the measured growth and fecundity parameters of *O. meridionalis* (Tables 1 and 2; Figures 2 & 3). Mortality also differed between inundation treatments, with no plant mortality in the Exposed, Shallow and Intermediate treatments, but four dead plants (one each from four different pots) under the Deep treatment (Table 3).

Table 1: Results of ANOVA between the 4 inundation treatments for each *O. meridionalis* plant parameter. df effect = 3; df error = 32. Refer to Figures 2 and 3 for the data.

Plant parameter	Transformation	MS effect	MS error	F	p
Height	-	9981.3	25.5	391.04	<0.001
Number of basal stems	-	856.8	9.9	86.16	<0.001
Dry weight	-	280.9	7.6	36.93	<0.001
Total inflorescences per plant	Log	0.803	0.051	15.75	<0.001
Incipient inflorescences per plant	Log	0.052	0.003	16.38	<0.001
Spikelets per inflorescence	Log	0.287	0.0089	32.29	<0.001
Spikelets per plant	-	3200748	128952	24.82	<0.001

Table 2: Results of Tukey's HSD *post hoc* testing, showing significance of differences between mean values for each parameter. 1 = Exposed, 2 = Shallow, 3 = Intermediate, and 4 = Deep treatments. '>' indicates a significantly higher value, '<' indicates a significantly lower value, and '=' indicates no significant difference between mean values. Refer also to Figures 2 and 3.

Plant parameter	Significance of differences between mean values for Treatments 1, 2, 3 & 4
Height	1 < 2 < 3 < 4
Number of basal stems	1 > 2 > 3 > 4
Dry weight	1 = 2 = 3 > 4
Total inflorescences per plant	1 = 2 = 3 > 4
Incipient inflorescences per plant	1 < 2 = 3 = 4
Spikelets per inflorescence	2 = 3 > 4 > 1
Spikelets per plant	2 = 3 > 1 > 4

Inundation significantly changed the morphology of plants. Plants growing in damp soil or shallow water were shorter and produced more stems than those growing in deeper water (Figure 2 a,b; Table 2). The morphological trade-off between stem height and number did not significantly affect the dry weight of plants grown at the Exposed, Shallow and Intermediate treatments. However, plants grown at the deepest level of inundation were not able to maintain the same level of vegetative production, with dry weights of these plants being significantly less than those grown at other treatment levels (Figure 2 c).

Table 3: Mortality rates for each inundation treatment. (Note that the value of 14.6% for Deep Treatment (-120 cm), equates with the death of one plant in each of four replicate pots).

