





# Growth of the invasive Navua sedge (*Cyperus aromaticus*) under competitive interaction with pasture species and simulated grazing conditions: Implication for management

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## Abstract

Navua sedge (*Cyperus aromaticus*), a perennial monocot plant native to tropical Africa, is a major weed in pasture and cropping areas in the wet tropical regions of Australia and South Pacific countries. In grazing pasture lands, rapid growth and reproduction of unpalatable Navua sedge leads to displacement of co-occurring pasture species and depletion of livestock carrying capacity and production. Understanding the interspecific competitive ability of Navua sedge with co-occurring desirable grasses and in response to varying ecological scenarios (e.g., grazing and plant density) is critical for the management of the weed in pasture situations. In a glasshouse setting, two co-occurring pasture species—humidicola (*Urochloa humidicola*) and Rhodes grass (*Chloris gayana*) were grown with Navua sedge, in pots using a replacement series model. For each Navua sedge weed–pasture species pair, the experimental setup comprised of four ratios in two densities under simulated grazing and nongrazing conditions of the pasture grasses. Navua sedge growth and reproduction was highest when it grew as a monoculture or when co-occurring pastures were exposed to simulated grazing as this action, reduced the competitiveness of the pasture grasses. Overall and using biomass gained, tiller production and relative yield as indices of growth dynamics, Rhodes grass was more competitive against Navua sedge than humidicola in both grazed and nongrazed conditions especially under high plant density. These results suggest the potential to include competitive pastures in integrated management strategies for Navua sedge, but species selection and grazing practices may influence the effectiveness of this approach.

## KEYWORDS

competition, management, Navua sedge, pasture grasses, replacement ratio design

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## 1 | INTRODUCTION

Plant species native to an area can cross geographical barriers and spread into new areas through various pathways, including water, air, hitchhiking on other organisms (especially alien insects), trade/commerce and via many anthropogenic activities such as habitat destruction and/or afforestation (Foxcroft et al., 2017; Roiloa et al., 2020). These species are often named as invaders, invasive species, alien species or exotic species. Irrespective of nomenclature attached, they can have a devastating impact on the biodiversity and ecology in their introduced areas (Gallardo et al., 2017; Osunkoya et al., 2019). For example, several sedges in the *Cyperus* species complex (e.g., *Cyperus rotundus*, *Cyperus difformis*, *Cyperus esculentus* and *Cyperus iria*) are among the world's most problematic weeds in various parts of the world (Holm et al., 1977); *Cyperus rotundus* especially is considered as one of the top 10 worst weeds of the world (Mannarreddy et al., 2017; Robert, 1981).

Navua sedge (*Cyperus aromaticus* [Ridley] Mattfeld & Kükenthal) is a member of *Cyperus* genus that is becoming problematic progressively around the world. It is native to African where it is also known synonymously as *Kyllinga polyphylla* Willd. Ex Kunth, *Kyllinga erecta* var. *polyphylla* (Kunth) S.S. Hooper and *Kyllinga aromatica* Ridley (Bruhl, 1995; Parsons & Cuthbertson, 2001; USDA, 2019). It has been recognized as a problematic invasive weed for decades in pastures, along rail- and road-sides, in lawns and cropping (e.g., sugarcane) farms of tropical areas (Benson, 1992; Black, 1984; CABl, 2019; Shi et al., 2021; Vitelli et al., 2010). Many humid and tropical Asian-pacific regions, such as Fiji, Vanuatu, Sri Lanka, India, Thailand, Hong Kong, Taiwan, Malaysia, Vietnam, Solomon Islands and coastal areas of north Queensland, Australia are infested with Navua sedge (Parsons & Cuthbertson, 2001; Shi et al., 2021). In its invaded ranges, Navua sedge is now a growing concern due to a lack of promising management techniques (AVH, 2019; Black, 1984; Karan, 1976; Shi et al., 2021; Vitelli et al., 2010).

Tropical pastures are especially prone to the development of monocultures of Navua sedge since chemical as well as physical management of Navua sedge is not actively undertaken by many landowners because of unintentional environmental impacts and financial constraints of such tactics (Karan, 1976; Vitelli et al., 2010). Mechanical measures, including regular slashing and mowing, tend to promote seed dispersal and further spread of Navua sedge (Benson, 1992; Shi et al., 2021; Vitelli et al., 2010). Equally, in Queensland, current chemical control options are unable to reduce the recurrence and spread of the weed (Vitelli et al., 2010; Vogler

et al., 2015). The only registered herbicide against Navua sedge in Australia is Halosulfuron Methyl (e.g., Sempra®); general broad-spectrum herbicides such as Glyphosate and Paraquat, are also used for control of Navua sedge (Chadha et al., 2022; Vitelli et al., 2010), but these herbicides have been found to be of limited success. It is usually recommended to apply these herbicides at least three times a year to achieve >90% population reduction, but such a reduction is rarely achieved by farmers using Halosulfuron Methyl due to the cost (Shi et al., 2021). Also, herbicide applications have been known to be temporary measures with minimal impact on subterranean rhizomes and dormant seeds which are the prime reason for Navua sedge's resurgence and contribution to its spread (Chadha et al., 2022; Vitelli et al., 2010). Moreover, after the herbicide application of Halosulfuron Methyl, pastures are restricted for cattle to graze upon (withholding period; spelling) for at least 10 weeks, which also imposes a significant impact and financial cost on beef and dairy enterprises. Considering the ineffective or uneconomical control measures highlighted above, the potential use of integrated weed management, including biological control is being explored (Dhileepan et al., 2022; Shi et al., 2021). Maintaining a healthy and competitive pasture is considered a useful approach, particularly as part of an integrated strategy to manage Navua sedge in grazed areas (Karan, 1976; Mune, 1959; Shi et al., 2021; Vitelli et al., 2010; Vogler et al., 2015). Hence, exploring the use of desirable pasture grasses that can compete with Navua sedge under varying ecological/land use scenarios will be informative and could offer long term control of the Navua sedge weed, especially when combined with biological and/or chemical control options (Shabbir et al., 2020).

