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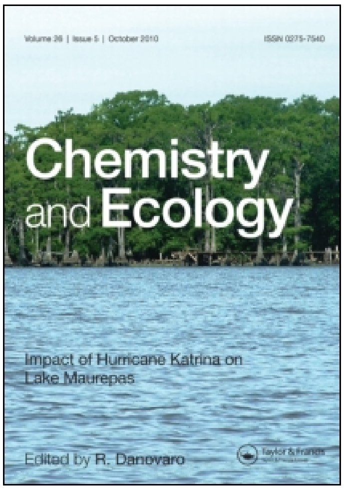

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# Effects of water depth and litter accumulation on morpho-ecological adaptations of *Eleocharis sphacelata*

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The morpho-ecological adaptations of *Eleocharis sphacelata* in response to water depth and the sequential effects of resultant differences in deep water conditions on the long term population dynamics were investigated based on the observations carried out in three stable homogeneous populations in Goulburn and Ourimbah, New South Wales, Australia from August 2003 to May 2005. The deep water populations attained a higher harvestable shoot biomass and a lower rhizome biomass with increased growth in root structure thus significantly enhancing the nutrient uptake rates leading to a higher accumulation of shoot bound macronutrients. However, the accretion of excessive amounts of autogenous shoot litter coupled with slower decomposition rates under anaerobic conditions in the two deep water populations led to higher nutrient enrichment in sediments and overlying water column causing subsequent eutrophication with signs of growth inhibition including typical stress symptoms like stunted growth and chlorotic shoots. The shallow water population that intermittently experienced alternative inundation-drawdown pattern depicted an unaffected continuation of seasonal growth affirming that strict water regime management practices coupled with timely mowing or the removal of accumulating litter are necessary to ensure long-term survival of healthy *E. sphacelata* stands when it is used in applications where deep water conditions prevail.

*Keywords*: *Eleocharis sphacelata*; Eutrophication; Litter accumulation; Morphological adaptations; Nutrient uptake

## 1. Introduction

Macrophytes are commonly used in constructed wetlands for the treatment of contaminated water [1, 2]. Assimilation of nitrogenous compounds and phosphorus in plant tissues and the potential to recover biomass after being harvested are amongst current criteria for species selection for macrophyte-based wastewater treatment systems [2, 3]. It has been noted that the ability of certain species to adjust to continuously changing conditions outside of life-history events serves as an important aspect of survival in variable environments [4]. Such

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adaptations allow those species to be used in a wide range of applications under varying biotic, abiotic, and edaphic conditions [5, 6].

The tall, stout sedge of Cyperaceae family, *Eleocharis sphacelata* R. Br., is a common emergent hydrophyte that colonizes littoral zones of rivers and shallow lakes throughout the Australasian region. This species has, in the recent past, been quoted as exemplar of the process of progressively adapting to shallow to 3 m depth in sheltered sites, by means of a range of morphological transmutations ensuing higher proportionate above- to belowground biomass allocation ratio [7, 8] coupled with anatomical differentiations like augmented tissue porosity in deep water [7–9]. *Eleocharis sphacelata* has also been recognized as a species apposite for macrophyte based wastewater treatment systems in view of its large biomass, invigorated regrowth after being harvested and higher nutrient uptake characteristics [8, 10, 11].

However, a large portion of the biomass produced by this aquatic macrophyte species remains in the area to decompose, with little exportation to other locations. The accumulation of excessive proportions of autochthonous litter is known to be detrimental for the long-term survival of plant communities [12–15]. Several studies have emphasised the functional responses of *E. sphacelata* of augmenting the proportionate biomass allocation to aboveground organs at the cost of diminishing rhizome structure in deep water [7, 8]. However, no detailed synopsis addressing the plausible consequences of resultant excessive litter accretion and altered nutrient dynamics due to imbalanced biomass allocation to shoot and rhizome structures on the long-term population dynamics of *E. sphacelata* has been published to date.

A strictly experimental approach was deemed unfeasible because ecological changes involve soil organic matter and nutrient pools with long turnover times, and because future conditions may include new combinations of demographic patterns, water stress, soil properties and temperature regimes [16]. Thus, we conducted a series of experiments on three stable monoculture populations of *E. sphacelata* established under different water regimes in Goulburn and Ourimbah, Australia to investigate and distinguish the associated morpho-ecological adaptations and subsequent interactive effects of diminished belowground structure on the seasonal nutrient dynamics and excessive shoot litter accretion on the long-term ecology and survival characteristics of individual populations.