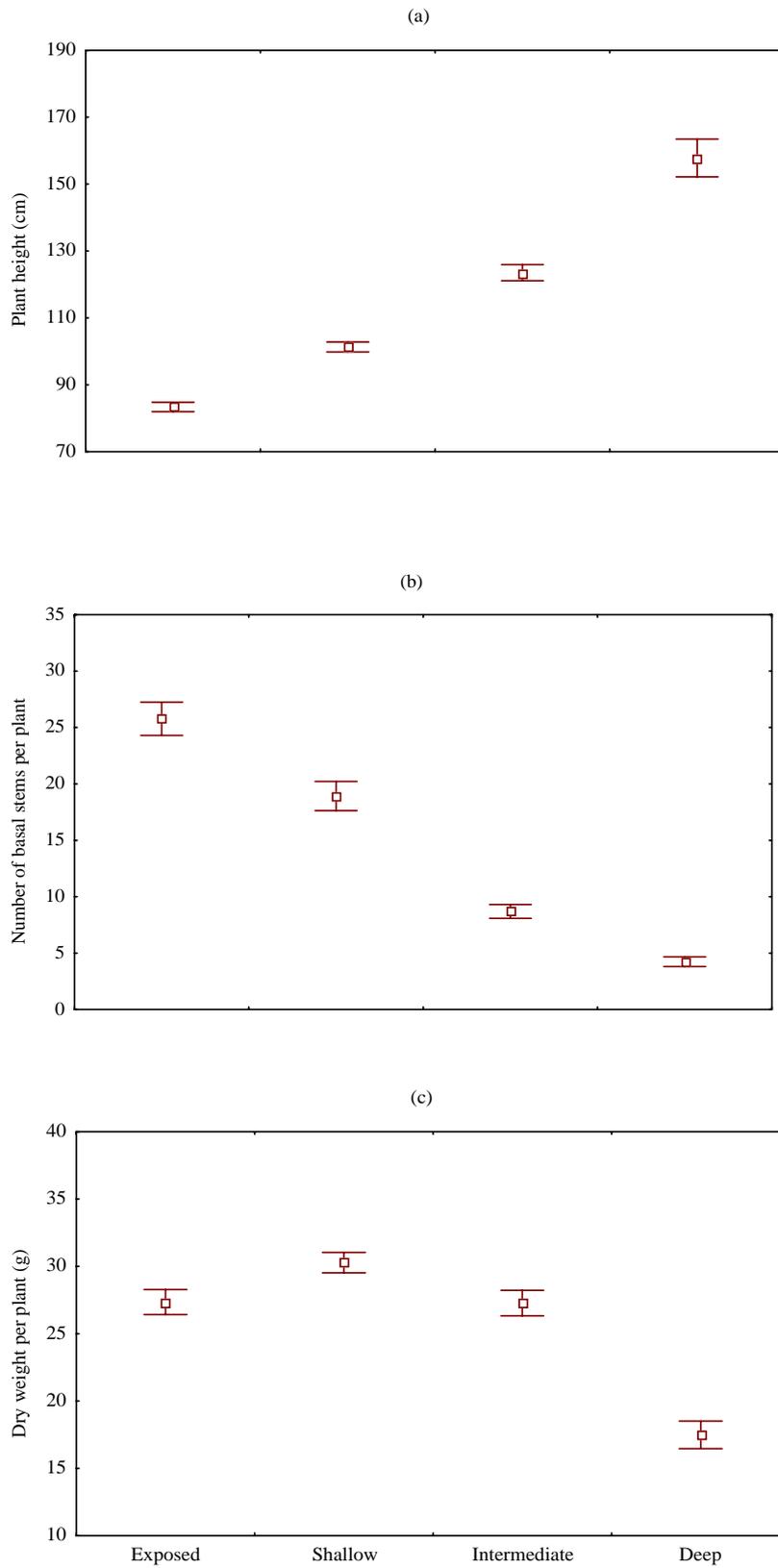| TREATMENT	% MORTALITY
Exposed treatment	0
Shallow Treatment	0
Intermediate Treatment	0
Deep Treatment	14.6 $\pm$ 17.7

Figure 2: Vegetative traits of plants grown under the four inundation treatments (mean ± standard error): (a) height, (b) number of basal stems, and (c) dry weight. Refer to Figure 1 for a description of each of the treatments.

Plants grown under the Deep treatment also had significantly fewer total (incipient + emerged) inflorescences per plant at the time of harvest than those from the three other inundation regimes (Figure 3 a; Table 2). In contrast there were significantly fewer incipient inflorescences on plants grown in exposed soil than for plants in other treatments. (Incipient inflorescences comprised a small proportion of the total inflorescences in all treatments at the time of harvest; Figure 3 b; Table 2).

The number of spikelets produced per inflorescence also varied significantly between treatments, with fewer from the Exposed treatment compared with the other treatments (Figure 3 c). Plants grown under the Shallow and Intermediate treatments (which did not significantly differ from each other) produced more spikelets per inflorescences than plants under the Deep treatment.