Plant growth, canopy structure, reproduction and biomass accumulation can be influenced by above and below ground competition (Mudr k et al., 2016; Savi c et al., 2021; Walsh et al., 2018). Some preliminary studies have been initiated to compare the competitiveness of desirable pasture species such as Rhodes grass (*Chloris gayana*), Signal grass (*Urochloa decumbens*), humidicola (*Urochloa humidicola*) and Setaria (*Setaria sphacelata* var. *sericea*) against Navua sedge, but the results have not been conclusive to date (Ellett, 2011; Moilwa, 2018). Rhodes grass is especially one of the most persistently productive and competitive grasses introduced into Queensland because it can readily establish and grow aggressively in grass mixtures as well as in monoculture (Jones et al., 1969; Manalil et al., 2020). Furthermore, it is highly palatable and hence, a desirable option for cattle grazing in Queensland and New South Wales, Australia (Ehrlich et al., 2003; Jones et al., 1969). Signal grass (*U. decumbens*) and humidicola (*U. humidicola*) have also

been introduced in the past to Australia (Cook & Dias, 2006; Redden et al., 2020), exploited as improved pastures and are known anecdotally to provide adequate competition to manage *Navua* sedge (Rob Pagano, Bernie English, Wayne Vogler, personal communications). We tested the hypothesis that where these desirable grasses are managed appropriately when grown in cattle paddocks or plots infested with *Navua* sedge, they will compete favorably, suppress the weed's growth and fitness, and thus consequently help to dampen the impact of the weed on production agriculture.

A glasshouse species replacement series experiment was conducted to study the competitive ability of two widely grown pasture species in far-north Queensland, Australia (Rhodes grass and *humidicola*) against *Navua* sedge. The use of a replacement series model for competition experiments has been one of the most common approaches used over the last five decades for the study of crop–weed interactions under certain conditions and with constant total plant density (De Wit, 1960; Rejmánek et al., 1989; Swanton et al., 2015; Szymura et al., 2018). Another method, the additive series competition design, has also become popular, but can produce obscure results about the effect of the weed on the crop and vice versa as the total plant density is altered in the trial (Rejmánek et al., 1989; Swanton et al., 2015). The overall conclusions of replacement series design are not significantly different from other methodologies (Jolliffe, 2000). In this study, we chose the former approach, that is, a replacement series model, which was implemented with four replacement ratios at two different densities with and without simulated grazing. The use of two different densities (and relatively small-medium pot size) was to minimize some of the inherent biases in the replacement series approach (see Sections 3 and 4). Thus, in this replacement experimental setup, growth performance of *Navua* sedge and two co-occurring pasture species (Rhodes and *humidicola* grass) were tested in diverse conditions of density (16 plants and 4 plants/pot) with four replacement ratios (25%, 50%, 75% and 100%) and under simulated and no grazing scenarios. Our proximate focus was to compare the biomass production and fitness components (flowering intensity, fruit production) of the *Navua* sedge in the presence of focal/desirable pasture grasses under varying ecological conditions. Taking cognizance of known significant results from a previous study on competition of Rhodes grass against *Navua* sedge under water-stressed conditions (Moiilwa, 2018) and Rhodes grass's response to grazing (Jones et al., 1969), the following specific objectives were defined for this study:

a. Evaluation of changes in biomass gained, partitioning patterns and fitness component of *Navua* sedge when

grown with Rhodes grass or *humidicola* and from the findings.

b. Exploration of which of the two desirable grasses can compete favorably against *Navua* sedge in relation to interspecific and intraspecific competition and simulated animal grazing of these grasses; the results could provide experimental evidence of which of the pasture species may be chosen for integrated management of the weed.

## 2 | MATERIALS AND METHODS

### 2.1 | Seedling production

Seeds of *Navua* sedge were sourced from infestation sites in South Johnstone, North Queensland, Australia while fresh seeds of Rhodes grass cv. *callide* and *humidicola* were procured from Barenbrug Pty Ltd, Australia. Seeds were stored in a cold room (4°C) until required. As germination time of a weed relative to a desirable plant (e.g., crops) may influence the outcome of competition (Gioria & Pyšek, 2017), a preliminary study was undertaken to determine the germination percentage and germination time for our three focal species. *Navua* sedge seeds germinated 1 and 2 weeks ahead of *humidicola* and Rhodes grass seeds, respectively.

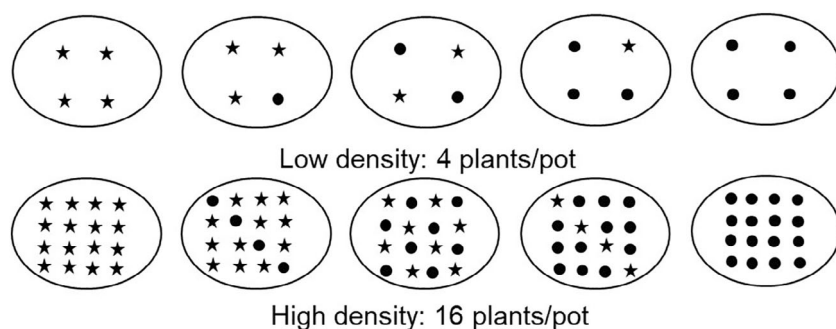
Based on the germination time and percentage results, to have at least 600 seedlings of each species required for a full factorial experiment (see below), approximately 2000 seeds of each species were sown in open seedling trays (dimension: 350 × 295 × 50 mm) containing 2.5 L of University of California potting mixture (consisting of peat moss, sand and added fertilizers) in the glasshouse located at the University of Queensland, St Lucia campus, Brisbane, Australia. Seedling trays and seedlings were irrigated twice a day throughout the duration of the experiment (16 weeks), while fertilizer (Scotts Osmocote® All Purpose General, 21.2% of nitrogen, 3.5% of phosphorus and 5.7% of potassium) was applied once in the last 2 weeks of seedling emergence stage. Due to differences in germination rates of the three focal species (see above), *Navua* sedge, *humidicola* and Rhodes grass seeds were sown on the March 14, 2019, March 20, 2019 and March 25, 2019, respectively. In this fashion, 2 weeks after exposure of seeds of the focal species to germination, their seedlings were of similar height and morphology and were ready to be transferred (transplanted) into pots for the competition trial. Initial biomass of both the shoot and root of transplanted plants were collected from 10 randomly selected seedlings of each species; these values were included in the analysis as covariates to adjust for their possible effects on growth parameters and for estimation of relative growth rates (RGRs, see below).

