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# Influences of simulated grazing and water-depth on the growth of juvenile *Bolboschoenus caldwellii*, *Phragmites australis* and *Schoenoplectus validus* plants

Nigel Hayball\*, Meryl Pearce

Strategic Policy, Department of Water, Land and Biodiversity Conservation,  
P.O. Box 240, Berri, SA 5343, Australia

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## Abstract

An experiment in a greenhouse was conducted over a 6-week period to investigate how simulated grazing (i.e. clipping) and submersion affects the growth of three juvenile emergent macrophytes: *Bolboschoenus caldwellii* (V. Cook) Sojak, *Phragmites australis* (Cav.) Trin. ex Steud. and *Schoenoplectus validus* (Vahl) A. Love & D. Love. Five plant traits (total plant length, number of shoots, above-ground biomass, root and rhizome biomass, tuber biomass) were recorded in response to different treatments. Treatments included clipping frequency (i.e. clipped once or clipped every 7 days), clipping intensity (i.e. no clipping, 50% clipped and 100% clipped), and submersion treatments (water-depth of 0 and 10 cm). The general response of the three species to increased clipping frequency and intensity was a greater reduction in above-ground biomass, total plant length and the number of shoots produced. Almost no growth occurred in all three species when clipped 100% every 7 days. Clipping and water-depth treatments had no significant effect on root growth in all three species. Compared to the clipping treatments, the change in water-depth had less effect on the three species growth response. Only the number of shoots produced by *P. australis* was significantly reduced with increased water-depth. The removal of 50% of *S. validus* plant tissue grown in damp conditions (water-depth of 0 cm), however, did not reduce above-ground biomass.

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\* Corresponding author. Tel.: +618-8595-2048; fax: +618-8595-2232.

E-mail address: [hayball.nigel@saugov.sa.gov.au](mailto:hayball.nigel@saugov.sa.gov.au) (N. Hayball).

## 1. Introduction

Emergent macrophytes, by the nature of their habitat, have to establish and survive in often varying water regimes (i.e. depth, rate, duration and timing, predictability) (Brownlow et al., 1994; Casanova and Brock, 2000). Similarly, wetlands attract a diversity of grazing fauna (Lodge, 1991; Jansen and Robertson, 2001; Kingsford and Norman, 2002; van den Wyngaert et al., 2003) that have direct and indirect effects on plant growth: trampling can cause loss of tissue, nutrient availability is altered through defecation, and defoliation leads to a loss of leaf area and nutrients (Crawley, 1983). In particular, the removal of tissue by defoliation can affect plant growth rate by reducing photosynthetic area, which in turn can reduce above-ground net primary production (Crawley, 1983; Heady and Child, 1994), and its ability to reproduce (Crosslé and Brock, 2002).

Grazing and water-depth could interact, leading, for example, to differential susceptibility to grazing along littoral inundation gradients. Deeper water stands may be less subject to cattle grazing from land (Menard et al., 2002), whereas some waterfowl, in contrast, attack from the water (Søndergaard et al., 1996). The degree of impact of this interaction would depend on circumstances such as the type of tissue removed (i.e. leaf, stem, meristem, seeds), the development stage of the plant, the frequency and intensity of defoliation, and flooding duration and depth. Blanch and Brock (1994) observed the effect of grazing and water-depth on two morphologically different aquatic plant species: *Myriophyllum variifolium* J. Hooker and *Eleocharis acuta* R. Br. The recorded changes in plant morphology in response to grazing were highly dependent on whether the plants were non-, partially-, or fully-submerged, and on the frequency and intensity of grazing. Both species were adversely affected by clipping below water levels. Results of a similar experiment by Middleton (1990), showed that individuals of emergent macrophyte species *Ipomoea aquatica* Forssk, *Paspalidium punctatum* A. Camus, and *Paspalum distichum* L. usually died when clipped underwater, but those of anchored floating-leaved *Nymphoides cristatum* Kuntze did not.