The different numbers of inflorescences produced per plant, spikelets produced per inflorescence, were reflected in significantly different numbers of spikelets per plant between treatments. *Post hoc* testing indicated there were significantly fewer spikelets produced per plant in the Deep treatment (947.1 $\pm$ 71.5), compared with plants from the three shallower regimes. Plants from the Exposed treatment produced a mean of 1,454.2 $\pm$ 84.4 spikelets per plant, which was significantly fewer than that for plants from the Shallow (2,315.3 $\pm$ 169.6) or Intermediate (1,955.0 $\pm$ 127.8) treatments, which were not significantly different.
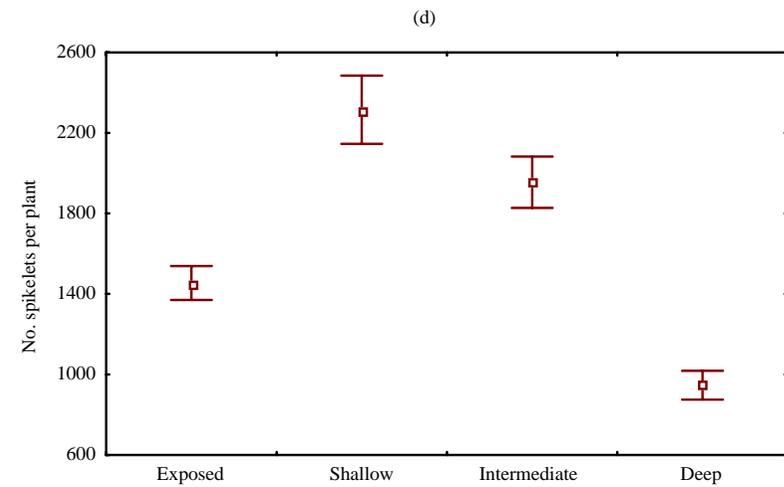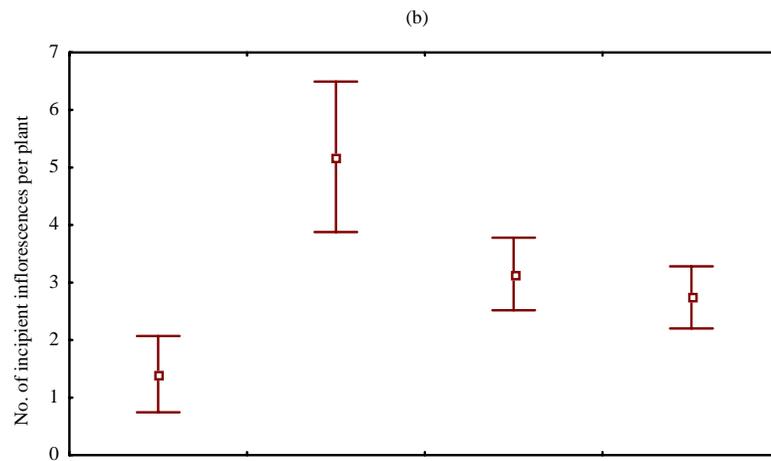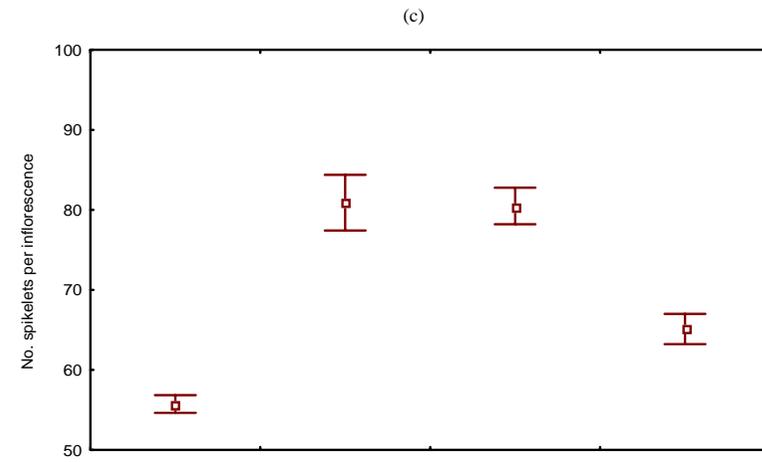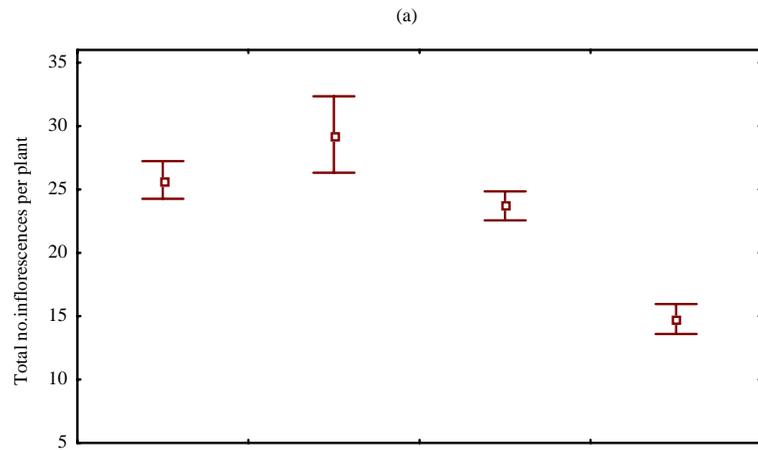
Figure 3: Reproductive traits of plants grown under the Exposed, Shallow, Intermediate and Deep inundation treatments (mean $\pm$ SE): number of (a) total inflorescences per plant, (b) incipient inflorescences per plant, (c) spikelets per inflorescence, and (d) spikelets per plant.