## 2. Methods and Materials

Two stable *E. sphacelata* populations in Rowes Lagoon, Goulburn in shallow (water depth of 0.3 m in spring and early summer, dry afterwards) and deep (water depth ∼0.95 m throughout) areas, respectively and another population in a permanent deep water pond (water depth ∼0.75 m throughout) in Ourimbah of New South Wales, Australia, were monitored during the investigation which spanned from August 2003 to May 2005, covering two annual growth cycles. Biomass sampling was carried out at monthly to bimonthly intervals until December 2004, and in situ shoot count data were collected again in May 2005 for comparative purposes.

### 2.1 *Study sites*

Rowes (Rose) Lagoon (34° 44′ S and 149° 44′ E, ∼702 m above MSL) is located 65 km north of Canberra, Australia. The shallow basin of the lagoon, with an area of nearly 100 ha was homogeneously covered with *E. sphacelata*. The mean annual precipitation of Goulburn is about 600 mm and the mean annual temperature is 14.1 °C, with the January (summer) mean being 26.6 °C, and the July (winter) mean being 6.1 °C. An additional study plot of *E. sphacelata* confined to a ∼0.95 m deep waterhole located about 500 m from the regular sampling area in Rowes Lagoon was monitored to envisage the effect of persistent waterlogged conditions on the stands under similar climatic conditions (hereafter referred to as Goulburn-deep site). Above- and belowground material were harvested only in September and December 2004 and in May 2005 from this site, to avoid causing strong disturbances to the patches relatively smaller in size. *Eleocharis sphacelata* in Ourimbah (33° 21′ S and 151° 22′ E, ~20 m above MSL) had established in a swamped pond of approximately 0.8 ha, and 0.75 m in depth. The mean annual precipitation of Ourimbah is about 1120 mm and the mean annual temperature is about 18.0 °C, with the January (summer) mean being 24.5 °C, and the July (winter) mean being 11.1 °C. All *E. sphacelata* monospecific areas had a ~15–20 cm thick layer of shoot detritus overlying the peaty sediment with a modicum of sand in the shallow water population and organic, soft bottom sediments in deep water, with moderate nutrient concentrations [8, 14] when measured at the beginning of the first growing season in October 2003. The thicknesses of the accreted detritus layers in two deep water populations were measured to be ~30–35 cm in the aftermath of the second growing season whilst that of the shallow-water population remained more or less unchanged.

### 2.2 *Sampling, sorting and morphological measurements*

Sampling was carried out in triplicate in quadrats of 0.125 $m^2$ (0.25 m × 0.50 m), periodically distributed at random. Whole plants were excavated with a garden spade to a minimum depth of 0.5 m and once moved to the laboratory, the rhizomatous soil blocks were washed and samples were separated into different organs. The aboveground biomass was classified into live and dead (more than 50% of the shoot height devoid of green tissues) shoot categories based on the shoot chlorophyllous composition whilst all broken, decaying shoots were classified as detritus. The belowground biomass with interconnected rhizomes and roots was separated by clipping, and the roots were sorted into live and dead portions respectively, based on the colour, texture and rigidity/sponginess. Rhizomes were sorted into four age categories: newly formed, full-grown, mature/senescing, and dead, adopting the rhizome age classification methodology earlier proposed for *Phragmites australis* [17] to the sturdy, less poriferous, auburn rhizomes of *E. sphacelata.* After categorizing, all materials were labelled, measured and counted, and then dried in a forced draught oven, at 65 °C for a minimum of 3 days or until a constant weight is attained. Measured biomass data are expressed in grams of dry weight per square meter (g DW $m^{-2}$).