## 2.2 | Growth and competition study

The 16 weeks study was undertaken in an evaporative cooled glasshouse located at the University of Queensland St Lucia Campus, Brisbane, Australia (27°29'42.7" S 153°00'31.4" E). A 2 × 2 × 4 × 2 × 2 factorial experiment was conducted using a completely randomized design with six replications for each treatment (Figure 1). The factors include (1) competition type (intraspecific and interspecific); (2) comparison of growth performance of two pasture species (Rhodes grass and humidicola), each grown in combination with Navua sedge; (3) four competition levels (at replacement ratios of 25%, 50%,

75% and 100%); (4) two plant densities (4 or 16 plants per pot) and (5) two grazing regimes (simulated grazing and no grazing conditions) (Figure 1). All pots were labeled with pasture species, competition levels (replacement ratio), density, grazing regime and replicate number.

Two hundred and forty pots (each of 25 cm in diameter; 23.5 cm in depth) were filled with "University of California" potting mixture. In each pot, either 4 or 16 seedlings were transplanted in the patterns required for the various species mixtures and plant densities (Figure 1). Automatic watering, lasting 5 min was implemented twice a day throughout the study to maintain the pots close to field capacity. The simulated grazing



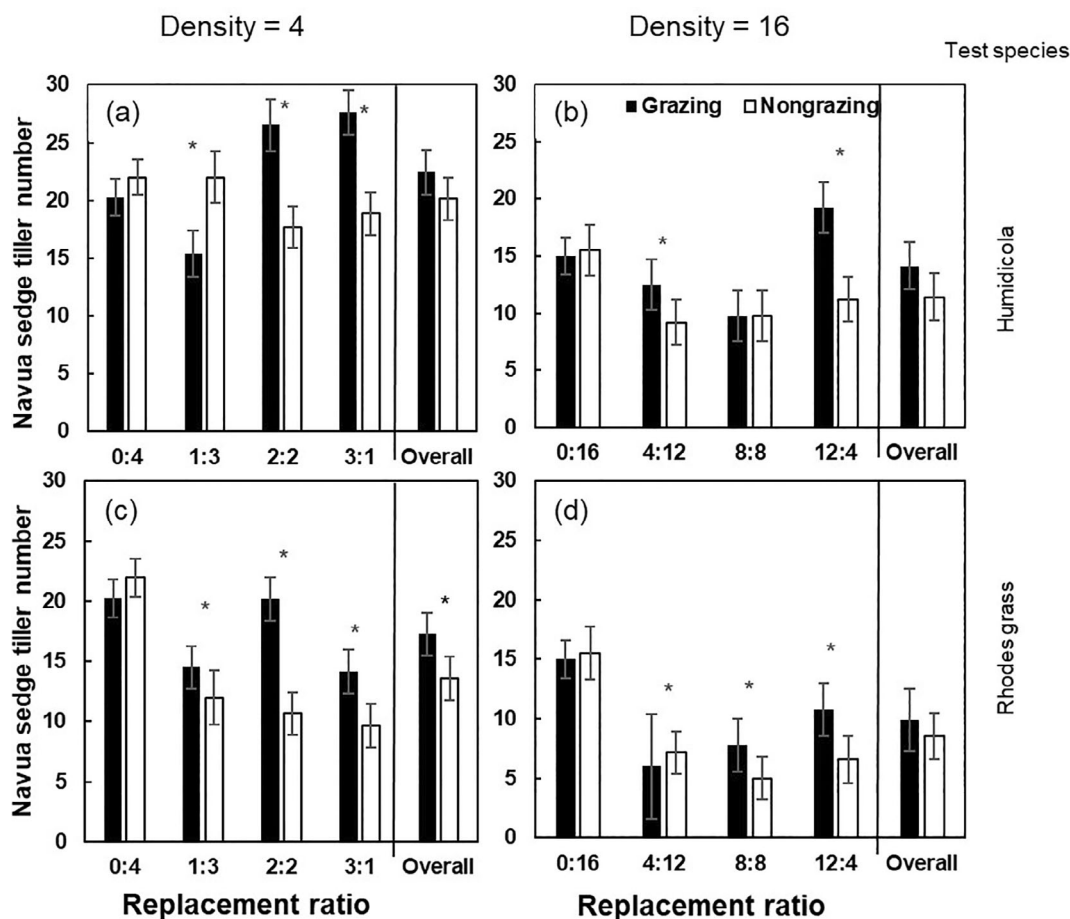
**FIGURE 1** A diagram showing the replacement ratios for the trial with either 4 or 16 plants per pot. The circle represents the test species (either humidicola or Rhodes grass) and the star represents Navua sedge species. Note that at either the low or high density, the first and last designs are mirror images of each other (i.e., they represent monocultures of either the test pasture species or the weed), thus accounting for a four-replacement ratio design.

**TABLE 1** Summary ANOVA of tests of effects of interspecific or intraspecific competition for Navua sedge and humidicola grass and Rhodes grass under two densities, four replacement ratios with and without simulated grazing. The error for the number of degrees of freedom range from 138 to 307. Note that the number of flowers is only recorded for Navua sedge.