Discussion

The growth habit, vegetative productivity, fecundity and mortality of *O. meridionalis* plants were significantly affected by inundation regime. As the level of inundation increases, individual plants respond by increasing stem height and decreasing stem number, while maintaining total vegetative productivity. However there is a limit to the capacity of the plant to maintain this morphological trade-off (Grace 1989; Stevenson & Lee 1987). For *O. meridionalis* this limit was reached between the intermediate and the deepest inundation. These inundation regimes equate in the field with deeper areas of the estuarine deltaic plain or in very wet years. Plants from the deepest inundation produced significantly less dry matter than other plants, and a small proportion of these plants died. The resources required to increase shoot length at a sufficient rate to compensate for increases in inundation precluded the production of additional axillary and basal stems. For deeply inundated aquatic plants, photosynthesis can be reduced because of light attenuation, resulting in reduced biomass accumulation (Mazaredo & Vergara 1982; Grace 1987; Stevenson & Lee 1987), and consequently fecundity. Water from the public water supply was used in this study. However, in the field, attenuation of light penetration is likely to be more pronounced, due to the accumulation of plant detritus in the water column, for example.

Changes in vegetative productivity due to inundation were translated into changes in the development of inflorescences. In this study, plants grown under the deepest inundation did not match the inflorescence production of plants grown under shallower conditions. Plants grown under deeper conditions also produced a fewer stems. In the field, plants in deep water may compensate for this through the development of axillary shoots and additional inflorescences along recumbent stems as the water levels recede. This potential was also demonstrated in this experiment, with a significantly larger number of incipient inflorescences present at the conclusion of the experiment on plants from the Shallow, Intermediate and Deep treatments. Under exposed conditions the shorter time for inflorescence production was compensated to a certain degree by the higher number of inflorescences arising from the larger number of stems. Under natural conditions seed production at deeper sites may ultimately be the same as that from shallower sites.

The experiment identified an optimal inundation regime, with respect to total spikelet production. The two intermediate inundation treatments (with maximum depths of 15 and 74 cm) resulted in the largest number of spikelets per plant (a mean range of 1,900 and 2,300 spikelets per plant). Both the exposed and deepest treatments resulted in significantly fewer spikelets per plant. This preferred inundation regime agrees with the field observations of Wilson et al. (1991), where the distribution of *O. meridionalis* populations correlated with "intermediate" depths, bearing in mind that the actual depth at an "intermediate" site can be expected to vary between years.