### 2.3 *Total nitrogen (TN) and total phosphorous (TP) concentrations*

Representative portions of dried rhizome and shoot material were finely ground in a stainless steel Wiley mill to pass through a number 40 screen and homogenized subsamples were analyzed in triplicate for nutrient concentrations. TN was determined by CHN Elemental Analyzer (Yanako CHN Corder® MT-5, Auto Sampler® MTA-3), while TP was determined spectrophotometrically (Hach® DR/4000U) following the molybdenate method for liberated $PO_4$ from solutions obtained from respective organs by wet digestion [17]. TN and TP standing stock per unit area (1 $m^2$) were calculated from the measured dry mass of each rhizome and shoot categories and concentrations of the aforementioned compounds. Sediment cores of the top 5 cm after removing the overlying detritus were collected in triplicate, dried, ground and homogenised before testing for organic content, total nitrogen and total phosphorus concentrations.

### 2.4 *Water quality parameters*

The *in situ* water quality measurements of temperature, pH, conductivity and dissolved oxygen were conducted on each sampling date in two deep water populations using a multi probe data logger (Yeocal® 606-SDL). Colour was measured spectrophotometrically (Hach® DR/4000U) at 400 nm. Laboratory tests for total nitrogen and phosphorous were performed in triplicate on subsamples transported and stored in cold boxes, following standard laboratory procedures [18].

### 2.5 *Data analysis and statistics*

The data were statistically analyzed using analysis of variance (ANOVA) with Tukey's multiple comparison and Bonferroni's post hoc pair-wise comparison as post-tests. Unpaired *t*-test was used to evaluate differences between two independent means. Data were pre-analyzed to ensure normality and log transformed when required to approach homogeneity of variance. Statistical analyses were performed with SPSS for Windows (release 11, SPSS Inc., Chicago, IL) statistical software package. All the mean values presented herein are given as mean ± 1SD.

## 3. Results and Discussion

Table 1 illustrates the sediment physicochemical characteristics in March 2004 and May 2005.

The two deep water populations in Goulburn and Ourimbah portrayed similar growth and biomass development characteristics but the Goulburn-shallow population depicted a distinctive growth form (table 2a,b), asserting that the water level posed a predominant effect in determining the ecology, reproductive behaviour and resource partitioning of *E. sphacelata*, in comparison to the overall influence of geographical variations between Goulburn and Ourimbah.

Table 1. Sediment total nitrogen, total phosphorous, organic content (determined as loss of ignition at 550° C) and water content (forced oven drying at 105° C for 48 hrs) in the three study sites (mean ± SD).

a) As measured in March 2004

| | Goulburn-shallow | Ourimbah | Goulburn-deep |
|---|---|---|---|
| Total nitrogen (mg/kg) | 3070 ± 222 | 3100 ± 181 | 2970 ± 240 |
| Total phosphorous (mg/kg) | 231 ± 34 | 110 ± 15 | 174 ± 23 |
| Organic content (%) | 13.1 ± 1.2 | 24.8 ± 2.7 | 19.7 ± 2.3 |
| Water content (%) | 7.1 ± 1.6 | 39.8 ± 3.6 | 43.8 ± 5.1 |

b) As measured in May 2005

| | Goulburn-shallow | Ourimbah | Goulburn-deep |
|---|---|---|---|
| Total nitrogen (mg/kg) | 3427 ± 316 | 7263 ± 326 | 8321 ± 430 |
| Total phosphorous (mg/kg) | 318 ± 53 | 914 ± 171 | 1229 ± 197 |
| Organic content (%) | 16.3 ± 2.2 | 33.2 ± 3.4 | 41.6 ± 4.9 |
| Water content (%) | 11.1 ± 2.3 | 46.8 ± 4.7 | 53.7 ± 6.3 |

Table 2. Live and dead (including detritus) biomass and rhizome, shoot, root morphological characteristics of *E. sphacelata* in the populations studied (mean ± SD).

a) Maximum values observed in Goulburn-shallow and Ourimbah (deep) populations, month observed and significant differences between means as revealed by *t*-test