Factor (source of variation)	df	F ratio and probability							Flowers number
		Tiller number	Crown size	Shoot length	Root length	Total biomass	Shoot/root ratio (biomass)	RGR	
Species (S)	2	83.221***	75.211***	173.432***	1.008	54.001***	5.634**	52.169***	—
Competition (C)	1	2.932	0.403	1.852	0.690	13.682***	0.441	182.099***	21.864***
Density (D)	1	29.782***	33.711***	26.493***	70.956***	55.294***	0.413	106.789***	50.947***
Grazing (G)	1	12.548***	17.396***	437.919***	0.076	193.565***	2.357	206.997***	0.293
S × C	2	7.821***	11.232***	8.917***	5.889**	23.975***	1.512	27.440***	—
S × D	2	4.615**	0.432	8.763***	0.862	0.397	2.015	0.074	—
S × G	2	15.330***	9.694***	138.536***	17.783	104.336***	4.221*	100.868***	—
C × D	1	0.005	0.992	0.241	0.226	0.936	0.976	3.843*	1.029
C × G	1	0.031	1.244	1.379	2.913	1.951	2.612	0.313	8.343**
D × G	1	3.370	0.543	0.562	0.202	1.403	1.360	0.296	0.284
S × C × D	2	0.502	0.722	4.762	1.596	0.632	0.196	0.583	—
S × C × G	2	3.483*	8.867	3.583	8.729***	13.416***	2.795	9.525***	—
S × D × G	2	0.612	1.970	6.024**	0.342	1.293	0.166	2.996	—
C × D × G	1	0.024	3.387	0.092	0.750	0.352	0.764	0.910	3.094
S × C × D × G	2	0.149	0.300	2.006	0.047	0.357	0.372	0.599	—

Abbreviations: ANOVA, analysis of variance; RGR, relative growth rate.

\* $p \leq 0.05$ ; \*\* $p \leq 0.02$ ; \*\*\* $p \leq 0.00$ .



**FIGURE 2** Mean response of tiller number of the invasive *Navua* sedge when grown at a low (4 plants per pot; *a* and *c*) and a high (16 plants per pot; *b* and *d*) density, with each density at 4 replacement ratios (0:4 or 0:16, 1:3 or 4:12, 2:2 or 8:8, 3:1 or 12:4) of combination of humidicola or Rhodes grass with *Navua* sedge. The graphs also show tiller number of *Navua* sedge under grazing and nongrazing treatments. Bars represent two standard error of the mean calculated with six replicates at each replacement ratio. “\*” indicates significant difference ( $p < 0.05$ ) between treatments at a given replacement ratio. “Overall” refers to mean plant performance, irrespective of replacement ratio. The significance of differences at the overall level can be found in Table 1.

treatment was imposed by manually cutting the tillers of only the grass species (Rhodes grass and humidicola) and not that of co-occurring *Navua* sedge weed in the pots twice at time intervals of 4 and 8 weeks after the initiation of the experiment. Each time during the simulated herbivory, plants of Rhodes grass and humidicola were trimmed at approximately 5 cm above ground level.

### 2.3 | Growth measurement and collection

For seedlings of all treatments, plant height was measured at monthly intervals. All plants were harvested 16 weeks after treatment applications. At this stage, plants were carefully removed from the pots (shoots and roots) by gently washing the soil away from the roots using running water. For each plant, various growth indices were measured and recorded, including crown diameter, root length, shoot

length, number of tillers; for *Navua* sedge only, flower numbers were also recorded. The root and shoot material were then separated, placed into individual paper bags and dried in ovens at 60°C for 96 h prior to determination of their dry weights. Shoot to root ratio was calculated using above ground biomass/root biomass, and RGR was calculated via  $(\ln W_2 - \ln W_1)/(t_2 - t_1)$ , where  $\ln W$  is the natural logarithm of biomass,  $t$  is the time (weeks) and the subscript refers to initial (1) and final (2) harvest. For each treatment condition, relative yield (RY) for each species was calculated using the formula below,

$$RY = \text{Yield in mixed culture} / \text{Yield in monoculture}.$$

### 2.4 | Data analysis

To evaluate the growth of the three focal species, all data parameters were subjected to multiway analysis of

variance (ANOVA) and linear regression models using SPSS statistics package (IBM version 27). From the data compiled, analyses of plant growth performance (the response variables; e.g., biomass gained, RGR and tiller number) were based on 5 factors of (i) competition type (intraspecific [monoculture] or interspecific [mixed culture]); (ii) test species (Navua sedge, Rhodes grass or humidicola); (iii) simulated grazing treatment (grazing or no-grazing); (iv) replacement ratios (100%, 75%, 50% and 25%); and (v) 2 plant densities (16 or 4 plants per pot). In all, for simplicity and ease of data interpretation, we examined effects of main and multiway interactions of all factors. In some cases, there were no significant differences among 25%, 50% and 75% of replacement ratios, so the data analyses and results for these individual ratios were collapsed and hence not shown in the results. Replacement series curves—that is, plots of RYs of each species in relation to changes in its proportion in the experimental pots were also constructed for biomass gained, RGR and flower production in relation to simulated grazing condition and overall density. In all growth indices,

data were tested for homogeneity in variance distribution and data were log transformed where necessary (RY and biomass gained) to meet the assumption of parametric analyses (e.g., ANOVA; Osunkoya et al., 2005). Significant main effects and interactions were further subjected to the protected least significant difference test to find where differences lie among levels of a given factor.

