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Livestock Grazing and Dense Willow Shading Negatively Impact Instream Plant Growth

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ABSTRACT

Human impacts have degraded riverine environments worldwide. In south-eastern Australia, livestock grazing and non-native *Salix* spp. (Willow) infestations throughout riverine environments commonly degrade instream conditions on which instream plants rely. However, the effects of livestock grazing and *Salix* spp. infestations on instream plants remain uncertain. We investigated the responses of two submerged and two emergent instream plant species to different levels and combinations of simulated grazing and shading. In a glasshouse experiment, we tested the response of *Cycnogeton procerum, Juncus usitatus, Schoenoplectus tabernaemontani*, and *Vallisneria australis* to combinations of clipping (simulated grazing) and shading (low (30%) and high (90%)) over a 14-week period. Plant length, above- and below-ground biomass, and vegetative output were measured in response to the different treatments. Most plants recovered in length following clipping, except *V. australis*, while shading either had minimal effects or increased plant length. Clipping reduced biomass for all species, while shading produced varying effects on above- and below-ground biomass. *S. tabernaemontani* and *V. australis* tended to have reduced rates of new leaf/stem production under clipped or high shade conditions. The combined effects of clipping and high shade on *J. usitatus* led to plant death. Our results show that clipping and shading can change the growth characteristics of instream plants, leading to general declines in plant fitness and in some cases, plant death. Although some species may tolerate clipping and low shading, the long-term effects of grazing, high shading, and combinations of the two are likely deleterious. Our study provides support for restoration efforts involving livestock exclusion and non-native *Salix* spp. removal from waterways.

1 | Introduction

Humans have degraded riverine environments globally by altering flow regimes, farming hard-hooved grazers nearby to waterways, and introducing exotic species (Richardson et al. 2007; Riis et al. 2008). Increasing human demands from riverine environments, and impacts of a drier, warmer climate are likely to result in reductions in water availability and further declines to river ecosystem health (Grill et al. 2019; IPCC 2022). River managers must balance several goals, such as conserving and restoring riverine diversity, promoting resilience to climatic extremes and providing resources for human activities (Postel and Richter 2003). Greater knowledge regarding the impacts of common land management practices on riverine environments is required to better manage and restore rivers globally (Grill et al. 2019).

Instream (submerged and emergent) plants play critical roles in riverine environments. They provide food and habitat for aquatic fauna, and regulate the structure, water quality and nutrient cycles of riverine environments (Carpenter and Lodge 1986; Newman 1991; Rejmankova 2011). Many species of instream plants also support cultural values and are an important source of food, textiles, instruments and medicines (Jackson

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et al. 2012). However, human impacts on riverine environments have led to declines in distributions and diversity of instream plant communities (Richardson et al. 2007).

As a region that relies heavily on agriculture, riverine environments across south-eastern Australia have experienced substantial changes due to altered hydrological regimes and land use (Greet et al. 2013; Jones et al. 2022). The hydrological regime is understood as a critical driver of instream plant communities (Rea and Ganf 1994; Blanch et al. 1999; Riis et al. 2008). However, the distribution of instream plants is highly variable in regulated river systems, suggesting that multiple drivers and interactions play a role in their occurrence (Vivian et al. in press). There has been increasing concern that livestock grazing and *Salix* spp. infestations can negatively impact riverine environments in south-eastern Australia, leading to efforts to exclude livestock and remove *Salix* spp. from waterways (Brooks and Lake 2007; Jones et al. 2022). However, these interventions are contentious socio-economic issues (Curtis and Robertson 2003). Therefore, it is important to gain a better understanding of the effects of livestock grazing and shading by *Salix* spp. on instream plants to inform waterway management in south-east Australia.

Hard-hooved grazers such as cattle and sheep were absent from Australian waterways until European agricultural practices were introduced in the 1830s (Bacon et al. 1994). Since their introduction, cattle and sheep have expanded in staggering numbers over a relatively short timeframe and now cover approximately 37% of Australia's naturally vegetated area, congregating around water sources where there is shade, vegetation and water available (Hobbs and Hopkins 1990; ABARES 2023). Cattle and sheep have many direct effects (consumption and trampling) and indirect effects (erosion, soil compaction, declines in water quality) to riverine environments (Clary 1995; Robertson and Rowling 2000; Prober et al. 2002). The resultant impacts to riverine environments vary depending on grazer population density, local environmental conditions and individual plant species responses (McIntyre and Lavorel 1994).

The effects of livestock grazing vary across instream plant species (Blanch and Brock 1994). Grazing removes a large proportion of photosynthetic leaf or stem area from the plant consumed, resulting in reduced oxygen to support respiration (Hayball and Pearce 2004). Studies have attempted to classify the response of instream plants to grazing according to growth form, however their mixed findings indicate that responses are likely to be species-specific (Middleton et al. 2015). For example, submerged plants with similar basal growth forms yielded variable compensatory growth and reproductive outputs when subjected to clipping (as simulated grazing) (Crosslé and Brock 2002). While previous studies have indicated that growth is generally negatively affected by grazing (Middleton 1990; Crosslé and Brock 2002), research on instream plant species that inhabit varied hydrological niches, particularly in the presence of potentially compounding impacts such as dense canopy shading, is lacking.

The spread of *Salix* spp. throughout south-eastern Australian waterways also poses a potential threat to native instream plant communities. *Salix* spp. were originally introduced in the late 19th Century to mitigate erosion along waterways and are currently considered favourably by many landholders to provide shade for livestock and stabilise banks where native vegetation has been cleared (Cremer 2003). The post-colonisation modification to riverine environments in south-eastern Australia arguably provided ideal conditions for the versatile reproductive abilities of *Salix* spp., leading to their rapid expansion along waterways (Stokes 2008). Direct impacts of *Salix* spp. include the obstruction of waterways and formation of dense canopies that limit the growth of native flora (Cremer 2003; Stokes 2008), and indirect impacts include erosion, diversion of floods and declines in water quality due to the substantial contribution of leaf litter during leaf senescence in autumn (Schulze and Walker 1997; Cremer 2003). Compared with native riparian trees such as the widespread *Eucalyptus camaldulensis* (River Red-gum) which produce 20%–45% shading year-round (Specht 1981), *Salix* spp. form a dense canopy of 70%–90% shading during late spring and summer, and almost no shade after leaf senescence in autumn and throughout winter (Ladson 1997). The reduced light availability in riverine environments associated with dense canopies formed by *Salix* spp. is likely to reduce the growth and survival of instream plants.

Light availability is a key determinant of photosynthesis in instream plants (Kirk 2010), but their specific responses to canopies formed by *Salix* spp. and *E. camaldulensis* are not known. Light availability is altered by seasonal day length, turbidity, and shading, and controls the rate of photosynthesis, plant growth, biomass allocation, and reproductive outputs of instream plants (Middelboe and Markager 1997; Kirk 2010). Studies have shown that instream plants morphologically adapt to highly shaded conditions by leaf elongation, reduced below-ground biomass, and decreased branching compared to plants under low shade (Barko and Smart 1981; Riis et al. 2012; Chou 2022). These traits appear to reduce respiratory costs and maximize the opportunity to capture light for photosynthesis, increasing the time required for communities to establish, yet not overall establishment success (Riis et al. 2012). Whilst it is understood that submerged instream plants can tolerate low to moderate levels of shade (Lu et al. 2013), the tolerance of instream plants to dense shading and the combined effects of livestock grazing and shading has not been tested under controlled conditions.