Although inundation regime had a significant effect on growth and fecundity, reproductive output was still > 700 spikelets per plant in all treatments. This illustrates the plasticity of growth of *O. meridionalis* in response to inundation. As plants were grown at an equivalent density of 43 m^{-2}, 700 spikelets per plant in this experiment equates with 30,100 spikelets m^{-2} in the field. This is far in excess of the measured seed bank (750 and 1,090 seeds m^{-2}; Wurm 1998) and the maximum recorded emergent seedling density (1,056 seedlings m^{-2}, Boggy Plains in 1994, Wurm 1998), but comparable to the spikelet production recorded at Boggy Plains in 1994 (21,109 $\pm$ 2,300 spikelets m^{-2}; Table 2.22, Wurm 1998).

Inundation regime experienced by established plants can significantly influence the sexual reproduction of annual and perennial plants (Grace 1989; Rea & Ganf 1994 a,b; Stevenson & Lee 1987). However, the distribution of *O. meridionalis* populations in areas of intermediate depth is unlikely to be explained by limits to its tolerance of inundation alone (e.g. Campbell et al. 1991). Although spikelet production for *O. meridionalis*, was significantly decreased by the driest and wettest inundation treatments, it was still high (>700) under a 120 cm range of inundation regimes. The study was conducted in the absence of inter-specific competition and density-dependent effects, both of which would be expected to be present in the field. Thus in the field inundation may interact with these edaphic and biotic factors to limit spikelet production and *O. meridionalis* population size. Ability to tolerate abiotic "stress" is frequently inversely related to competitive ability (Carter & Grace 1990), and this high reproductive effort under a range of inundation regimes may at the expense of the competitive ability of *O. meridionalis* (Harper 1977; Grace & Wetzel 1981). However if habitat variability, in the form of inundation regime, limits the growth and reproduction of perennial species, then *O. meridionalis* would be well placed to occupy any vacated space.

The results of the field and experimental studies are consistent. In the field, significant differences in growth and fecundity were also detected between years of different inundation. For example, spikelet production (per unit area and per plant) was significantly higher in 1994 than in 1992 at Water Recorder Point, despite plant survivorship being the same in those years (Wurm 1998). The depth and duration of inundation differed between these two years. The 1992 inundation level was similar to the Exposed treatment and 1994 was similar to the Intermediate treatment. In the tank, spikelet production of plants in the Exposed and Intermediate treatments also varied significantly, with more spikelets per plant produced in the Intermediate treatment. The duration of inundation also differed in those two years, with the 1992 wet season commencing in January in 1992, and the 1994 the wet season in the first week of December 1993. Assuming that flowering is initiated by photoperiod (Tsunoda & Takahashi 1984), this meant an additional 6 weeks of growth prior to flowering in 1994. This potential additional vegetative accumulation prior to the initiation of inflorescences also may have contributed to higher spikelet production in the field populations. Further experimentation would clarify whether the time of commencement and the rate of inundation also control growth and spikelet production.