Published results (Middleton, 1990; Oesterheld and McNaughton, 1991; Blanch and Brock, 1994), indicate that the interaction of grazing and water-depth on emergent macrophyte growth has only been examined in a few species. The focus of this study was to determine, in a controlled environment, the influence of water-depth and simulated grazing (i.e. different clipping frequencies and intensities) on the growth of juvenile plants of three, relatively common, emergent macrophyte species: *Bolboschoenus caldwelli* (V. Cook) Sojak, *Phragmites australis* (Cav.) Trin. ex Steud. and *Schoenoplectus validus* (Vahl) A. Love and D. Love.

## 2. Materials and methods

### 2.1. Species description

*B. caldwelli* (V. Cook) Sojak is a narrow-leaved perennial with triangular stems, and grows to a height of 1.2 m. In Australia, this species forms extensive, dense stands and is observed to dominate where flooding is less frequent on the elevated perimeters of wetlands (Blanch et al., 1999), whereas *S. validus* (Vahl) A. Love and D. Love mostly occurs at lower elevations

in permanently flooded, stable water level habitats (Chambers et al., 1995). *S. validus* habitats include inland waters, wet depressions and estuaries on coastal plains (Sainty and Jacobs, 1994; Chambers et al., 1995). *P. australis* (Cav.) Trin. ex Steud. is a widespread (Clevering and Lissner, 1999) and abundant perennial that forms large monoclonal stands ranging from the permanently flooded littoral to high on the floodplain (Haslam, 1972; Weisner and Ekstam, 1993).

## 2.2. Experimental design

All seedlings were obtained as juveniles from a local, native plant nursery. The seedlings were grown outside in small rectangular pots (3 cm × 3 cm × 5 cm deep) from seed (*P. australis* and *S. validus*) and from cuttings < 5 cm in height (*Bolboschoenus caldwellii*) collected from local habitats in Adelaide, South Australia: River Torrens (*S. validus* and *P. australis*) and Wingfield (*B. caldwellii*). Previous experiments have shown pot size can limit the growth of a species (McConnaughay et al., 1993). Thus, to enable both below and above-ground growth, seedlings were transplanted from the nursery pots into larger cylindrical pots (10×10×10 cm deep), which had drainage holes. A slow-releasing fertilizer (100 g N m<sup>-2</sup> annum<sup>-1</sup>) was applied to the soil (sand/organic soil mixture) during transplantation of the seedlings. Plants were watered using mains water with a total dissolved solids of 509 mg l<sup>-1</sup>.

A randomized block-design was conducted in a greenhouse (Middleton, 1990; Blanch and Brock, 1994). Each species had 25 seedlings randomly allocated to one tray (damp treatment: water-depth of 0 cm), and 25 seedlings randomly allocated to one perspex tank (submerged treatment: water-depth of 10 cm above the soil surface). After acclimation to depth for 3 weeks, plants were matched for above-ground biomass, shoot length and number of shoots. Five clipping treatments (no clipping (control), clipped once 50%, clipped once 100%, clipped weekly 50%, clipped weekly 100%) were applied to each species in both damp and submerged treatments. For each treatment there were five replicates. The clipping treatments were applied over a 6-week period.

To simulate grazing, each plant was clipped by pulling the plant upwards while it was being snipped by a pair of serrated scissors (Middleton, 1990). Water levels were maintained throughout the experiment. To remove algae and surface scum, water in the tanks was replaced every 7 days (Brock, 2000). Seedlings in the damp treatments were watered every 2–3 days. The temperature of the greenhouse ranged from 10 to 30 °C, simulating normal diurnal temperature fluctuations in the plant species environment during the growing season (September–March). The photoperiod (6 h per day) was however, less than that typical of the growing season (8.25 h per day).