In this study, we investigated the responses of two submerged and two emergent instream plant species with varied hydrological niches occurring in south-east Australian riverine environments to different combinations of simulated grazing and shading. We tested growth responses of the four species to six combinations of simulated grazing by clipping and varied levels of shading, reflective of various land management scenarios present across south-east Australian riverine environments. In a nursery-based experiment, we tested how these different combinations of clipping and shading affected plant length, biomass and vegetative output. We hypothesised that clipping and increasing levels of shade would negatively affect plant growth resulting in reduced plant growth in terms of: (1) plant length, (2) plant biomass, and (3) vegetative output of plants, compared to those that were not clipped or shaded. We expected minor

differences in outcomes of single treatments of shading or clipping, such as the potential for leaf elongation when plants were shaded and not clipped.

2 | Materials and Methods

2.1 | Study Species

For this study, four perennial plant species with different hydrological niches were selected: *Cycnogeton procerum* (Water Ribbons), *Juncus usitatus* (Common Rush), *Schoenoplectus tabernaemontani* (River Clubrush) and *Vallisneria australis* (Eel Grass). All species are native and common to riverine environments in south-eastern Australia, capable of surviving in, or adjacent to permanent surface water, are all found in waterways with areas of dense *Salix* spp. stands and are palatable to livestock (pers. obs.). While instream plants are known to be vulnerable to livestock grazing (Jansen and Healey 2003), we were unable to source primary literature for the palatability of the study species aside from direct observation of grazing at sites within the study area. All species have linear leaf morphology but have varying physiological attributes.

Cycnogeton procerum is an herbaceous perennial with roots that end in tubers and strap-like leaves growing up to 2 m long. In shallow, slow-moving or still water, *C. procerum* leaves often emerge from the water surface, with broader and shorter leaves than individuals in deeper, faster-flowing water, which often have longer, narrower leaves that trail on the water surface (Aston 1977). *C. procerum* can tolerate water depths up to 1.5 m and a wide variety of hydrological conditions such as high turbidity (Rea and Ganf 1994), its tolerance to grazing and shade has not been tested.

Juncus usitatus is a tufted perennial rush that grows in damp to saturated soil in stands up to 1 m tall along the margins of riverine environments. It is shortly rhizomatous with dense fibrous root systems and rigid stems emergent from waterlogged soil (Sculthorpe 1967). The tolerance of *J. usitatus* to grazing and shade has not been tested.

Schoenoplectus tabernaemontani is a perennial rush with tall, soft stems up to 2 m high, spreading vegetatively by rhizomes and forming dense matted root systems (Sculthorpe 1967). It can grow in water depths up to 60 cm and is often found emerging from shallow water along the edge of waterways (Vanderbosch and Galatowitsch 2011). Simulated grazing (clipping) has been shown to reduce the above-ground biomass, plant length, and production of new stems by juvenile plants (Hayball and Pearce 2004). Neither its tolerance to shading nor to the combination of shading and clipping has been investigated.

Vallisneria australis is a submerged perennial that forms dense meadow-like stands of submerged strap-like leaves by stoloniferous growth from a basal cluster. Its leaves can range from a few cm up to 2 m long, growing in still to swift-flowing waters of 0.3–3 m depth (Aston 1977). *Vallisneria* spp. can tolerate low light levels for extended periods of time. Populations of *V. australis* can be negatively affected by herbivory (by grazing waterfowl and turtles), the effects of livestock grazing on this species are not well understood (Carter and Rybicki 1985; Chou 2022).

2.2 | Plant Preparation and Experimental Conditions

Plants for the experiment were obtained from local native plant nurseries (Australian Ecosystems and Ecodynamics). *C. procerum, J. usitatus*, and *S. tabernaemontani* were obtained as tubestock, and *V. australis* as entire plants floating in tubs of water. We obtained 60 plants of each species (total 240 plants). We potted the plants into medium-sized cylindrical pots (135 × 135 × 140 mm) with drainage holes using a media mix of 1 part soil (Grass Mix, Daisy's Garden Supplies) to seven parts sand (Vivian et al. 2020; Main et al. 2022). All plants were then transferred to a temperature-controlled glasshouse at the University of Melbourne, Burnley, Australia, where ambient temperature was maintained above 20°C during the day and above 10°C overnight. *C. procerum* and *V. australis* plants were inundated to a depth of 20 cm in rectangular tubs (37 × 65 × 41 cm). *J. usitatus* and *S. tabernaemontani* plants were placed in rectangular tubs of the same dimensions and filled until the water level was 5 cm above the base of the pot. The plants were left in the glasshouse for two weeks before the experiment began.

2.3 | Experimental Setup

The experiment ran from 18 May to 31 August 2023 (after the two-week acclimation period) using a randomised block-design conducted in the glasshouse (Blanch and Brock 1994). To each of 18 large round tubs (72 × 50 cm), three plants of each of the four species were randomly allocated, such that there was a total of twelve plants in each tub. Within each tub, a tiered design with *C. procerum* and *V. australis* plants placed on the bottom of the tubs, and *S. tabernaemontani* and *J. usitatus* plants elevated by placing them on top of stacked plant trays at two different levels. The tubs were filled with tap water to a depth of 40 cm, with *C. procerum* and *V. australis* completely submerged, *S. tabernaemontani* partially inundated to 13 cm of the pot height and *J. usitatus* partially inundated to 5 cm of the pot height (Figure 1).

We implemented six treatments with three replicate tubs per treatment: control (unshaded, unclipped), low shade and unclipped, high shade and unclipped, no shade and clipped, low shade and clipped and high shade and clipped. Thus, for each treatment, there were nine replicate plants of each species.

A further six plants of each species were harvested to measure initial biomass. To do this, plants were removed from their pots and washed to remove all soil. Above- and below-ground plant parts were separated with secateurs and oven-dried at 80°C for 72 h and weighed.

To simulate different levels of riparian shading, a PVC structure was constructed over the tubs and six tubs were covered with 30% shade cloth (low shade treatments, similar to the level of canopy shading by *E. camaldulensis*) and another six tubs with 90% shade cloth (high shade treatments, similar to the level of canopy shading by *Salix* spp. in late spring and summer). The



FIGURE 1 | Photos demonstrating experimental setup. A tiered design was constructed so that *J. usitatus* plants were emergent, *S. tabernaemontani* plants were partially inundated and *C. procerum* and *V. australis* plants were submerged (top, left). The tubs were filled with tap water to a depth of 40 cm, with *C. procerum* and *V. australis* completely submerged, *S. tabernaemontani* partially inundated to 13 cm of the pot height and *J. usitatus* partially inundated to 5 cm of the pot height (top, middle). Clipping was implemented by cutting plant leaves at 2–5 cm from the soil surface with secateurs once per week, for the first three weeks of the experiment (top, right). Shading was used to simulate different levels of riparian shading. Six tubs were covered with 30% shade cloth (low shade treatments, similar to the level of canopy shading by *E. camaldulensis*). Six tubs were covered with 90% shade cloth (high shade treatments, similar to the level of canopy shading by Salix spp.). The remaining six tubs were not shaded (bottom). [Color figure can be viewed at wileyonlinelibrary.com]

remaining six tubs were not shaded (Figure 1). Clipping treatments were applied to plants in half of the tubs in all levels of shading (i.e., three tubs in each of no, low and high shade).