A model providing an overview of the effect of environmental factors on the growth of *O. meridionalis* is given in Figure 4.
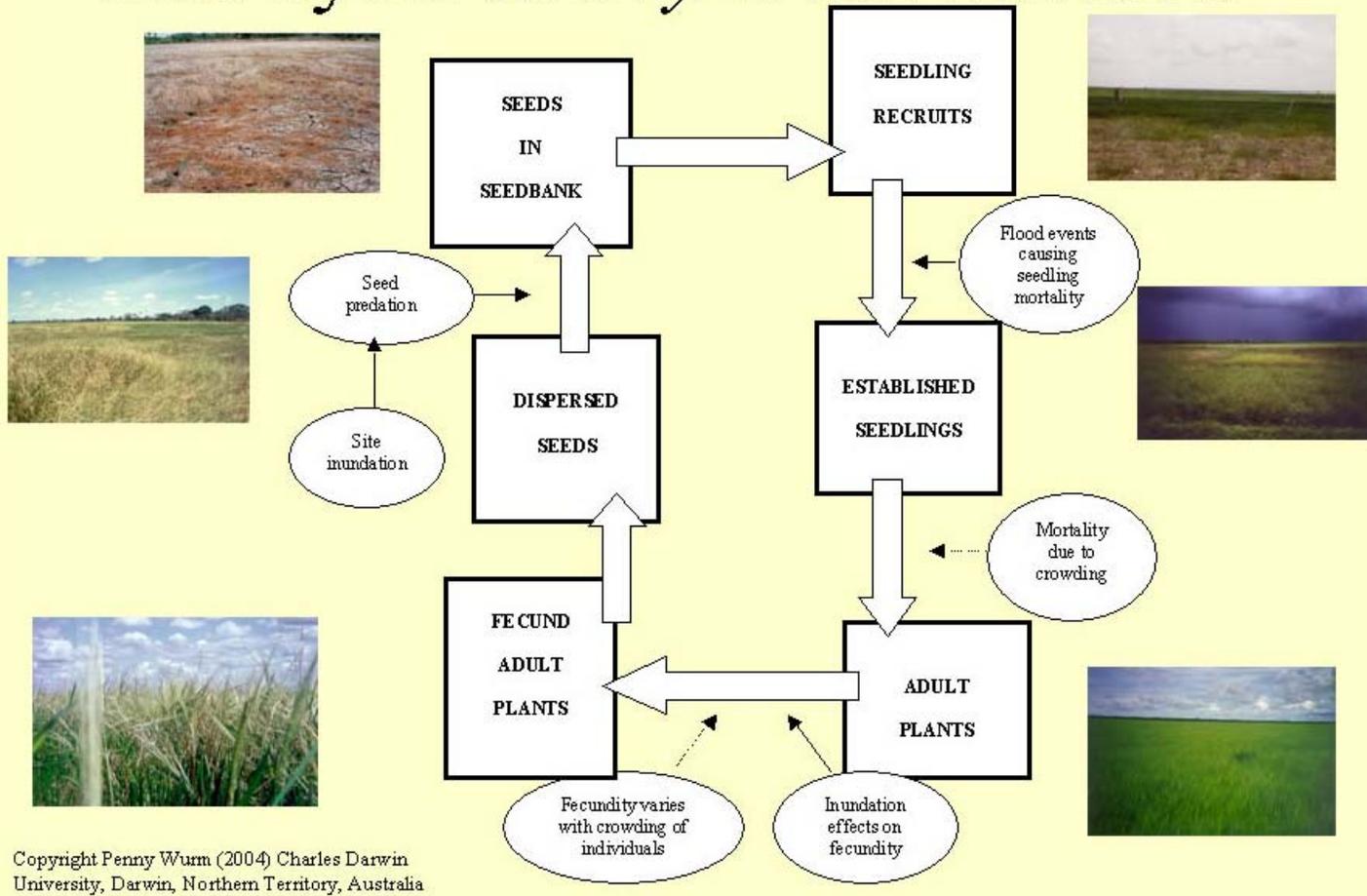
Figure 4. Conceptual model of the life-cycle of *Oryza meridionalis*. Life-cycle stages are represented in squares, regulating effects in shaded ovals and external variables in unshaded ovals. Transitions between life-cycle stages are represented by block arrows, impacts of external variables on transition probabilities are indicated by line arrows, and influences of population regulating factors are indicated by broken lined arrows. The returned arrow at the seed-bank stage of the life-cycle represents those seeds which persist in the soil for more than one dry season. Penny Wurm PhD Thesis 1998.

The results of this study comprise a chapter of a PhD thesis:

Wurm P.A.S. (1998). The population ecology of *Oryza meridionalis* Ng on the South Alligator River floodplain, Kakadu National Park, monsoonal Australia. PhD Thesis, Charles Darwin University, Darwin.

References

Bayliss P. & Yeomans K.M. (1990). Seasonal distribution and abundance of magpie geese, *Anseranus semipalmata* Latham, in the Northern Territory, and their relationship to habitat, 1983-86. *Australian Wildlife Research* **17**: 15-38.

Blom C.W.P.M., BogemannG.M., Laan P., van der Sman A.J.M., van de Steeg H.M. & Voesenek L.A.C.J. (1990). Adaptation to flooding in plants form river areas. *Aquatic Botany* **38**: 29-47.

Botts P.S. & Cowell B.C. (1988). The distribution and abundance of herbaceous angiosperms in west-central Florida marshes. *Aquatic Botany* **32**: 225-238.