At the end of the sixth week, five plant traits (total plant length, number of shoots, above-ground biomass, root and rhizome biomass, tuber biomass) were recorded to measure the plant growth response to each treatment. The final standing plant material (of both treated, and control plants, i.e. damp, clipped 0%) was then harvested, weighed and analyzed. All plant material was washed over a 1 mm sieve and sorted via the flotation technique. Where possible, dead roots were excluded. Plants were separated into above-ground, roots and rhizomes, and tuber biomass. Plant material was oven dried at 80 °C for 72 h and weighed.

The main factors (i.e. water-depth, clipping frequency and clipping intensity) and their interactive effects on all plant growth response indices were examined by a three-way ANOVA. Data transformations were applied when necessary to meet the assumptions of ANOVA (i.e. normality of distribution and homogeneity of variance). Clipping intensity was the only main factor that comprised more than two levels (i.e. clipped 0, 50 and 100%). If the clipping intensity result was significant then Bonferroni’s post hoc pair-wise comparison test was applied to determine the location of the difference between the means of the variables.

3. Results

For total plant length (Fig. 1a) and number of shoots produced of *B. caldwellii* (Fig. 1b), analysis of variance indicated significant interaction between clipping frequency and clipping intensity (Table 1). With total plant length, a significant interaction also occurred between clipping intensity and water-depth (Fig. 1a). Clipping frequency and clipping intensity had a significant effect on the above-ground biomass (Fig. 1c).

In *P. australis*, clipping intensity significantly reduced total plant length (Fig. 2a), number of shoots (Fig. 2b) produced and above-ground biomass (Fig. 2c; Table 1). Only total plant length was significantly reduced with increased clipping frequency (Fig. 2a). Water-depth significantly affected the number of shoots produced (Fig. 2b). For both damp

Table 1  
Three-way ANOVA of six juvenile plant growth traits after 6 weeks of greenhouse growth for three emergent macrophyte species: *B. caldwellii*, *P. australis* and *S. validus*

Trait	Factor	d.f.	Species					
			<i>B. caldwellii</i>		<i>P. australis</i>		<i>S. validus</i>	
			SS	P	SS	P	SS	P
Plant length	<i>D</i>	1	74	0.275	89	0.400	2572	<0.001
	<i>F</i>	1	11628	<0.001	2016	<0.001	12852	<0.001
	<i>I</i>	2	2804	<0.001	7267	<0.001	8632	<0.001
	<i>D</i> × <i>F</i>	1	160	0.112	29	0.630	1677	<0.001
	<i>F</i> × <i>I</i>	1	1877	<0.001	123	0.324	1381	<0.001
	<i>D</i> × <i>I</i>	2	1017	0.001	430	0.186	472	0.011
	Error	40	2425		4910		1883	
Number of shoots	<i>D</i>	1	97	<0.001	99	0.004	45	0.287
	<i>F</i>	1	68	0.001	10	0.334	116	0.091
	<i>I</i>	2	232	<0.001	410	<0.001	4002	<0.001
	<i>F</i> × <i>I</i>	1	44	0.005	23	0.150	96	0.122
	Error	40	198		418		1544	
Above-ground biomass	<i>D</i>	1	3	0.231	0.134	0.678	43	<0.001
	<i>F</i>	1	23	0.003	1	0.228	16	0.009
	<i>I</i>	2	110	<0.001	38	<0.001	379	<0.001
	Error	40	88		31		86	

Presented are degrees of freedom (d.f.), sums of squares (SS), and level of significance (*P*). Three-way interactions are not presented since they were never significant. *D*, *F* and *I* are explained in Fig. 1.