### 3 | RESULTS

#### 3.1 | Overall (general pattern)

Tiller production, crown size, shoot length, total biomass and RGR, all varied significantly among the three tested species, between plant density and simulated grazing condition (Tables 1 and Table S1). For each species, the influence of competition (intraspecific or interspecific) type was only manifested on RGR, total biomass gained and on number of flowers produced by Navua sedge (Table 1). Shoot/root ratio (mean  $\pm$  SE) only differed among our

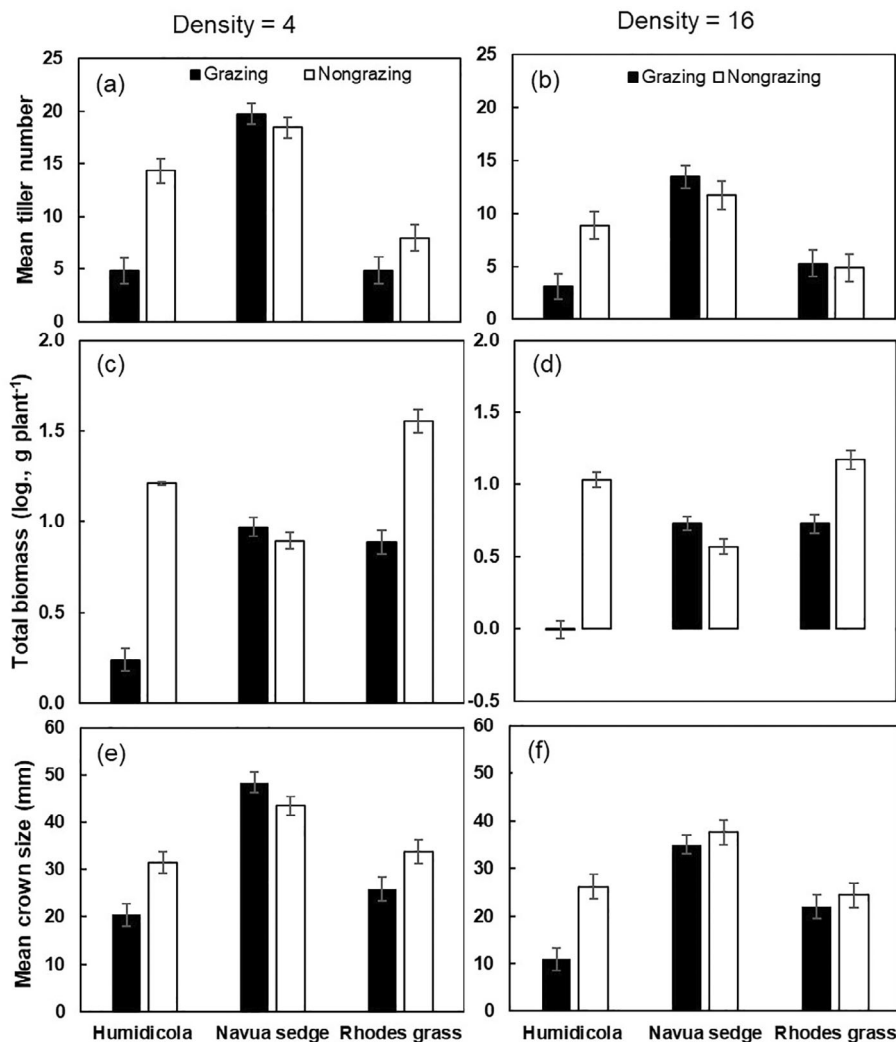
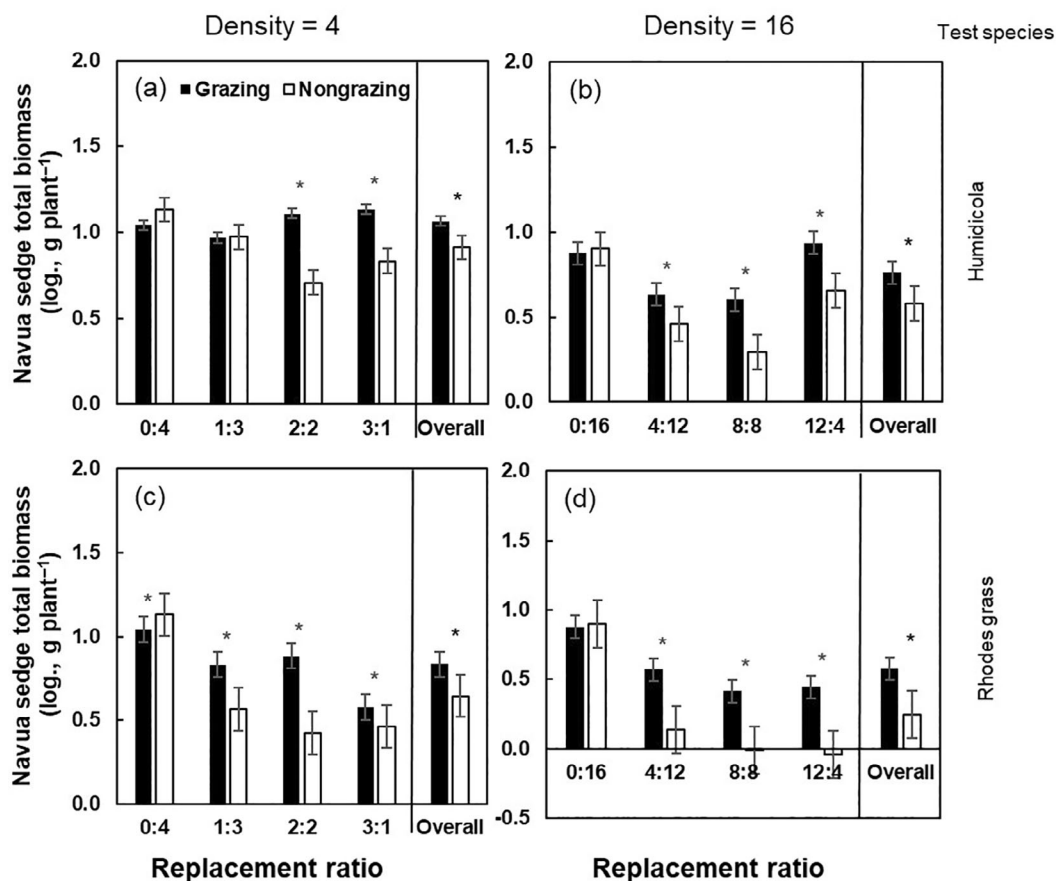


FIGURE 3 Mean ( $\pm$  SE) response of the tiller numbers (a and b), total biomass (ln-transformed, c and d) and crown size (e and f) of invasive Navua sedge and two pasture grasses (humidicola and Rhodes grass) under grazing and nongrazing conditions.