| | Units | Goulburn-shallow | | Ourimbah | | *t*-test |
|---|---|---|---|---|---|---|
| AGB – living | $g\,m^{-2}$ | 1601 ± 248 | Feb. 04 | 2488 ± 181 | Feb. 04 | $< 0.05$ |
| AGB – dead | $g\,m^{-2}$ | 3270 ± 727 | May 04 | 2667 ± 487 | Sep. 04 | $> 0.05$ |
| BGB – living | $g\,m^{-2}$ | 7280 ± 1480 | Feb. 04 | 2902 ± 778 | Mar. 04 | $< 0.05$ |
| BGB – dead | $g\,m^{-2}$ | 1435 ± 190 | Dec. 04 | 876 ± 234 | Dec. 04 | $< 0.01$ |
| AGB/BGB (Total) | ratio | 0.57 ± 0.07 | Dec. 04 | 2.05 ± 0.46 | Dec. 04 | $< 0.01$ |
| AGB/BGB (Live) | ratio | 0.25 ± 0.03 | Dec. 04 | 1.46 ± 0.32 | Dec. 04 | $< 0.01$ |
| Rhizome length | $m\,m^{-2}$ | 40.2 ± 6.7 | Feb. 04 | 14.7 ± 2.7 | Feb. 04 | $< 0.05$ |
| Root biomass | $g\,m^{-2}$ | 817 ± 214 | Feb. 04 | 1195 ± 240 | Mar. 04 | $> 0.05$ |
| Root/rhizome (biomass) | % | 15.2 ± 2.3 | Jan. 04 | 77.5 ± 24.3 | Feb. 04 | $< 0.05$ |
| Live shoots | no. $m^{-2}$ | 1451 ± 366 | Jan. 04 | 643 ± 69 | Feb. 04 | $< 0.05$ |
| Dead shoots | no. $m^{-2}$ | 2960 ± 681 | May 04 | 1603 ± 424 | May 04 | $> 0.05$ |
| Total shoots | no. $m^{-2}$ | 4107 ± 82 | Jan. 04 | 2069 ± 422 | May 04 | $< 0.05$ |
| FL/NFL shoots | % | 12.9 ± 3.1 | Feb. 04 | 44.8 ± 8.9 | Dec. 03 | $< 0.01$ |
| Avg. shoot height | cm | 95.9 ± 31.6 | Jan. 04 | 190.2 ± 41.2 | Feb. 04 | $< 0.05$ |
| Max. shoot height | cm | 145.0 ± 31.3 | Feb. 04 | 305.0 ± 57.7 | Dec. 04 | $< 0.05$ |

AGB, BGB: above-, belowground biomass;
FL/NFL: ratio of flowering/non-flowering shoots

b) Values observed in the three *E. sphacelata* populations in September 2004

| | Units | Goulburn-shallow | | Ourimbah (deep) | | Goulburn-deep | |
|---|---|---|---|---|---|---|---|
| AGB – live | $g\,m^{-2}$ | 68 ± 34 | a | 693 ± 333 | a,b | 840 ± 159 | b |
| AGB – dead | $g\,m^{-2}$ | 3021 ± 399 | a | 2667 ± 487 | a | 2992 ± 878 | a |
| BGB – live | $g\,m^{-2}$ | 4635 ± 713 | a | 1439 ± 300 | b | 2601 ± 661 | a,b |
| BGB – dead | $g\,m^{-2}$ | 1435 ± 190 | a | 876 ± 234 | b | 747 ± 114 | b |
| AGB/BGB (Total) | ratio | 0.51 ± 0.02 | a | 1.45 ± 0.15 | b | 1.17 ± 0.33 | b |
| AGB/BGB (Live) | ratio | 0.01 ± 0.01 | a | 0.37 ± 0.15 | b | 0.30 ± 0.11 | b |
| Rhizome length | $m\,m^{-2}$ | 35.2 ± 4.4 | a | 10.5 ± 2.4 | b | 16.0 ± 4.8 | b |
| Root biomass | $g\,m^{-2}$ | 494 ± 84 | a | 655 ± 103 | b | 648 ± 50 | b |
| Root/rhizome (biomass) | % | 10.9 ± 3.2 | a | 55.1 ± 19.6 | b | 26.4 ± 4.9 | b |
| Live shoots | no. $m^{-2}$ | 432 ± 123 | a | 235 ± 100 | a | 365 ± 17 | a |
| Dead shoots | no. $m^{-2}$ | 1725 ± 718 | a | 1088 ± 166 | a | 1357 ± 201 | a |
| Total shoots | no. $m^{-2}$ | 2157 ± 829 | a | 1323 ± 133 | a | 1723 ± 200 | b |
| Avg. shoot height | cm | N/A | – | 200.7 ± 49.3 | a | 237.2 ± 26.0 | a |
| Max. shoot height | cm | N/A | – | 238.3 ± 7.6 | a | 297. ± 27.8 | a |

AGB, BGB: above-, belowground biomass; N/A: No aboveground biomass
Different letters within each row indicate significant differences between means as revealed by ANOVA and Tukey tests ($P < 0.05$).