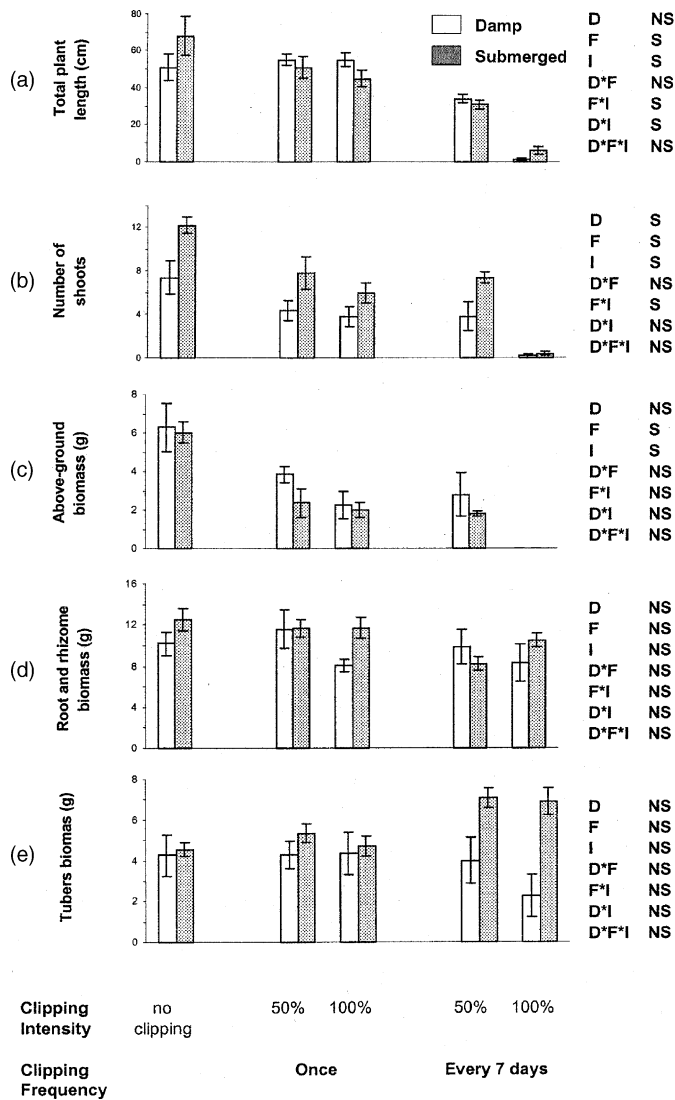


Fig. 1. *B. caldwellii*: (a) total plant length, (b) number of shoots, (c) above-ground biomass, (d) root and rhizome biomass, and (e) tuber biomass (*B. caldwellii* only) from different clipping and water-depth treatments in a greenhouse experiment. Water treatments were: damp (0 cm) (open columns) and submerged (10 cm water-depth) (grey columns). Treatments were applied for 6 weeks and then growth measurements were recorded at the end of the sixth week. All data are given as mean  $\pm$  standard error. Five replicates per treatment (D, depth; F, clipping frequency; I, clipping intensity). Analysis was conducted using ANOVA (see Table 1). Significant levels: NS, not significant; S,  $P < 0.05$ .