**FIGURE 4** Mean response of total biomass (logged) of Navua sedge when grown at a low (4 plants per pot; *a* and *c*) and a high (16 plants per pot; *b* and *d*) density, with each density at 4 replacement ratios (0:4 or 0:16, 1:3 or 4:12, 2:2 or 8:8, 3:1 or 12:4) of combination of humidicola or Rhodes grass with Navua sedge. The graphs also show biomass gained by Navua sedge under grazing and nongrazing treatments. Bars represent two standard error of the mean calculated with six replicates at each replacement ratio. “\*” indicates significant difference ( $p < 0.05$ ) between treatments at a given replacement ratio. “Overall” refers to mean plant performance, irrespective of replacement ratio. The significance of differences at the overall level can be found in Table 1.

three focal species (Navua sedge [ $1.85 \pm 0.12$ ], humidicola [ $2.35 \pm 0.15$ ], Rhodes grass [ $2.43 \pm 0.16$ ];  $F_{2,307} = 5.63$ ,  $p < 0.004$ ) and was unaffected by competition, density or grazing conditions. Equally, there were no significant interaction effects between species and other tested factors on this trait, except for species  $\times$  grazing treatment ( $p = 0.02$ ; Table 1). There were significant interactions between species and competition type (S  $\times$  C), or species and simulated grazing (S  $\times$  G) for most growth parameters examined (RGR, number of tillers, number of flowers and total biomass), suggesting that species growth trait responses were largely affected by the nature of competition and/or grazing condition. In contrast, density effect on species growth response (S  $\times$  D) was limited/minimal as it affected only the tiller production ( $F = 4.62$ ;  $p < 0.02$ ) and shoot length ( $F = 8.76$ ;  $p < 0.02$ ) (Table 1), indicating minimal density effect and/or consistency in the direction of the effect of low (4 plants/pot) or high (16 plants/pot) on species growth performance.

### 3.2 | Individual species response to treatments and their interactions

Navua sedge produced significantly fewer tillers with increased replacement ratios (i.e., with increasing presence of grass species) and hence competition intensity, especially when grown with Rhodes grass as compared to humidicola (Figure 2). This trend of decreased Navua sedge tiller production with increasing interspecific competition appeared clearer (and hence significant) under nongrazing condition than when pasture species are grazed. As expected, both Rhodes grass and humidicola produced fewer tillers in simulated grazing condition and under high density than in low density (Figure 3a,b). Interestingly and overall, in the high density of 16 plants per pot, Rhodes grass produced significantly more tillers under simulated grazing than in the nongrazed conditions (4% increase,  $p < 0.05$ ; Figure 3b).

In general, Rhodes grass produced significantly more total biomass ( $83.3 \text{ g} \pm 6.37$ ) than humidicola ( $41 \text{ g} \pm 5.02$ ) (Figure 3c,d). Again, and as expected, both grasses produced significantly more biomass under nongrazed than grazed condition. Both Rhodes grass and humidicola also produced less biomass in high density than under low-density competitions (Figure 3c,d). Overall, Navua sedge produced much less total biomass when growing with Rhodes grass than with humidicola (Figure 4).

For Navua sedge, similar to tiller production and total biomass gained, crown size and hence space pre-emption, decreased with increasing competition in the presence of Rhodes grass than when the weed was grown with humidicola (Figure 5). This trend manifests itself more in the absence of simulated grazing (Figure 5). In all, Rhodes grass

exhibited significantly more crown size growth ( $25.95 \text{ cm} \pm 2.49$ ) than humidicola ( $20.42 \pm 2.38$ ) ( $p < 0.02$ ) under both grazed and nongrazed conditions when grown at the lower density of four plants per pot (Figure 3e); at high density, the difference in crown size between the two grasses was minimal (Figure 3f). However, Navua sedge showed higher crown diameters than both Rhodes and humidicola under both grazed and nongrazed conditions in the two plant densities (Figure 3e,f).

The number of flowers were only recorded for Navua sedge. Navua sedge produced significantly fewer flowers per plant (Table 1) under high-density (mean  $\pm$  SE:  $5.96 \pm 1.46$ ) than low-density ( $12 \pm 1.51$ ) conditions with either humidicola or Rhodes grass (Figure 6). However, more flowers were found under grazing than nongrazing