Brock M.A. (1986). Adaptation to fluctuations rather than to extremes of environmental parameters. *In* P. De Deckker and W.D. Williams (eds) *Limnology in Australia*, 671 pages. CSIRO, Melbourne and Dr W. Junk Publishers, Dordrecht.

Campbell B.D., Grime J.P.K, Mackey J.M.L. & Jalili A. (1991). The quest for a mechanistic understanding of resource competition in plant communities: the role of experiments. *Functional Ecology* **5**: 241-253.

Carter M.F. & Grace J.B. (1990). Relationships between flooding tolerance, life history and short-term competitive performance in three species of *Polygonum. American Journal of Botany* **77**: 381-387.

Cook G.D. & Heerdegen R.G. (2001). Spatial variation in the duration of the rainy season in monsoonal Australia. *International Journal of Climatology.* **21**: 1723-1732.

Counts R.L. & Lee P.F. (1988a). Patterns of variation in Ontario wild rice *Zizania aquatica* L. 2. Differential responses of populations to varying cultivation conditions. *Aquatic Botany* **31**: 37-55.

Counts R.L. & Lee P.F. (1988b). Patterns of variation in Ontario wild rice *Zizania aquatica* L. 3. Similarity between source and introduced population pairs under experimental and field conditions. *Aquatic Botany* **31**: 37-55.

Cowie I.D., Short P.S. & Osterkamp Madesen M. (2000). Floodplain flora: a flora of the coastal floodplains of the Northern Territory. Flora of Australia Supplementary Series Number 10. Environment Australia, Canberra.

Friend G.R., Dudzinski M.L. & Cellier K.M. (1988). *Rattus coletti* (Rodentia: Muridae) in the Australian wet-dry tropics: seasonal habitat preferences, populations dynamic and the effects of buffalo (*Bubalus bubalis*). *Australian Journal of Ecology* **13**: 51-66.

Frith H.J. & Davies S.J.J.F. (1961). Ecology of the magpie goose *Anseranus semipalmata* Latham (Anatidae). *CSIRO Wildlife Research* **6**: 91-141.

Gopal B. (1986). Vegetation dynamics in temporary and shallow freshwater habitats *Aquatic Botany* <u>23</u> : 391 - 396.

Grace J.B. (1989). Effects of water depth on *Typha latifolia* and *Typha domingensis*. *American Journal of Botany* **76**: 762-768.

Grace J.B. & Wetzel R.G. (1981). Phenotypic and genotypic components ofd growth and reporduction in *Typa latifolia*: experimental studies in marshes of differing successional maturity. *Ecology* **62**: 789-801.

Greening H.S. & Gerritsen J. (1987). Changes in macrophyte community sturcture following drought in the Okefenokee Swamp, Georgia, U.S.A. *Aquatic Botany* **28**: 113-128.

Harper J.L. (1977). *Population ecology of plants*. Academic Press, New York.

HilleRisLambers D. & Seshu D.V. (1982). Some ideas on breeding procedures and requirements for deepwater rice improvement. <u>In</u> *Proceedings of the 1981 International deepwater rice workshop*, pp 29-44. International Rice Research Institute, Philippines.

Humphrey C.L., Bishop K.A. & Brown V.M. (1990). Use of biological monitoring in the assessment of effect of mining wastes on aquatic ecosystems of the Alligator Rivers region, tropical northern Australia. *Environmental Monitoring and Assessment* **14**: 139-181.

Lieffers V.J. & Shay J.M. (1989). The effects of water level on the growth and reproduction of *Scirpus maritimus var. palidosus*. *Canadian Journal of Botany* **59**: 118-121.

Madsen, T. & Shine R. (1996). Seasonal migration of predators and prey - a study of pythons and rats in tropical Australia. *Ecology* **77**: 149 - 156.

Mazaredo A.M. & Vergara B.S. (1982). Physiological differences in rice varieties tolerant of and susceptible to complete submergence. In *Proceedings of the 1981 international deepwater rice workshop,* pp 327-341. International Rice Research Institute, Philippines.