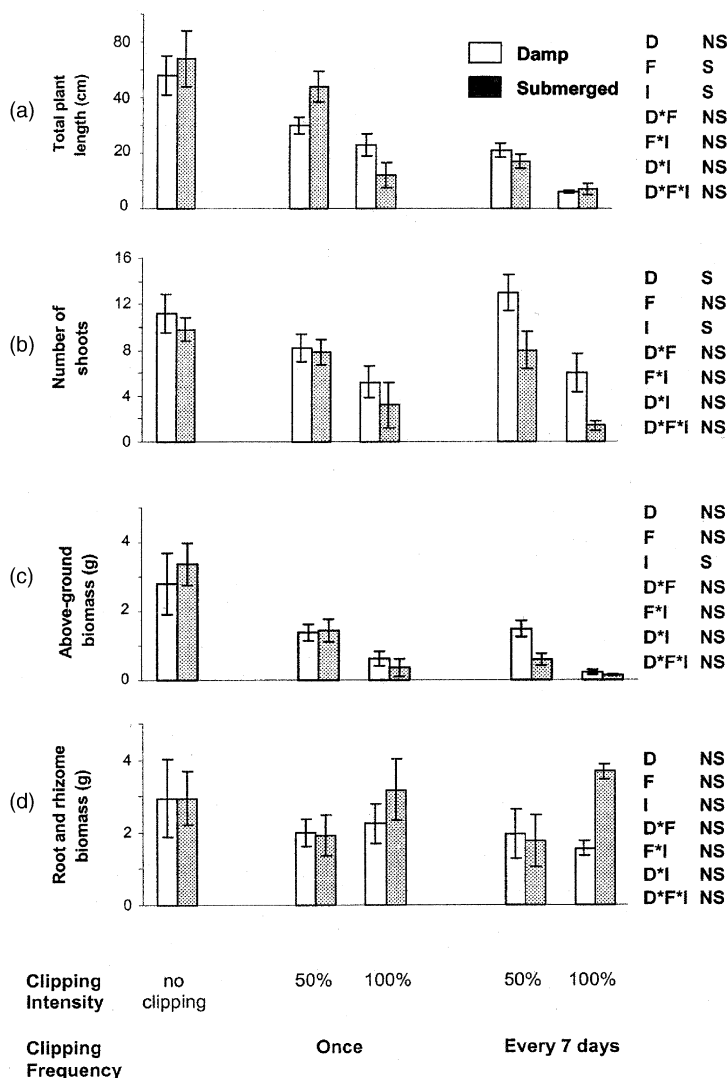


Fig. 2. (a–d) Plant responses in *P. australis* further as Fig. 1.

and submerged plants, total plant length (Fig. 2a) and above-ground biomass (Fig. 2c) were at their lowest when clipped 100% every 7 days.

Analysis of variance indicated a significant two-way interaction (Table 1) between all main factors for total plant length of *S. validis* (Fig. 3a). For example, total plant length (Fig. 3a) was reduced when clipped 100% every 7 days compared to being clipped 100% once. Furthermore, regardless of water-depth, the greatest difference in total plant length occurred between 50 and 100% clipping intensity when clipped every 7 days (Fig. 3a).