Clipping was conducted to simulate the large amount of understorey vegetation typically grazed by cattle and sheep when given access to waterways. Drawing on work by Blanch and Brock (1994) and Hayball and Pearce (2004), clipping was implemented by cutting plant leaves/stems at 2–5 cm from the soil surface with secateurs (Figure 1). To simulate stock rotation on a paddock, plants in the clipping treatment were cut once per week for the first three weeks only.

The plants were left in situ for the duration of the experiment. Evaporative losses were replaced throughout the experiment by refilling the tubs on a weekly basis to a depth of 40 cm, with each species maintained at its respective depth. Algae and surface scum were removed on a weekly basis using a fine fishnet.

Water temperature and light levels were recorded hourly using automatic pendant loggers (HOBO, UA-002-64) secured at the water surface level and the soil surface of *J. usitatus* (two loggers per tub). A full summary of the temperature and light data is provided in Appendix A (Figures A1, A2). For all treatments, the mean temperature was $<1°C$ hotter at the soil surface of

the high pots than the water surface. Mean temperatures across the entire study period were 15.5°C, 17.8°C, and 16.9°C from no shade to high shade, respectively, at the water surface. Light levels were 30%–50% lower at the water surface and declined with shading, resulting in mean lux levels of 2716, 1503, and 202 from no shade to high shade, respectively, at the water surface. Dissolved oxygen, pH, and specific conductivity were measured using a water quality metre towards the conclusion of the experiment to compare with average conditions of local regulated riverine environments.

Throughout the experiment, the temperature in the glasshouse ranged from 9°C to 27°C, simulating normal diurnal temperature fluctuations during the growing season of south-eastern Australia (September–March). As the experiment was conducted over the austral winter (April–August, Victoria, Australia), the average photoperiod was 8 h per day, which is less than in the typical growth season (10 h per day).

2.4 | Plant Measurements

Plant height, numbers of new *C. procerum* leaves, *S. tabernaemontani* stems, and *V. australis* leaves were recorded on a weekly basis, and the final number of *V. australis* plantlets was recorded at the end of the experiment. Flowers produced by *J. usitatus* were also recorded to indicate reproductive output. Plant height was measured by recording the height of the longest stem/leaf to the nearest centimetre. After 14 weeks, plants were harvested to assess above- and below-ground biomass as per the initial harvest.

2.5 | Statistical Analysis

We conducted statistical analyses on plant length, biomass and vegetative output variables to evaluate treatment effects using R (version 4.2.0, R Core Team 2023) via R Studio (R Studio Team 2020). Data evaluation was conducted as visual summaries of the data (mean ± confidence intervals or boxplots) followed by statistical analysis of treatment effects.

Plant growth was assessed at the conclusion of the experiment (week 14) for each species in each treatment. Change in biomass was assessed by comparing the above- and below-ground biomass for all species at the start of the experiment with above- and below-ground biomass for each species in each treatment at the conclusion of the experiment. Vegetative outputs were assessed by comparing the number of new leaves/stems for each species in each treatment.

We used linear mixed effects models to assess the effects of clipping and shading on (1) plant length for all species, (2) above- and below-ground biomass for all species, and (3) vegetative outputs for *C. procerum, S. tabernaemontani*, and *V. australis* only. Linear mixed effects models were run separately for each species using the *lme4* package (Bates et al. 2015), with *lmerTest* (Kuznetsova et al. 2017) used for significance testing. Clipping (2 levels) and shading (3 levels) were modelled as interacting fixed factors to enable assessment of clipping and shading independently, and tub identity was included as a random effect for all models. We examined plots of raw data, model residuals, quantile-quantile regression plots, and R^2 via *MuMIn* (Bartoń 2020) to assess normality and model fit. No data transformations were used, and a significance threshold of $p < 0.05$ was used when interpreting model estimates. The full model outputs are presented in Appendices B–D (Tables B1, C1, D1), and only *p*-values are referred to in the Results.

3 | Results

3.1 | Plant Growth

The length of all control plants changed minimally across the duration of the experiment, with the exception of *V. australis* plants, which decreased slightly in length from week 10 onward (Figure 2).

Clipping alone reduced plant length for the first three weeks of the experiment, as to be expected (Figure 2). Following 3 weeks of clipping, the length of clipped plants typically increased as the experiment progressed, but the rate of increase varied across the study species. For example, the length of clipped *C. procerum* plants recovered (30–47 cm) and was similar in length to unclipped plants (30–50 cm) at the conclusion of the experiment without shading ($p > 0.05$). Clipped *J. usitatus* plants recovered steadily; however, they were 55%–80% shorter in length (24–39 cm) than unclipped plants (43–50 cm) by the end of the experiment ($p < 0.001$). Clipped *S. tabernaemontani* plants responded quickly and eventually exceeded (59–88 cm) the length of unclipped *S. tabernaemontani* plants (45–58 cm, $p = 0.047$) by 30%–60%. The length of clipped *V. australis* plants increased steadily but slowly over time (reaching 8–21 cm) but did not recover their leaf length to that of unclipped *V. australis* (15–44 cm), resulting in a strong negative effect (~50% shorter) of clipping on leaf length for this species ($p < 0.001$).

Shading plants with no clipping treatment yielded variable effects on plant length. *C. procerum* plants tended to grow 10%–30% longer under high shade (41–54 cm) than without shade (30–50 cm), whereas *J. usitatus* plants tended to grow longer under low shade (42–64 cm) than without shade (43–50 cm), however these effects were small ($p = 0.01$ and $p = 0.012$ respectively) (Figure 2). Shading of *S. tabernaemontani* resulted in plants growing 50%–140% longer (82–130 cm under low shade and 68–140 cm under high shade) than those unshaded (45–58 cm) ($p < 0.001$), which was stronger than the observed effect of clipping. Shading (low or high) did not affect the plant length of *V. australis*.

There was a significant interaction between clipping and shading for *J. usitatus* and *S. tabernaemontani* but only for the high shade treatment ($p < 0.001$ and $p = 0.031$ respectively). Clipped *J. usitatus* plants under high shade did not recover and died at week 10. *S. tabernaemontani* plants that were clipped and highly shaded were shorter than unclipped and highly shaded plants. For both species, the combination of clipping and high shade had a severe negative impact on the plants.

3.2 | Biomass

Above- and below-ground biomass of control plants increased over the course of the experiment for all species (Figure 3).