McAlpine J.R. (1976).   Climate and water balance. In R. Story, R.W. Galloway, J.R. McAlpine, J.M. Aldrick & M.A.J. Williams (eds) *Lands of the Alligator Rivers area, Northern Territory.* CSIRO Land Research Series No. 38. CSIRO, Melbourne.

Neill C. (1993). Growth and resource allocatin of whitetop (*Scolochloa festucacea*) along a water depth gradient. *Aquatic Botany* **46**: 235-246.

Rea N. (1992). *The influence of water regime on the population ecology of two emergent macrophytes in South Australia.* PhD Thesis, University of Adelaide, South Australia.

Rea N. & Ganf G.G. (1994a).   How emergent plants experience water regime in a Mediterranean-type wetland. *Aquatic Botany* **49***: 117-136.*

Rea N. & Ganf G.G. (1994b).   Water depth changes and biomass allocation in two contrasting macrophytes. *Australian Journal of Marine and Freshwater Research* **45***: 1459-1468.*

Rea N. & Ganf G.G. (1994c). The role of sexual reproduction and water regime in shaping the distribution patterns of clonal emergent aquatic plants. *Australian Journal of Marine and Freshwater Research* **45***: 1469-1479.*

Redhead T.D. (1979).   On the demography of *Rattus sordidus colletti* in monsoonal Australia. *Australian Journal of Ecology* **4**: 115-136.

Statsoft Incorporated. (1996).   STATISTICA for Windows Version 5.0 Computer programme and manuals. Statsoft Inc., Tulsa Oklahoma.

Stevenson S.C. & Lee P.F. (1987). Ecological relationships of wild rice *Zizania aquatica*. 6. The effects of increases in water depth on vegetative and reproductive production. *Canadian Journal of Botany* **65**: 2128-2132.

Taylor J.A. & Tulloch D. (1985). Rainfall in the wet-dry tropics: Extreme events at Darwin and similarities between years during the period 1870-1983. *Australian Journal of Ecology* **10**, 281-295.

Tsunoda S. & Takahashi N. (1984). *Developments in crop science (7): Biology of rice.* Japan Scientific Societies / Elsevier, Tokyo.

Tulloch D., Cellier K.M. & Hertog A.L. (1988). The distribution of the nests of the magpie goose (*Anseranus semipalmata* Latham) at Kapalga, NT: a four year study. *Australian Journal of Wildlife Research* **15**: 211-21.

van der Valk A.G. & Davis C.B (1980). The impact of a natural draw-down on the growth of four emergent species in a prairie glacial marsh. *Aquatic Botany* **6**: 301-322.

Walker L.R., Zasada J.C. & Chapin F.S. (1986). The role of life history processes in primary succession on an Alaskan floodplain. *Ecology* **67**: 1243-1253.

Weisner S.E.B., Graneli W. & Ekstam B. (1993). Influence of submergence on the growth of seedlings of *Scirpus lacustris* and *Phragmites australis*. *Freshwater Biology* **29**: 371-375.

Whitehead P. & Tschirner K. (1990). Magpie goose *Anseranus semipalmata* nesting on the Mary River floodplain, Northern Territory, Australia: extent and frequency of flooding losses. *Australian Wildlife Research* **17** 147-157.

Williams C.K. (1991). Dusky Rat: *Rattus colletti*. In: *The Complete Book of Australian Mammals* (ed. R.Strahan) pp 441-442. Collins Angus and Robertson Publishers, Australia.

Wilson B.A., Brockelhurst P.S. & Whitehead P.J. (1991). *Classification, distribution and environmental relationships of coastal floodplain vegetation,* Northern Territory, Australia. Technical memorandum no. 91/2, Land management Unit, Conservation Commission of the Northern Territory, Palmerston.

Wurm P.A.S. (1998). The population ecology of *Oryza meridionalis* Ng on the South Alligator River floodplain, Kakadu National Park, monsoonal Australia. PhD Thesis, Charles Darwin University, Darwin.