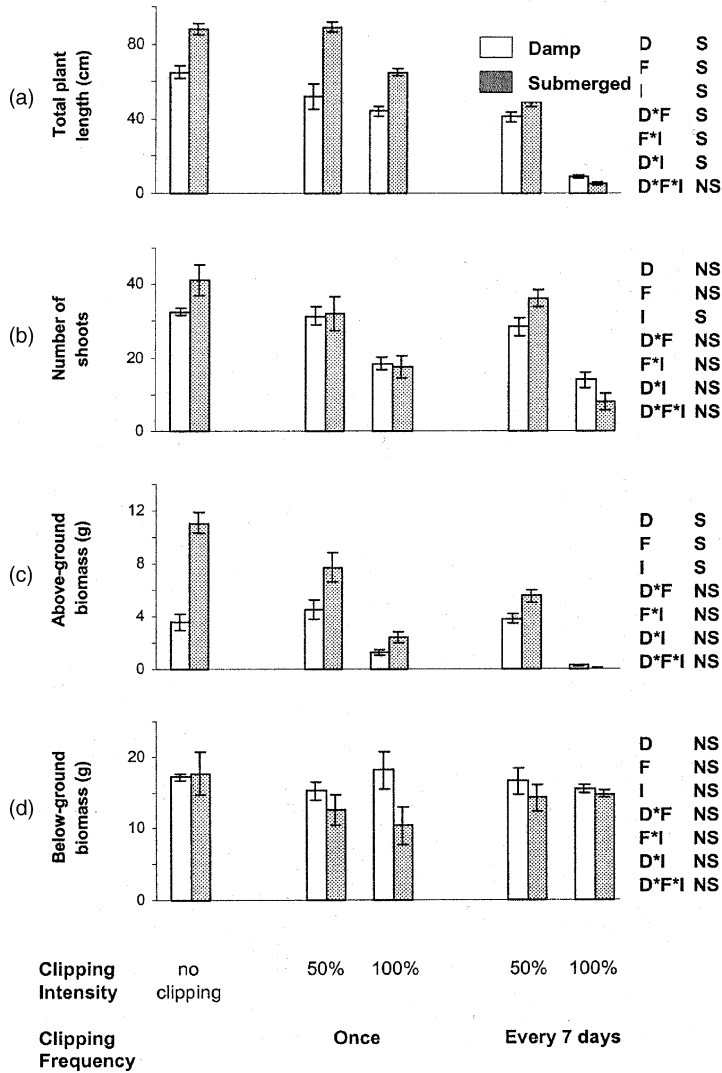


Fig. 3. (a–d) Plant responses in *S. validus* further as Fig. 1.

Clipping frequency, clipping intensity and water-depth had a significant effect on above-ground biomass of *S. validus* (Fig. 3c). However, clipping intensity was the only main factor to significantly reduce the number of shoots produced (Fig. 3b).

In all three species, water-depth, clipping frequency and clipping intensity had no significant effect on root and rhizome biomass (Figs. 1d, 2d and 3d) or tuber biomass (*B. caldwelii* only) (Fig. 1e).

#### 4. Discussion

Previous studies have shown that removal of above-ground biomass tissue affects plant access to a number of resources (i.e. carbon, oxygen and light). For example, [Cížková-Koncalova et al. \(1992\)](#) showed that above-ground photosynthetic tissue is crucial for providing access to atmospheric carbon dioxide in order to produce carbohydrates and support respiration. In this study, the greater removal of above-ground biomass as clipping frequency and clipping intensity increased, could have resulted in plants becoming starved of carbon and their growth being severely affected. Thus, the limited growth that occurred in treatments where almost all above-ground tissue was repeatedly removed at a high clipping intensity (i.e. clipped 100% every 7 days) is not unexpected. Lack of exposed tissue and consequent carbon starvation has also been cited as a cause of reed decline in many European lakes ([Cížková-Koncalova et al., 1992](#)).

The removal of above-ground biomass would also have resulted in the removal of meristems (i.e. intercalary, lateral, apical). Regrowth after apical meristem removal requires an initiation of axillary buds and the development of a new apical meristem from a new bud located on the rhizome, tuber or corm ([Taiz and Zeiger, 1991](#)). The success of regrowth is likely to depend on the relative growth rate (RGR) of individual emergent macrophytes and the frequency of grazing (i.e. clipping).

*B. caldwellii* plants produced a greater number of shoots in submerged grazing treatments than in damp treatments. The temperature in the greenhouse and the submersion of *B. caldwellii* may have simulated optimal growth conditions, i.e. those of early spring (September). However, when the plants were not submerged, greenhouse conditions may have simulated late spring or early summer (December) and the end of the growing season, thereby possibly inducing fewer growth points.

A result that could be misleading was that total plant length of *B. caldwellii* grown in damp conditions increased when clipped at a low frequency and intensity ([Fig. 1a](#)), thus suggesting that growth of *B. caldwellii* was favored by grazing. However, despite the increase in total plant length, grazing pressure reduced the number of shoots produced and above-ground biomass decreased.

Unlike *B. caldwellii* and *S. validus*, *P. australis* grown in damp conditions produced significantly more shoots than when submerged ([Fig. 2b](#)). [Mauchamp et al. \(2001\)](#) found that an increase in submergence inhibited growth of *P. australis*. The authors suggested that *P. australis* had a limited ability to photosynthesize under water. [Weisner and Granéli \(1989\)](#) demonstrated that above-ground growth of *P. australis* is hampered by reducing-substrates and shoot grazing, that impair oxygen transport to the roots. Therefore, it is possible that the additional stress of clipping reduced oxygen transport through the flooded shoots to the below-ground organs. The reduction in oxygen to below-ground organs could impair root functioning, inhibiting growth of *P. australis* and the number of shoots produced ([Vretare and Weisner, 2000](#); [Vretare et al., 2001](#)).