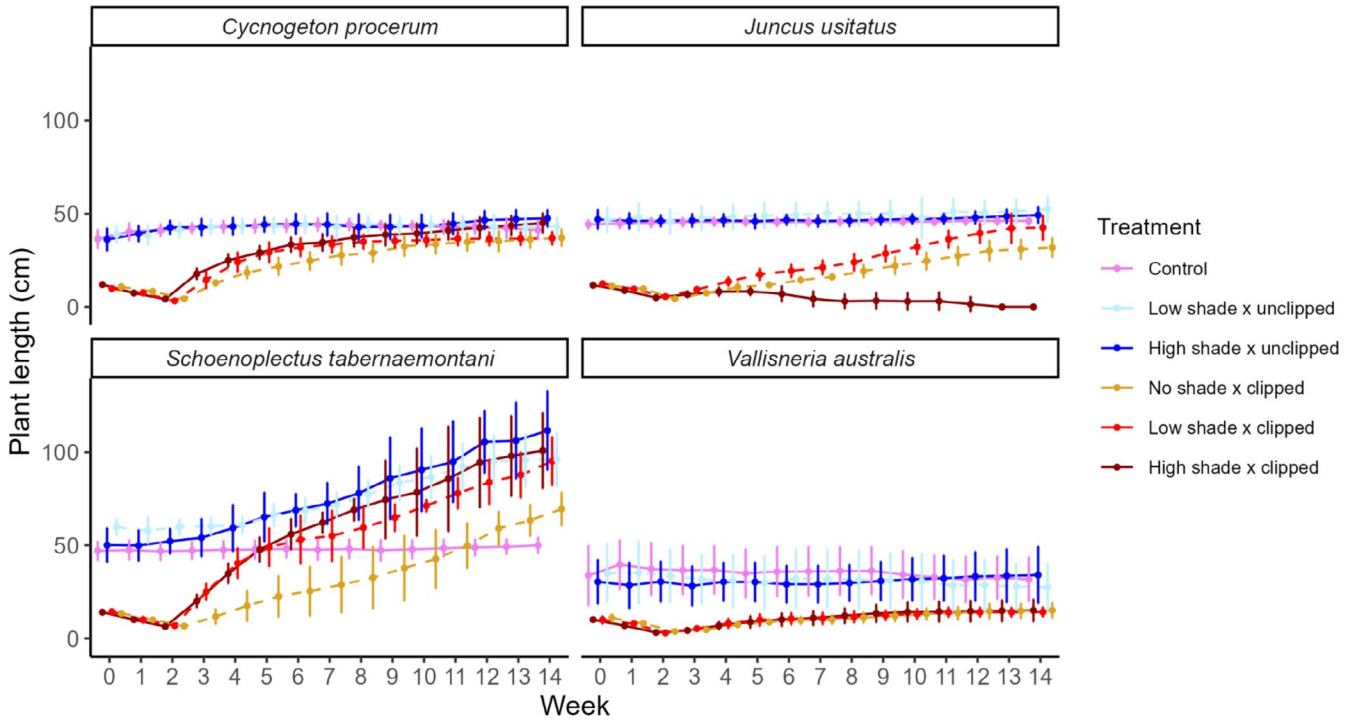


FIGURE 2 | Plant length over time during the experiment, showing varied rates of leaf/stem length increase for all species. Treatments are represented by different colours. Raw data are shown as points. Dashed lines indicate clipped treatments with increasing levels of shade (orange, red, maroon), and solid lines indicate treatments with increasing levels of shade applied without clipping (light blue, dark blue). Control plants (pink) were neither clipped nor shaded. Error bars are ±1 SE. [Color figure can be viewed at wileyonlinelibrary.com]

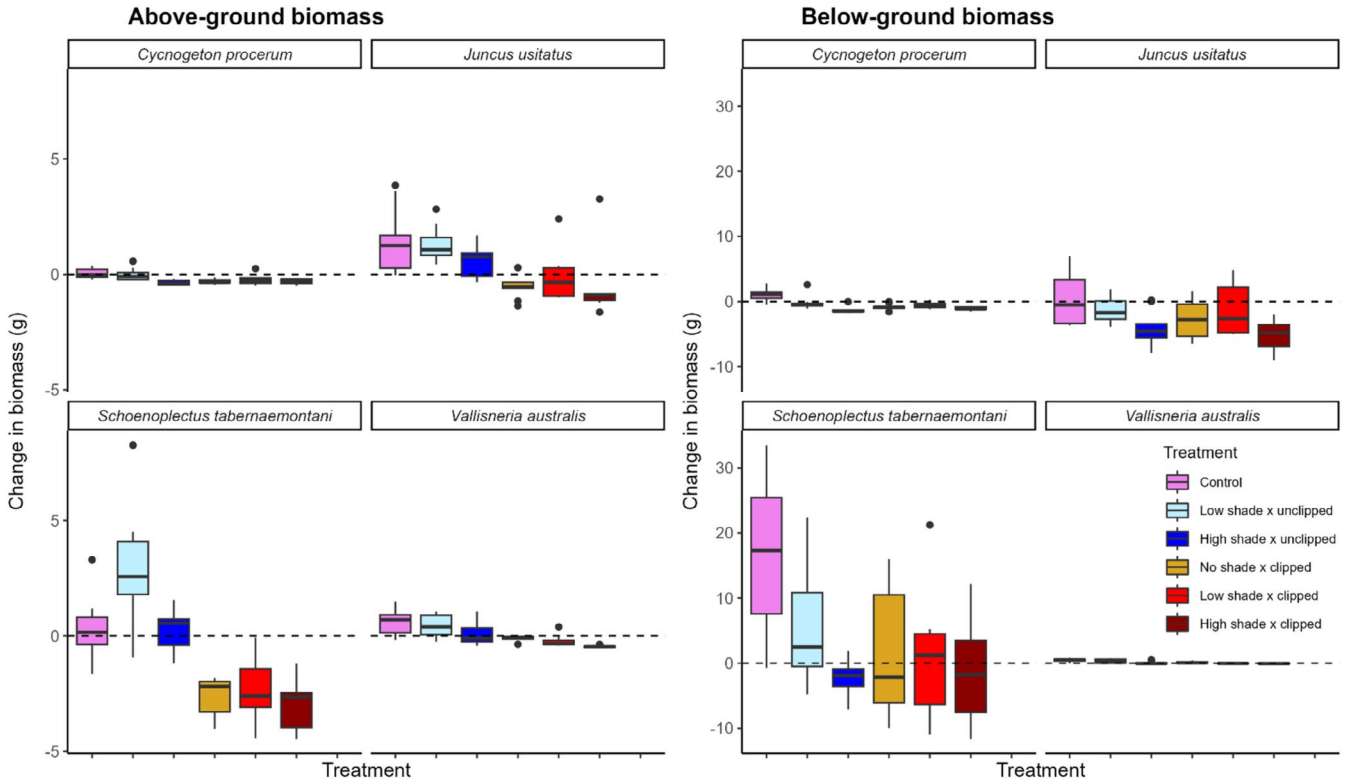


FIGURE 3 | Change in above-ground and below-ground biomass for the study species at the end of the experiment. Change in biomass for each species was calculated as biomass for each plant minus average biomass at the start of the experiment ($n = 6$). Treatments are represented by different coloured boxes across the x-axis. Clipped treatments had increasing levels of shade applied (orange, red, maroon), and shaded treatments had increasing levels of shade applied (light blue, dark blue). Control plants (pink) were neither clipped nor shaded. The dashed line (0 g) indicates no change in biomass, negative values indicate reduced biomass and positive values represent increased biomass. Boxes show the interquartile range (25th to 75th percentile) with a line for the median and whiskers extend to the furthest data point. [Color figure can be viewed at wileyonlinelibrary.com]

Regardless of shading treatment, clipping typically resulted in a net loss of both above- and below-ground biomass for all species (Figure 3). There was a particularly strong negative effect of clipping on the above- and below-ground biomass of *S. tabernaemontani* plants when no shading was applied ($p < 0.001$). Clipped *S. tabernaemontani* plants lost above-ground biomass (-2.64 ± 0.83 g) between the beginning and end of the experiment (compared with control plants that gained 0.03 ± 1.66 g), and gained minimal below-ground biomass, 1.22 ± 9.41 g between the beginning and end of experiment (compared with control plants that gained 14.94 ± 12.30 g).