### 3.1 *Growth and morphological adaptations*

The *E. sphacelata* population in Goulburn-shallow site produced a larger number of fine, wiry shoots in contrast to the longer, robust shoots observed in two deep water populations in Goulburn and Ourimbah. The deep water populations attained a significantly higher peak aboveground biomass (figure 1) and maintained higher root/rhizome and above-/belowground biomass ratios (*t*-test, all $P < 0.05$) throughout the period of investigation. The maximum belowground biomass observed for the Ourimbah (deep) population in late summer was $\sim$2.5 times lower than that of shallow water population in Goulburn. The above morphological adaptations observed in shallow versus deep water populations for *E. sphacelata* during the period of investigation matched with those reported by Sorrell *et al.* [8].

The distinct patterns of biomass production and accumulation in shallow versus deep water portray the capacity of *E. sphacelata* to effectively acclimatise to deep water with phenotypic

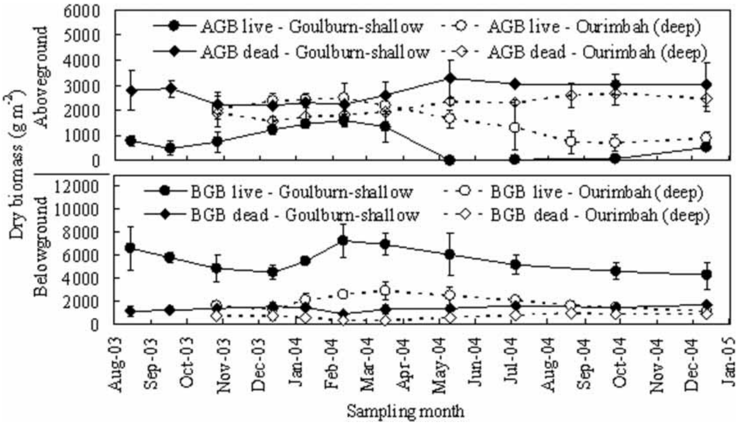

Figure 1. Seasonal variation of above- and belowground live and dead (including detritus) dry biomass (AGB, BGB) as observed in Goulburn-shallow and Ourimbah (deep) populations (mean ± SD).

plasticity through allocating more resources to shoot weight by producing fewer but taller shoots to maintain a positive carbon balance and an effective gas exchange between aerial and belowground parts [7, 8].

### 3.2 *Total nitrogen and total phosphorous (TN, TP) uptake and retention dynamics*

Amongst the aboveground organs, TN and TP concentrations were higher in newly formed shoots over the growing season in January–February 2004, and the shoots of Ourimbah (deep) population contained slightly higher TN, TP concentrations for all measured categories (table 3). The formation of fresh adventitious roots immediately preceding a growing season enhances the plant nutrient uptake rates [20], causing newly formed shoots to contain higher nutrient concentrations. The mean aboveground maximum TN stocks in Goulburn-shallow and Ourimbah populations were $18.2 \pm 0.51$ and $35.9 \pm 2.5\,\mathrm{g\,TN\,m^{-2}}$ whilst the maximum TP stocks were $0.760 \pm 0.342$ and $1.645 \pm 0.342\,\mathrm{g\,TP\,m^{-2}}$, correspondingly in March 2004.

The nutrient uptake and storage behaviour of *E. sphacelata* populations in shallow versus deep water differed significantly (ANOVA, $P < 0.05$) and different age categories of rhizomes had varying nutrient concentrations (figure 2). The decrease in shoot and rhizomatous nutrient concentrations over the growing period is ostensibly due to the dilution in a growing high aboveground biomass [21]. The TN dynamics of Goulburn-shallow population seemingly had an annual pattern that is coherent with translocation to shoots in spring and early summer causing depletion in rhizomes, suggesting a limited root uptake. Either the higher availability or higher uptake rates of TN in Ourimbah population conceivably demoted the need for an

Table 3. Maximum aboveground total nitrogen (TN), total phosphorous (TP) concentrations (dry w/w) observed in Goulburn-shallow and Ourimbah (deep) populations (mean ± SD).