There was no significant change in *B. caldwellii* ([Fig. 1d](#)), *P. australis* ([Fig. 2d](#)) and *S. validus* ([Fig. 3d](#)) root biomass throughout the experiment. The addition of a slow-releasing nutrient fertilizer to stimulate the growth of seedlings at the start of the experiment, would have influenced this result (c.f. [Squires and van der Valk, 1992](#); [Coops et al., 1996](#)). The tuber biomass of *B. caldwellii* did not significantly change during the experiment. Studies



(Čižková-Koncalova et al., 1992; Grace, 1993) have reported emergent plant tubers being viable after 2 or more years. In considering this result, Grace (1993) postulated that this response might be a strategy aimed at surviving destructive disturbances such as inundation and grazing.

It is unlikely that temperature and photoperiod were as influential in reducing growth in the three juvenile species as either grazing pressure or water-depth. The diurnal temperature in the greenhouse matched the optimal growth temperatures (September–October) for all three species. Furthermore, the photoperiod for most of the experiment was equivalent to the early regrowth photoperiod.

In conclusion, results from this study demonstrate, at least in a controlled environment (i.e. greenhouse), that grazing can have a detrimental effect on the growth of juvenile *B. caldwelii*, *P. phragmites* and *S. validus* plants. The interaction of water-depth and grazing (i.e. clipping intensity and frequency), however, has less of an effect on juvenile emergent macrophyte growth than grazing alone; these findings are similar to those of Middleton (1990), Oosterheld and McNaughton (1991), and Blanch and Brock (1994). Furthermore, our results suggest that a mild grazing regime (i.e. clipped 50%) may not affect the growth of juvenile *S. validus* plants.

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## References

- Blanch, S.J., Brock, M.A., 1994. Effects of grazing and depth on two wetland plant species. *Aust. J. Mar. Freshwater Res.* 45, 1387–1394.
- Blanch, S.J., Ganf, G.G., Walker, K.F., 1999. Tolerance of riverine plants to flooding and exposure indicated by water regime. *Regul. River* 15, 43–62.
- Brock, M.A., 2000. How do water regime and grazing alter the reproductive capacity of aquatic plants? Final Report, National Wetland R&D Program, Environment Australia/LWRRDC, Canberra.
- Brownlow, M.D., Sparrow, A.D., Ganf, G.G., 1994. Classification of water regimes in systems of fluctuating water level. *Aust. J. Mar. Freshwater Res.* 45, 1375–1386.
- Casanova, M.T., Brock, M.A., 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecol.* 147, 237–250.
- Chambers, J.M., Fletcher, N.L., McComb, A.J., 1995. A Guide to Emergent Wetland Plants of South-Western Australia. The Marine and Freshwater Research Laboratory, Murdoch University, Perth.
- Čižková-Koncalova, H., Kvet, J., Thompson, K., 1992. Carbon starvation: a key to reed decline in eutrophic lakes. *Aquat. Bot.* 43, 105–113.
- Clevering, O.A., Lissner, J., 1999. Taxonomy, chromosome numbers, clonal diversity and population dynamics of *Phragmites australis*. *Aquat. Bot.* 64, 185–208.
- Coops, H., van den Brink, F.W.B., van der Velde, G., 1996. Growth and morphological responses of four helophyte species in an experimental water-depth gradient. *Aquat. Bot.* 54, 11–24.
- Crawley, M.J., 1983. *Herbivory: The Dynamics of Animal–Plant Interactions*. Blackwell Scientific, Oxford.