Shading generally resulted in smaller increases in biomass (or even losses) but had variable effects on above- and below-ground biomass across the four species. The above-ground biomass of unclipped *C. procerum* plants was negatively affected only when highly shaded ($p = 0.005$) while there was a strong negative effect on below-ground biomass under both low (-0.21 ± 1.03 g, $p < 0.001$) and high shade (-1.35 ± 0.49 g, $p < 0.001$) (control *C. procerum* plants gained 1.05 ± 0.91 g in below-ground biomass). The above-ground biomass of unclipped *J. usitatus* plants was unaffected by shading; however, below-ground biomass decreased under high shade ($p = 0.005$). Unclipped *S. tabernaemontani* under low shade were the only plants that increased in above-ground biomass (2.83 ± 2.52 g, compared to the above-ground biomass of control *S. tabernaemontani* that gained 0.03 ± 1.59 g, $p = 0.002$). However, below-ground biomass of *S. tabernaemontani* plants reduced under both low ($p = 0.016$) and high shade ($p < 0.001$). Both the above- and below-ground biomass of *V. australis* plants were relatively unaffected by low shade ($p > 0.05$) but reduced under high shade ($p = 0.017$ and $p = 0.001$ respectively).

Clipped plants showed very different responses to shading than unclipped plants because the effect of clipping overwhelmed the effect of shading (Figure 3). Interactions were therefore generally relatively weak for biomass models. In contrast to the general reduction of biomass with greater shade cover when unclipped, the biomass of unshaded and high shaded treatments was similar when clipped, while low shade yielded higher biomass than both for all species except *V. australis* (Figure 3). For below-ground biomass of *C. procerum*, there were strong positive interactions for clipping with low shade ($p = 0.002$) and clipping with high shade ($p < 0.001$). These positive interactions indicated the reversal of patterns where shading decreased biomass in unclipped plants but increased biomass (slightly) in clipped plants.

3.3 | Vegetative Output

Control plants of *C. procerum*, *S. tabernaemontani*, and *V. australis* produced vegetative outputs in the form of leaves (*C. procerum* and *V. australis*), stems (*S. tabernaemontani*), or plantlets (*V. australis*) over the course of the experiment; however, the rate and number of vegetative outputs varied across study species (Figure 4). Control *C. procerum* plants produced 1–5 new leaves, control *V. australis* plants produced 3–14 new leaves, and control *S. tabernaemontani* produced 4–18 new stems by the conclusion of the experiment. *V. australis* plants in the control treatment tended to produce numerous plantlets (up to four), whereas plants that were subjected to clipping and shading produced none or few (up to two).

Clipping did not affect the number of new *C. procerum* leaves produced. Generally, clipped *S. tabernaemontani* plants

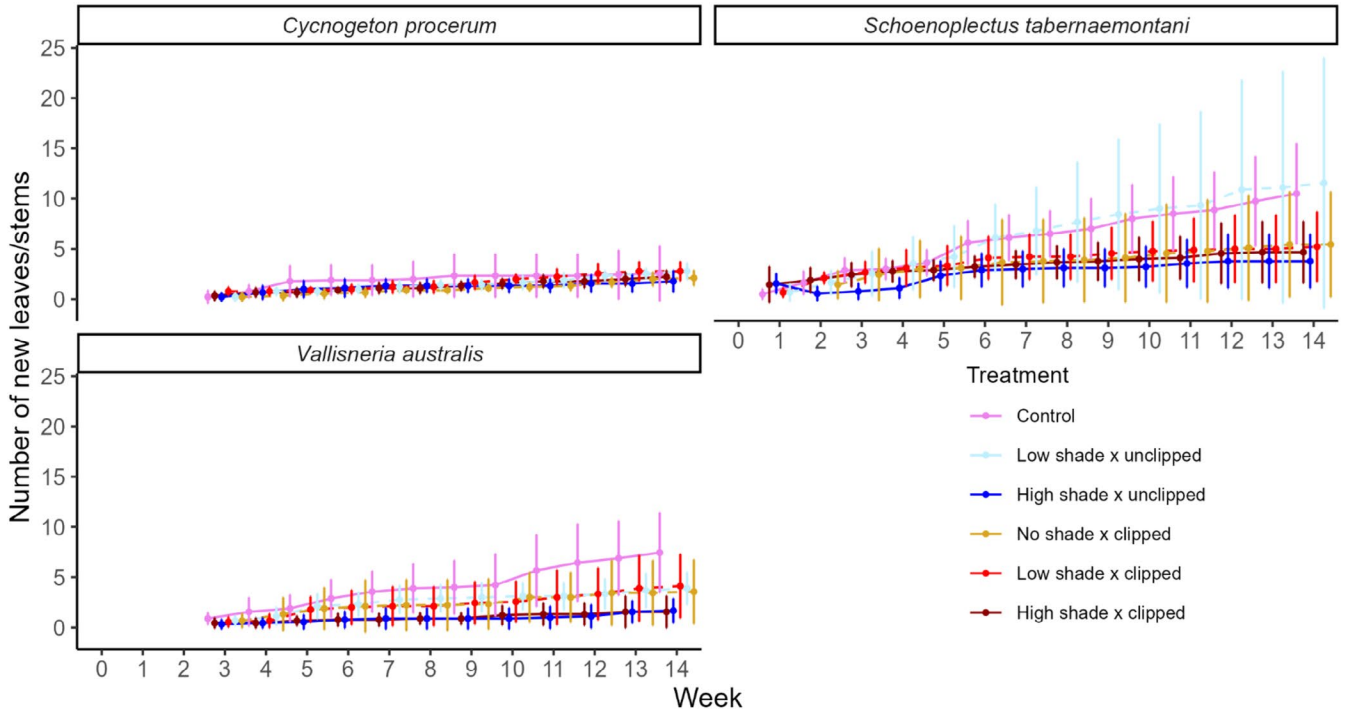


FIGURE 4 | Number of new leaves/stems produced by *C. procerum*, *S. tabernaemontani* and *V. australis* over time during the experiment, showing varied rates and numbers of vegetative outputs across species. Treatments are represented by different colours. Raw data are shown as points. Dashed lines indicate clipped treatments with increasing levels of shade (orange, red, maroon), and solid lines indicate treatments with increasing levels of shade applied without clipping (light blue, dark blue). Control plants (pink) were neither clipped nor shaded. Error bars are ±1 SE. [Color figure can be viewed at wileyonlinelibrary.com]

produced few new stems, but clipping did not have a significant main effect ($p = 0.10$) because of large variability in the number of stems produced (Figure 4). On the other hand, clipping unshaded *V. australis* plants resulted in significantly fewer (1–7) new leaves ($p = 0.030$).