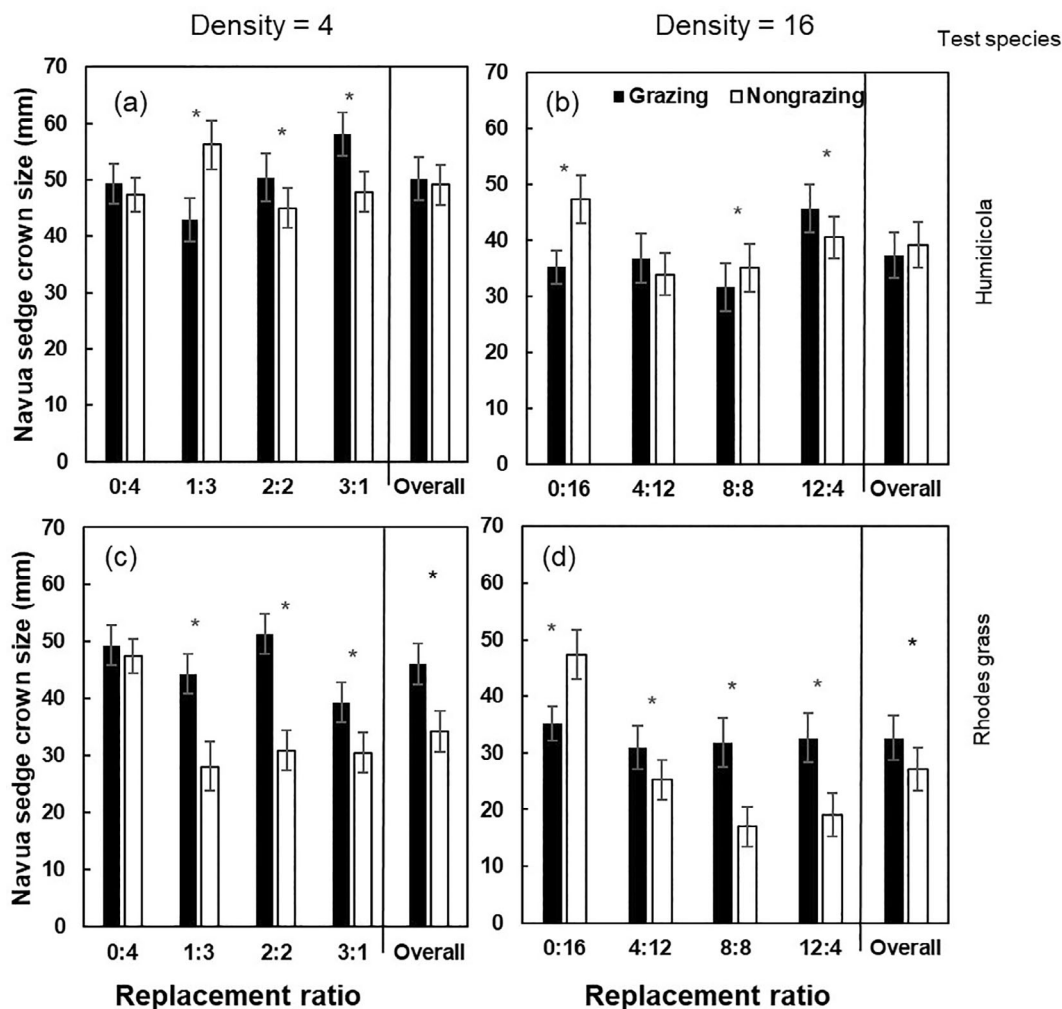
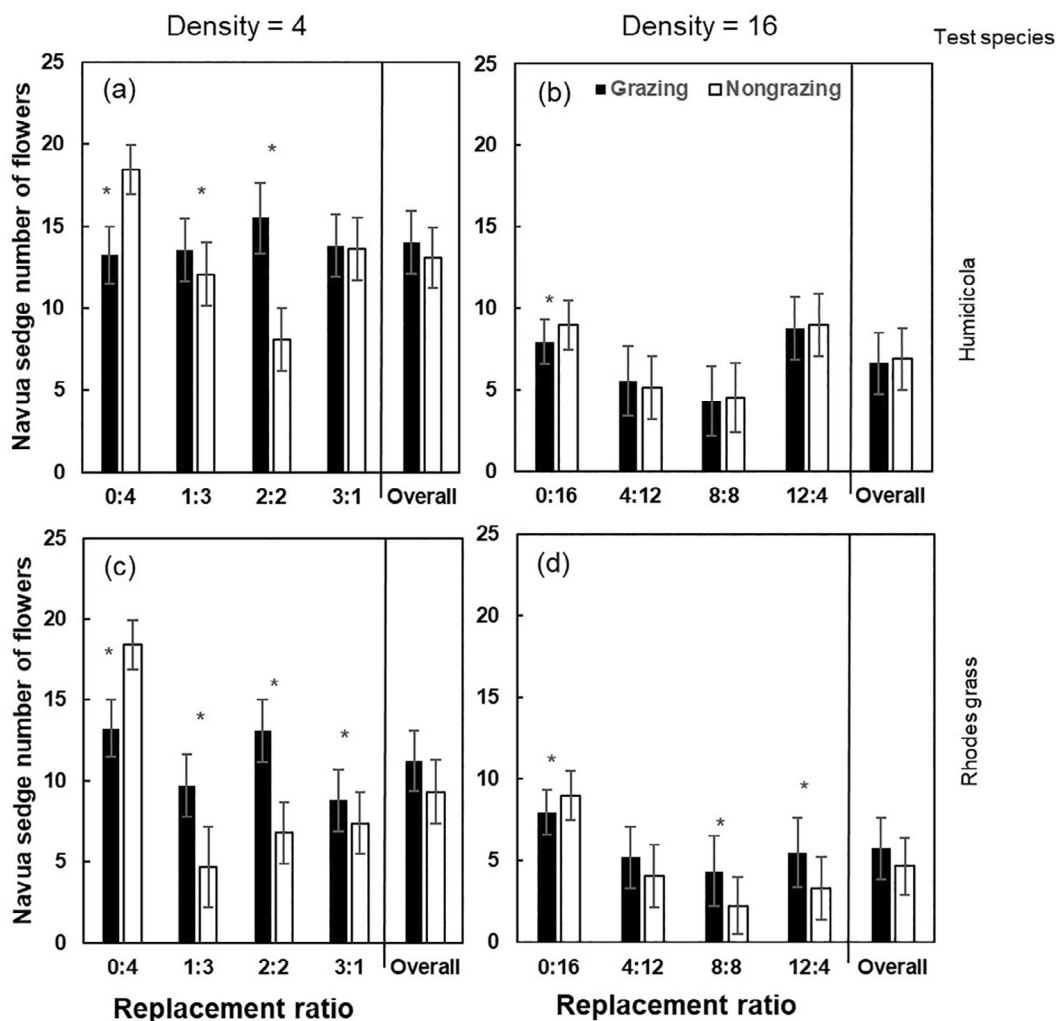


FIGURE 5 Mean response of crown diameter of Navua sedge when grown at a low (4 plants per pot; a and c) and a high (16 plants per pot; b and d) density, with each density at 4 replacement ratios (0:4 or 0:16, 1:3 or 4:12, 2:2 or 8:8, 3:1 or 12:4) of combination of humidicola or Rhodes grass with Navua sedge. The graphs also show crown diameter of Navua sedge under grazing and nongrazing treatments. Bars represent two standard error of the mean calculated with six replicates at each replacement ratio. “\*” indicates significant difference ( $p < 0.05$ ) between treatments at a given replacement ratio. “Overall” refers to mean plant performance, irrespective of replacement ratio. The significance of differences at the overall level can be found in Table 1.