| | Goulburn-shallow | | Ourimbah (deep) | |
|---|---|---|---|---|
| Shoot category | TN (%) | TP (%) | TN (%) | TP (%) |
| Newly formed | 2.01 ± 0.57 | 0.092 ± 0.019 | 2.37 ± 0.61 | 0.135 ± 0.013 |
| Full-grown | 1.132 ± 0.185 | 0.056 ± 0.011 | 1.566 ± 0.422 | 0.074 ± 0.009 |
| Mature/senescing | 0.463 ± 0.114 | 0.025 ± 0.004 | 0.582 ± 0.099 | 0.038 ± 0.007 |
| Dead/detritus | 0.295 ± 0.067 | 0.017 ± 0.003 | 0.451 ± 0.031 | 0.021 ± 0.004 |

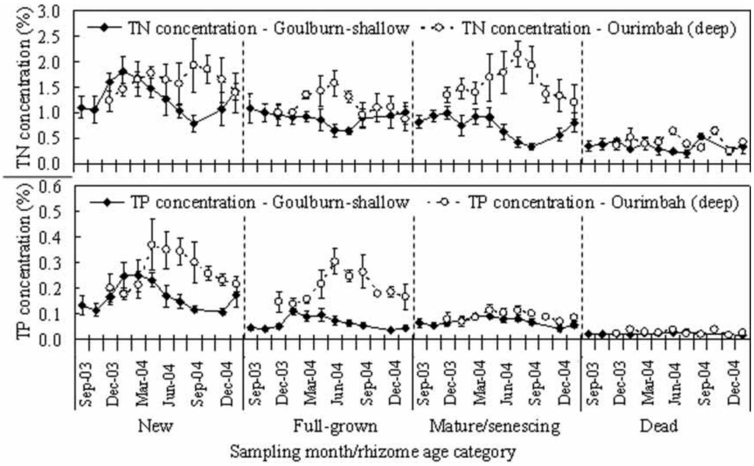

Figure 2. Seasonal variation in age specific rhizomatous total nitrogen and total phosphorous (TN, TP) concentrations for Goulburn-shallow and Ourimbah (deep) populations (mean ± SD).

efficient internal recycling between shoots and rhizomes. However, the TP concentrations in live rhizome categories in both Goulburn and Ourimbah populations followed a similar accumulation-depletion pattern with all the rhizome categories of Goulburn population having relatively lower TP concentrations (ANOVA, $P < 0.05$).

Plants respond to waterlogged or reduced soil conditions by forming adventitious or water roots [19]. In contrast to the shallow water population, the two deep water populations produced larger biomass of fresh roots, longer and thicker in morphology. Based on the results of laboratory experiments using indicator gels with colorant tracers, Sorrell and Orr [20] detailed that only the new roots of *E. sphacelata* are active in nutrient and photon exchange with the rhizosphere sediments and that $NH_4^+$ is assimilated at a faster rate than $NO_3^-$ did. Therefore, *E. sphacelata*, grown in deep water where more anaerobic conditions prevail, is capable of maintaining higher nutrient uptake rates via overly developed new root biomass in comparison to its shallow water counterparts. The initial TN concentration in sediments did not differ amongst the sites studied (ANOVA, $P > 0.05$), but the TP and organic contents were lower in Goulburn-shallow site in comparison to Ourimbah and Goulburn-deep sites. Sorrell *et al.* [8] and Tanner [22] remarked that apart from the enhanced growth of emergent plants in organic substrates due to greater nutrient availability, even small additions of organic matter to mineral nutrient solutions that otherwise saturate growth can further endorse and boost up the growth of emergent macrophytes, perhaps due to chelation effects [23]. In addition to the higher fresh root biomass, the overall percent root biomass was also significantly higher in the deep water *E. sphacelata* populations compared to the shallow water counterparts and in contrast to the reduced overall belowground biomass. *Eleocharis cellulosa* is known to show a similar behaviour to flooding and P-enrichment as *Typha domingensis* with a strong response of root density to P-availability, reaching higher root density with higher P-availability [24] and alternatively, root and rhizome biomass and length determining the utilization of nutrient resources in the soil [6].