Shading did not affect the number of new *C. procerum* leaves produced throughout the experiment. *S. tabernaemontani* plants under high shade produced fewer stems (0–8, $p = 0.033$), whereas plants under low shade were unaffected. In contrast, shading had no effect on the number of new stems produced by *S. tabernaemontani* plants when clipped. The number of new leaves produced by *V. australis* was reduced under both low (1–6, $p = 0.043$) and high shade (0–4, $p = 0.003$), with the effect stronger under high shade. There were no significant interactions between clipping and shading for any species (Figure 4).

One *J. usitatus* plant was observed to flower during the experiment and that plant was in the control group (unclipped and unshaded), which flowered in the second week of the experiment.

4 | Discussion

Plant growth responses to clipping and shading varied across the study species, but in general, clipping and high shade negatively impacted plant growth. Plants mostly recovered leaf/stem length following clipping (except *V. australis*), while shading had either minimal effects or increased plant length, contrary to our first hypothesis. However, the combined effect of clipping and high shade led to plant death in *J. usitatus*. Biomass was reduced for all species when clipped, in line with expectations, while shading produced varying effects on above- and below-ground biomass across species. Notably, below-ground biomass was reduced under high shade for all species. *Schoenoplectus tabernaemontani* and *V. australis* (but not *C. procerum*) tended to produce fewer new leaves/stems when clipped or highly shaded, supporting our third hypothesis. These findings have important implications for land management practices and restoration efforts in riverine environments. They demonstrate that, while species across different hydrological niches employ diverse responses to grazing and shading, the overall impacts of cattle grazing and dense shading by *Salix* spp. on instream plants are likely deleterious.

4.1 | Effects of Grazing on Instream Plants

Species responded to clipping (as simulated grazing) with varied rates of leaf/stem recovery. Clipped *C. procerum* and *S. tabernaemontani* plants responded with immediate growth after the 3-week clipping period ended, whereas the recovery of *J. usitatus* and *V. australis* plants was slow from weeks 4–5 onwards. The removal of above-ground biomass during clipping would have decreased light and oxygen acquisition and subsequent carbohydrate production from photosynthesis (Hayball and Pearce 2004), which appears to have stimulated leaf/stem growth in *C. procerum* and *S. tabernaemontani*. The presence of tubers in *C. procerum* and rhizomes in *S. tabernaemontani* may have increased the resilience of the clipped plants by releasing energy within these specialised storage organs to stimulate growth (Grace 1993). Furthermore, the rapid rate of leaf turnover exhibited by *C. procerum* may have supported its recovery after clipping (Rea and Ganf 1994). These adaptive capacities may explain the common occurrence of *C. procerum* throughout regulated Victorian riverine environments (Vivian et al. in press). The elongation of clipped *S. tabernaemontani* plants suggests that adult plants with well-established rhizomes may have a better ability to recover than juveniles (Grace 1993), as our results using relatively mature plants contrast with Hayball and Pearce's (2004) results where the length of juvenile *S. tabernaemontani* decreased with clipping. It was also observed that the elongated *C. procerum* leaves and *S. tabernaemontani* stems in clipped plants were more fragile than in plants that had not been clipped. These observations are consistent with findings by Armstrong et al. (1994), who observed longer, weaker stems in stressed wetland plants due to increased ethylene production, stimulating cell production and increasing elasticity of cell walls. The short duration of our experiment did not allow us to investigate how these longer, weaker stems would fare over a longer period. However, our results imply that *C. procerum* and *S. tabernaemontani* may be resilient to short periods of grazing by livestock via the elongation of leaves/stems, whereas *J. usitatus* and *V. australis* are less so.

Notably, clipping resulted in reduced above- and below-ground biomass for all species. The reduced biomass of clipped *C. procerum* and *S. tabernaemontani* plants is despite them having responded quickly by elongating leaves/stems following clipping, demonstrating that elongation came at an energetic cost (Rejmankova 2011). For *V. australis*, above- and below-ground biomass was reduced when plants were clipped, and plant length was shorter. This lack of resilience is understandable given the absence of specialised resource-storage organs such as tubers. Our results are consistent with Middleton (1990) who found that, in general, instream plants declined in above- and below-biomass when clipped. For all our study species, it appears that the removal of above-ground biomass during clipping resulted in plants drawing on stored reserves to replace lost photosynthetic tissue, which led to reductions in below-ground biomass. Therefore, even short periods of grazing are likely to reduce the fitness of instream plants.

4.2 | Effects of Shading on Instream Plants

In all species except *V. australis*, shading tended to result in increased plant length. *V. australis* inhabits the deepest hydrological niche of all study species and is able to photosynthesize under low-light conditions, explaining the similar leaf length of shaded and unshaded *V. australis* plants in our experiment (Chou 2022). The increased plant length in the other species reflects previous findings of leaf elongation by instream plants under low-light conditions to increase the available leaf area to acquire light and ensure photosynthesis (Barko and Smart 1981). Such adaptation has been referred to as "foraging", whereby plants produce longer leaves/stems with fewer branches and reduce below-ground biomass to improve resource acquisition and reduce respiratory costs when shaded (de Kroons and Hutchings 1995). Our findings indicate that *C. procerum, J. usitatus*, and *S. tabernaemontani*

responded to shade by "foraging". However, the stamina of these species to compensate for decreases in light availability remains undetermined.

Our results suggest that the study species have varied tolerances to increasing levels of shade. Whilst the length of *S. tabernaemontani* stems increased under both levels of shade, *C. procerum* leaves grew longer under high shade only. This suggests that the threshold for stimulating stem/leaf elongation is lower in *S. tabernaemontani* than *C. procerum*. This concords with Lu et al.'s (2013) findings that growth stimulation of *Vallisneria natans* and *Myriophyllum spicatum* is dependent on light intensity. It is likely that plant growth responses to low-light conditions are both intensity-dependent and species-dependent, and that some species may be more resilient than others when light availability is reduced by dense *Salix* spp. canopies.

Shading also yielded variable effects on above- and below-ground biomass across the study species. For *C. procerum*, above-ground biomass was reduced under high shade only, whereas below-ground biomass was reduced under low and high shade. This is consistent with the plant length results where *C. procerum* leaves were longer, yet weaker under high shade and suggests that leaves elongated at the cost of biomass (Armstrong et al. 1994; de Kroons and Hutchings 1995). On the other hand, above-ground biomass of *S. tabernaemontani* under low shade increased, which aligns with the strong positive effect on plant length of low shade. The reduction in below-ground biomass in *C. procerum, S. tabernaemontani* and *J. usitatus* plants under high shade suggests that the "foraging" employed by these species as a response to decreased light intensity comes at a cost of reduced plant fitness (Riis et al. 2012).