- Crosslé, K., Brock, M.A., 2002. How do water regime and clipping influence wetland plant establishment from seed banks and subsequent reproduction? *Aquat. Bot.* 74, 43–56.
- Grace, J.B., 1993. The adaptive significance of clonal reproduction in angiosperms: an aquatic perspective. *Aquat. Bot.* 44, 159–180.
- Haslam, S.M., 1972. Biological flora of the British Isles. *Phragmites communis* Trin. *J. Ecol.* 60, 585–610.
- Heady, H.F., Child, D.R., 1994. *Rangeland Ecology and Management*. Westview Press, Oxford.
- Jansen, A., Robertson, A.I., 2001. Relationships between livestock management and the ecological condition of riparian habitats along an Australian floodplain river. *J. Appl. Ecol.* 38, 63–75.
- Kingsford, R.T., Norman, F.I., 2002. Australian waterbirds: products of the continent's ecology. *Emu* 102, 47–69.
- Lodge, D.M., 1991. Herbivory on freshwater macrophytes. *Aquat. Bot.* 41, 195–224.
- Mauchamp, A., Blanch, S., Grillas, P., 2001. Effects of submergence on the growth of *Phragmites australis* seedlings. *Aquat. Bot.* 69, 147–164.
- McConaughay, K.D.M., Bernston, G.M., Bazzaz, F.A., 1993. Limitations to CO<sub>2</sub> induced growth enhancement in pot studies. *Oecologia (Berl.)* 94, 550–557.
- Menard, C., Duncan, P., Fleurance, G., Georges, J.-Y., Lila, M., 2002. Comparative foraging and nutrition of horses and cattle in European wetlands. *J. Appl. Ecol.* 39, 120–133.
- Middleton, B., 1990. Effect of water depth and clipping frequency on the growth and survival of four wetland plant species. *Aquat. Bot.* 37, 189–196.
- Oosterheld, M., McNaughton, S.J., 1991. Interactive effect of flooding and grazing on the growth of Serengeti grasses. *Oecologia (Berl.)* 88, 153–156.
- Sainty, G.R., Jacobs, S.W.L., 1994. *Waterplants in Australia*, third ed. Sainty and Associates, Darlinghurst.
- Søndergaard, M., Bruun, L., Lauridsen, T., Jeppesen, E., Madsen, T.V., 1996. The impact of grazing waterfowl on submerged macrophytes: in situ experiments in a shallow eutrophic lake. *Aquat. Bot.* 53, 73–84.
- Squires, L., van der Valk, A.G., 1992. Water-depth tolerances of the dominant emergent macrophytes of the Delta Marsh, Manitoba. *Can. J. Bot.* 70, 1860–1867.
- Taiz, L., Zeiger, Z., 1991. *Plant Physiology*. Benjamin/Cummings, Redwood City.
- van den Wyngaert, I.J.J., Wienk, L.D., Sollie, S., Bobbink, R., Verhoeven, J.T.A., 2003. Long-term effects of yearly grazing by moulting Greylag geese (*Anser anser*) on reed (*Phragmites australis*) growth and nutrient dynamics. *Aquat. Bot.* 75, 229–248.
- Vretare, V., Weisner, S.E.B., 2000. Influence of pressurized ventilation on performance of an emergent macrophyte (*Phragmites australis*). *J. Ecol.* 88, 978–987.
- Vretare, V., Weisner, S.E.B., Strand, J.A., Granéli, W., 2001. Phenotypic plasticity in *Phragmites australis* as a functional response to water depth. *Aquat. Bot.* 69, 127–145.
- Weisner, S.E.B., Ekstam, B., 1993. Influence of germination time on juvenile performance of *Phragmites australis* on temporarily exposed bottoms – implications for the colonization of lake beds. *Aquat. Bot.* 45, 107–118.
- Weisner, S.E.B., Granéli, W., 1989. Influence of substrate conditions on the growth of *Phragmites australis* after a reduction in oxygen transport to below-ground parts. *Aquat. Bot.* 35, 71–80.