Whilst the observed results in the present study provide strong evidence of contrasting adaptive responses of *E. sphacelata* to varying water depths and associated nutrient conditions, only circumstantial evidence is available on the exact mechanisms that triggered the responses observed. However, the aforementioned accumulation-depletion behaviour and the higher nutrient concentrations in the detritus in Ourimbah population suggest that *E. sphacelata* in

Goulburn and Ourimbah adapted two different ecophysiological strategies in storage behaviour similar to that explained by Kühl *et al.* [16]; the "translocation type", more adapted on nutrient poor sites and the "assimilation type" that prefers to settle on nutrient rich sites, respectively. Greenway and Woolley [11] reported that cropping appeared to invigorate the growth in *E. sphacelata*, which took only two months to achieve the initial biomass standing stock with tissue nutrient concentrations reaching as high as $9.4\,\mathrm{mg\,P\,g^{-1}}$ and $31.7\,\mathrm{mg\,N\,g^{-1}}$ [10] in a waterlogged system; characteristics highly favourable for species apposite for macrophyte-based wastewater treatment schemes.

### 3.3 *Implications of eutrophication in deep water populations and plausible causes*

An abnormal declining rate of shoot growth and reduced plant vigour were observed in the two deep water populations of *E. sphacelata* over the spring and summer of 2004/2005. During the latter half of the investigation, the onset of shoot growth was delayed in all three populations owing to the delay in spring cloudbursts, however, the *in situ* observations and shoot count data in study areas in May 2005 in the aftermath of the second growing season disclosed that the Goulburn-shallow population had attained a shoot count as high as $78.3 \pm 6.1\%$ of that of the previous year, in contrast to the $24.7 \pm 3.9\%$ and $19.2 \pm 5.8\%$ (all $n \sim 6$–$9$) for Ourimbah (deep) and Goulburn-deep populations, respectively. The prolonged drought (March to July) afterwards of summer 2004 coinciding with seasonal formation of inflorescence of *E. sphacelata* in two deep water populations caused the aboveground shoot biomass to die off, declining by over 65–70% with a substantial concomitant increase in the accreted dead biomass overlying soft bottom sediments. Hunt *et al.* [25] elaborated that higher above- to belowground biomass allocation ratios, similar to that observed in two deep water populations of *E. sphacelata*, affect the subsequent decomposing process adversely, because of physicochemical differences between rhizomatous and shoot tissues, and because soil conditions are more favourable for decomposition than surface conditions. The refractory organic matter from shoots differs from the labile organic matter originating from algae and submerged macrophytes because it contains a high amount of lignin and cellulose. During the anaerobic decomposition of these compounds, phytotoxic organic acids such as acetic and butyric acid are released [26].

During December 2004 sampling in both deep water populations, scores of later-emerging shoots were observed to have died before reaching full maturity, and signs of growth inhibition including typical stress symptoms such as stunted growth and chlorotic shoots were also discerned. This decline of overall shoot biomass seemingly continued steadily despite the emergence of few new shoots as the spring and early summer growing season advanced and discolouration of pond water, predisposing of emerging eutrophic conditions, was observed in May 2005 in both Goulburn and Ourimbah deep water populations. The water quality and sediment characteristics measured on each sampling date for individual populations did not portray any significant difference over the time until March 2004 ($t$-test, all $P > 0.05$). Therefore, the March 2004 and May 2005 data sets were used for comparative purposes. The physicochemical analyses of sediment cores collected in May 2005 affirmed significant increases in organic content, water affinity, total nitrogen and total phosphorous concentrations in the deep water populations in comparison to the March 2004 data ($t$-test, all $P < 0.05$) (table 1a,b). In contrast, the physicochemical differences associated with sediment cores collected in March 2004 and May 2005 from Goulburn-shallow population were only trivial and statistically not significant ($t$-test, all $P > 0.05$).