4.3 | Combined Effects of Clipping and Shading on Instream Plants

Overall, growth responses of plants subjected to both clipping and shading indicated declines in physical condition beyond the impacts of single treatments. *S. tabernaemontani* and *J. usitatus* that were clipped and highly shaded did not recover in length. For all species except *V. australis*, clipped plants subjected to low shade yielded higher biomass when compared to clipped plants subjected to high shade, which suggests that a threshold for maintaining biomass was surpassed as shading increased. Furthermore, the production of new leaves/stems/plantlets tended to be lowest under clipped and shaded conditions. This was particularly notable for *V. australis*, where the effects of clipping and shading (low and high) resulted in the production of fewer new leaves and plantlets than unclipped and unshaded plants. Under low light conditions, the survival strategy of *Vallisneria* spp. focuses on reproducing to form an abundant population, than increasing leaf photosynthetic area (Lu et al. 2013; Chou 2022). In our study it appears that clipping and shading *V. australis* plants precluded the production of new leaves or plantlets, and the ability for plants to persist prolonged periods of clipping and shading is uncertain. Our results suggest a particularly low tolerance for *J. usitatus* to combined effects of clipping and shading, as plants subjected to clipping and high shade failed to survive. The growth responses to combined clipping and shading suggest that instream plant resilience within grazed and *Salix* spp.-infested areas is species-dependent. This was particularly evident for *J. usitatus* and *V. australis*, which failed to adapt to clipped and shaded conditions, despite the difference in growth forms and hydrological niches that the species inhabit. Our results suggest that individual species responses to grazing and shading, and the ability to sustain these responses, are likely to determine how instream plants persist under these stressors.

4.4 | Management Implications

The findings of our study support previous work that advocates for the exclusion of livestock and removal of *Salix* spp. infestations from waterways (Barko and Smart 1981; Cremer 2003; Curtis and Robertson 2003; Brooks and Lake 2007; Stokes 2008; Jones et al. 2022). Clipping resulted in varied recovery rates for plant length but reduced biomass of all species. This indicates that whilst some species may be resilient to short periods of livestock grazing, that the recovery potential is limited for all study species. While grazing reduction may be adequate to support instream plant communities, this requires careful stock management and grazing exclusion is the most effective way to prevent grazing impacts.

Tolerances to shading also vary across species. Morphological adaptation of leaves/stems to 'forage' and the presence of specialised below-ground storage organs may offer plants of some species resilience to the stress associated with dense shading. However, plant responses to high levels of shading often came at a cost of reduced fitness, and the stamina to withstand high shade by these species is undetermined but inherently limited. These findings suggest that the level of shade produced by *Salix* spp. infestations throughout south-eastern Australian riverine environments negatively impacts understorey plants and adds to a growing body of evidence to support willow-removal programmes (Brooks and Lake 2007; Stokes 2008). Isolated *Salix* spp. individuals will have limited impacts on instream plant populations but they can easily spread to form large mature stands, so we advocate for the complete removal of *Salix* spp. in areas where instream plant community recovery is sought.

Dense shading and grazing combined had the most severe impacts on plants, yet the removal of one threat through management is likely to yield marginal benefits to instream plant populations. Areas with these combined stressors are likely to require combined management of grazing and *Salix* spp. to facilitate adequate plant recovery.

There are other factors that affect both the likelihood that a plant is grazed and the responses by instream plants to grazing and shading that were not considered in this study. Livestock will selectively choose plants to consume based on several factors, including plant traits, size, palatability, and the relative abundance of plants (Jones and Vesk 2016). Plant responses appeared to vary according to several morphological traits; however, our experiment was focused on the responses of plant species inhabiting different hydrological niches. Future research could focus on investigating plant responses at the trait level. Livestock grazing in riparian zones can lead to major physical damage to plants as a result of trampling and pugging, and cause soil compaction and bank erosion—impacts that were not considered in this study (Robertson and Rowling 2000). Other environmental

factors such as water regime, water temperature, and nutrient loads also influence the growth of instream plants but were not considered in our study (Vivian et al. 2020; Main et al. 2022).

We simulated summer conditions over a 14-week period; however, the experiment was conducted over austral winter, which meant that the photoperiod was less than in summer. The study species would likely exhibit changes to growth and recession rates across usual annual seasonal conditions, and grazing and shading may have different effects on plants at different stages of their growth cycle, which we were unable to test (Wood et al. 2012). Future research could repeat our experiment in late spring/summer or simulate the variable shading provided by *Salix* spp. across a full year to investigate these seasonal effects. Furthermore, experiments simulating grazing over longer and more variable time periods could provide insights into the stamina of instream plants to withstand grazing impacts.

5 | Conclusion

Livestock grazing and dense shading are likely to negatively affect the growth, and even cause the death, of instream plants. While instream plant species have differing abilities to tolerate varied combinations of grazing and shading, the long-term effects of grazing and shading remain uncertain but are likely deleterious. Instream vegetation may become further stressed as human demands for water increase under projected hotter, drier conditions over the coming decades. Our findings provide further support for interventions such as livestock exclusion and non-native *Salix* spp. removal from waterways to help restore degraded riverine environments.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Appendix A

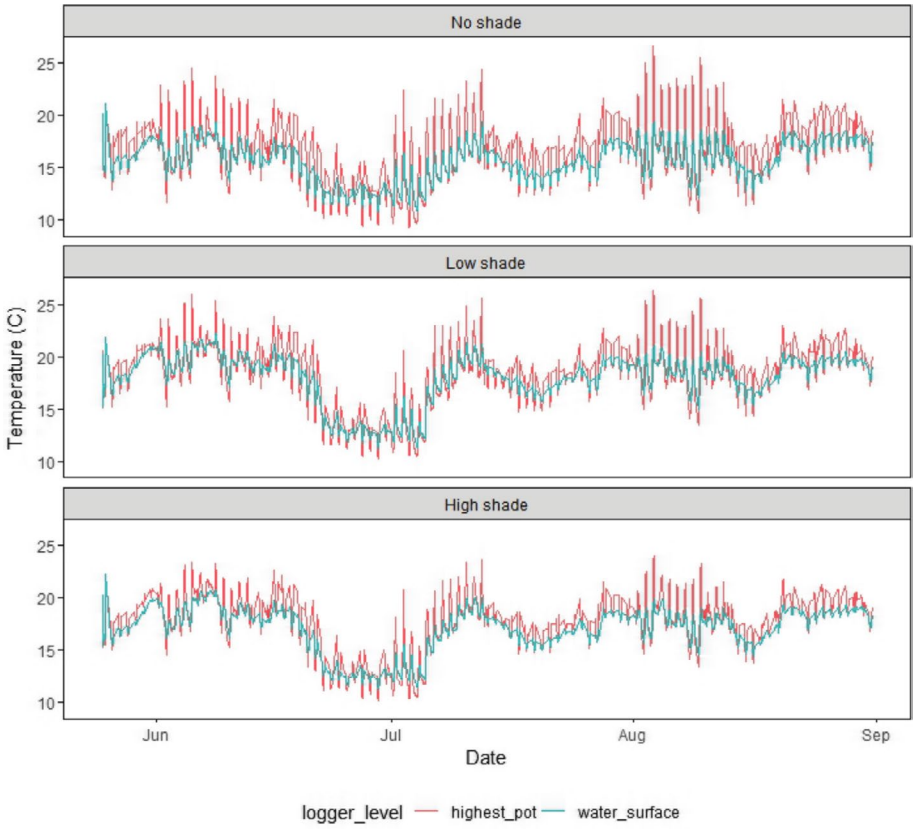


FIGURE A1 | Mean temperature values across tubs within each treatment type throughout the study period. Two logger positions were used: Water surface (blue) and soil level of the highest pot (red). [Color figure can be viewed at wileyonlinelibrary.com]