The surface layers of overlying water column in Ourimbah and Goulburn-deep populations indicated pH and dissolved oxygen in the range of $6.9 \sim 7.8$ and $7.5 \sim 8.7\,\mathrm{mg\,l^{-1}}$ in March

2004 and in the range of 7.6 ~ 8.9 and 10.1 ~ 11.5 mg $l^{-1}$ in May 2005 (all measurements were taken at midday at temperatures of ~16–20 °C) indicating an increased amount of microbial photosynthesis. The shoots of *E. sphacelata* are capable of substantially oxygenating the rhizosphere sediments and above-lying water column by diffusion and convective flow [8]. However, the shoot count data in May 2005 revealed that the number of shoots had decreased quite significantly compared to the previous season for both sites, leading to the derivation that the main cause of increased oxygenation was mainly due to the microbial photosynthesis. The bottom layers of the water column in Ourimbah *E. sphacelata* population, however, indicated slightly acidic and more anoxic conditions with pH and dissolved oxygen in the range of 5.4 ~ 6.7 and 4.5 ~ 5.9 mg $l^{-1}$ in May 2005, presumably symptomatic of ammonia and nitrite dynamics of decomposing autogenous shoot litter under further hypoxic conditions in deep most layers. The water column total nitrogen and total phosphorous of two deep water populations had increased from 0.41 ~ 0.48 mg $l^{-1}$ and 0.014 ~ 0.021 mg $l^{-1}$ in March 2004 to 1.06 ~ 1.22 mg $l^{-1}$ and 0.081 ~ 0.096 mg $l^{-1}$ in May 2005 and might have led to the increased microbial activities and subsequent eutrophication of the water bodies. Similarly, the conductivity of the surface layer water column in two deep water populations increased from 0.6 ~ 1.1 ms $cm^{-1}$ in March 2004 to 2.1 ~ 2.9 ms $cm^{-1}$ whilst the colour measurement varied from 164 ± 32 mgPt $l^{-1}$ ($n = 3$) in March 2004 to 427 ± 106 mgPt $l^{-1}$ ($n = 3$), clearly indicating a significant deterioration of the water quality. The contrast of physico-chemical characteristics of sediment cores collected from shallow and deep water populations in May 2005 further attested that decomposition of autogenous shoot litter progressed more effectively in Goulburn-shallow population under surface air conditions when the water level receded.

Field *et al.* [27] explicated that plant responses with the greatest potential to affect nutrient cycling included changes in total production, chemical composition and allocation between shoots and rhizomes. These plant responses affect decomposition rate, immobilization of nutrients into decomposing residues, nutrient mineralization and the future availability of nutrients for plants in turn affecting the associated plant communities adversely. There is increasing evidence that above the water level and hydraulic regime, productivity of individual species and standing crop often increase with organic matter content [28], but in flooded parts organic matter may provide adverse conditions for plant growth due to higher oxygen consumption by microbial which constrains the ability for rhizosphere oxidation [29]. The strong decline of *Phragmites australis* observed in many European wetlands, in some instances, has been related to the high production and accumulation of nutrient rich detritus [12]. However, the effects of eutrophication on *P. australis* were deemed indirect, via the accumulation and decay of litter and allogenous organic matter, rather than acting directly via disturbed carbohydrate cycling or reduced porosity of the aerenchymous plant tissue. It was further noted that remarkably, species such as *Typha latifolia* and *P. australis* with strong capacity for rhizosphere oxidation were also inhibited in the decomposed litter sediment indicating that in addition to the high oxygen demand of the litter sediment, phytotoxic organic acids such as acetic and butyric acid may also have reduced growth and plant vigour [30].

Based on the findings of an outdoor pot experiment on *P. australis*, Clevering [31] acquainted that only the water logging, flooding and fluctuating water table treatments caused growth reduction in substrate containing litter and when drained, no differences between substrate treatments were present. This was highlighted as one of the explanations for the disappearance of *P. australis* along the waterward side of littoral zones and can also be regarded as the reason for unaffected continuation of seasonal growth and healthy survival of *E. sphacelata* in Goulburn-shallow population that intermittently experienced alternative inundation-drawdown pattern. However, because vast amounts of nutrients and partially decomposed litter are accreted in and above the sediment, a prolonged inundation causing stagnant deep water ponding even in such population might cause the oxidation of the sediment releasing these nutrients, instigating substantial eutrophication with catastrophic damage to the littoral vegetation. This fact further affirms that strict water regime management practices coupled with timely mowing or the removal of accumulating litter are necessary to ensure long term survival of healthy *E. sphacelata* stands, to prevent the eruption of harmful eutrophic conditions when *E. sphacelata* is utilised in applications like macrophyte based wastewater treatment systems and other phytoremediaion related applications where deep water conditions prevail.

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