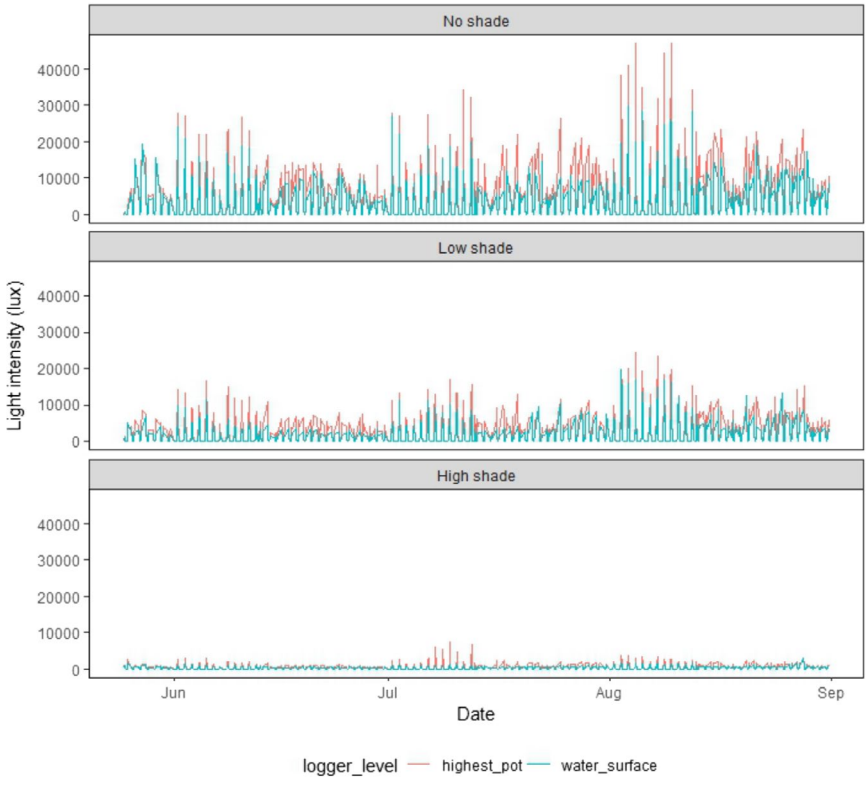


FIGURE A2 | Mean light intensity values across tubs within each treatment type throughout the study period. Two logger positions were used: Water surface (blue) and soil level of the highest pot (red). [Color figure can be viewed at wileyonlinelibrary.com]

Appendix B

TABLE B1 | Final plant length results summary (week 14), including model parameter estimates, standard error and *p*-values.

		Estimate	Standard error	*p*-value
Cycnogeton procerum	(Intercept)	41.33	1.64	< 0.001***
	Clipping	−4.22	2.32	0.08#
	Low shade	1.78	2.32	0.45
	High shade	6.22	2.32	0.01*
	Clipped × low shade	−2.00	3.28	0.55
	Clipped × high shade	1.78	3.28	0.59
Juncus usitatus	(Intercept)	46.22	1.71	< 0.001***
	Clipping	−14.33	2.41	< 0.001***
	Low shade	6.33	2.41	0.01*
	High shade	3.11	2.41	0.20
	Clipped × low shade	4.33	3.41	0.21
	Clipped × high shade	−35.00	3.41	< 0.001***
Schoenoplectus tabernaemontani	(Intercept)	50.06	6.39	< 0.001***
	Clipping	19.50	8.87	0.05
	Low shade	46.16	8.87	< 0.001***
	High shade	61.61	8.87	< 0.001***
	Clipped × low shade	−20.50	12.42	0.12
	Clipped × high shade	−30.27	12.42	0.03
Vallisneria australis	(Intercept)	31.78	3.35	< 0.001***
	Clipping	−16.67	4.74	0.001***
	Low shade	−4.22	4.74	0.38
	High shade	2.33	4.74	0.62
	Clipped × low shade	3.33	6.71	0.62
	Clipped × high shade	−2.33	6.71	0.73

Note: Significance codes: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, #$p < 0.100$.

Appendix C

TABLE C1 | Change in above-ground biomass at the end of the experiment (week 14), including model parameter estimates, standard error and *p*-values.

		Estimate	Standard error	*p*-value
Cycnogeton procerum	(Intercept)	0.03	0.08	0.68
	Clipping	−0.35	0.11	0.001**
	Low shade	−0.04	0.11	0.71
	High shade	−0.40	0.11	< 0.01**
	Clipped × low shade	0.12	0.16	0.48
	Clipped × high shade	0.41	0.16	0.03*
Juncus usitatus	(Intercept)	1.39	0.43	< 0.01**
	Clipping	−1.89	0.61	0.001**
	Low shade	−0.06	0.61	0.92
	High shade	−0.79	0.61	0.22
	Clipped × low shade	0.41	0.87	0.65
	Clipped × high shade	0.71	0.87	0.43
Schoenoplectus tabernaemontani	(Intercept)	0.35	0.54	0.53
	Clipping	−2.99	0.75	< 0.001***
	Low shade	2.48	0.75	< 0.01**
	High shade	−0.17	0.75	0.82
	Clipped × low shade	−2.09	1.04	0.05*
	Clipped × high shade	−0.28	1.04	0.79
Vallisneria australis	(Intercept)	0.63	0.15	0.001**
	Clipping	−0.75	0.21	< 0.01**
	Low shade	−0.20	0.21	0.34
	High shade	−0.57	0.21	0.02*
	Clipped × low shade	0.11	0.29	0.71
	Clipped × high shade	0.23	0.29	0.44

Note: Change in above-ground biomass for each species was calculated as biomass for each plant minus average biomass at the start of the experiment. Significance codes: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, $^{\#}p < 0.10$.

Appendix D

TABLE D1 | Change in below-ground biomass at the end of the experiment (week 14), including model parameter estimates, standard error and *p*-values.

		Estimate	Standard error	*p*-value
Cycnogeton procerum	(Intercept)	1.05	0.23	< 0.001***
	Clipping	−1.87	0.33	< 0.001***
	Low shade	−1.26	0.33	< 0.001***
	High shade	−2.40	0.33	< 0.001***
	Clipped × low shade	1.49	0.47	< 0.01**
	Clipped × high shade	2.11	0.47	< 0.001***
Juncus usitatus	(Intercept)	0.26	1.03	0.80
	Clipping	−3.07	1.45	0.04*
	Low shade	−1.50	1.45	0.31
	High shade	−4.32	1.45	< 0.01**
	Clipped × low shade	3.02	2.05	0.15
	Clipped × high shade	2.14	2.05	0.30
Schoenoplectus tabernaemontani	(Intercept)	16.94	3.20	< 0.001***
	Clipping	−15.79	4.40	0.001***
	Low shade	−11.03	4.40	0.02*
	High shade	−19.39	4.40	< 0.001***
	Clipped × low shade	10.49	6.13	0.09#
	Clipped × high shade	16.31	6.13	0.01*
Vallisneria australis	(Intercept)	0.43	0.07	< 0.001***
	Clipping	−0.30	0.11	< 0.01**
	Low shade	−0.13	0.11	0.24
	High shade	−0.36	0.11	0.001**
	Clipped × low shade	−0.03	0.15	0.84
	Clipped × high shade	0.18	0.15	0.24

Note: Change in below-ground biomass for each species was calculated as biomass for each plant minus average biomass at the start of the experiment. Significance codes: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, #$p < 0.10$.