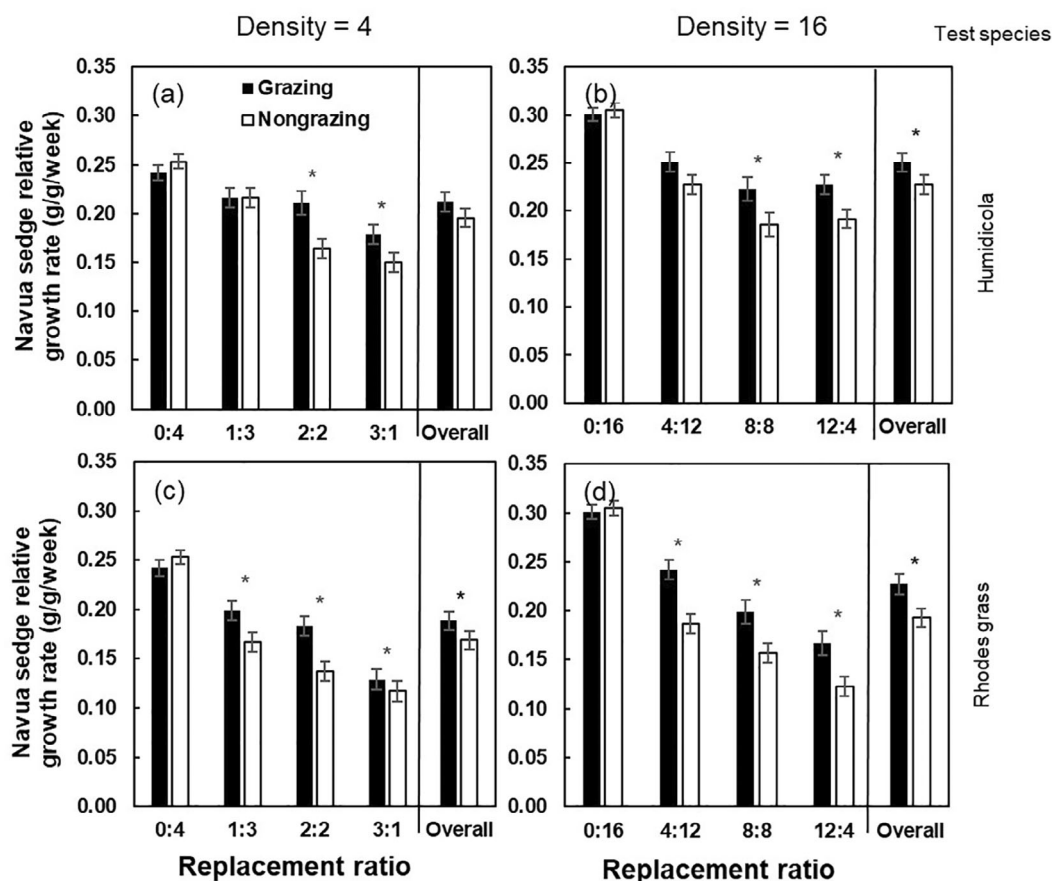
**FIGURE 6** Mean response of number of flowers of Navua sedge when grown at a low (4 plants per pot; *a* and *c*) and a high (16 plants per pot; *b* and *d*) density, with each density at 4 replacement ratios (0:4 or 0:16, 1:3 or 4:12, 2:2 or 8:8, 3:1 or 12:4) of combination of humidicola or Rhodes grass with Navua sedge. The graphs also show number of flowers of Navua sedge under grazing and nongrazing treatments. Bars represent two standard error of the mean calculated with six replicates at each replacement ratio. “\*” indicates significant difference ( $p < 0.05$ ) between treatments at a given replacement ratio. “Overall” refers to mean plant performance, irrespective of replacement ratio. The significance of differences at the overall level can be found in Table 1.

conditions (Figure 6). In the high density of 16 plants per pot, there was no significant difference in Navua sedge flower production in the presence of Rhodes grass or humidicola. In contrast, at low density of four plants per pot, Navua sedge produced marginally fewer flowers with Rhodes grass ( $10.27 \pm 1.91$  per plant) than humidicola ( $13.53 \pm 1.87$  per plant) (Figure 6;  $p = 0.07$ ).

Navua sedge showed significantly different RGR at the two densities of four and 16 plants per pot (Figure 7). In all cases, irrespective of species paired with Navua sedge and the grazing condition, the RGR of the focal weed decreased with increasing interspecific competition at both low and high density (Figure 7). However, it is safe to say that based on total biomass gained, the competition effect is felt more by Navua sedge under Rhodes grass

than under humidicola. It is also safe to acknowledge that the use of RGR gave a clearer picture of growth dynamics under various scenarios than that presented using total biomass gained (contrast Figure 4 vs. Figure 7).

The RY of biomass and tiller number of Rhodes grass in response to competition were significantly greater (higher concave in shape) than responses exhibited by humidicola (convex in shape) or Navua sedge (mildly concave in shape) under both grazed and nongrazed conditions (Figure 8a,b). Same trend was observed of greater performance for Rhodes grass compared to humidicola when each grass is in competition with Navua sedge in terms of tiller production and RGR, though the dynamics were not as clear-cut as that depicted using biomass gained (Figure 8). Thus, in summary it is noted that



**FIGURE 7** Mean response of relative growth rate (RGR, g/g/week) of Navua sedge when grown at a low (4 plants per pot; *a* and *c*) and a high (16 plants per pot; *b* and *d*) density, with each density at 4 replacement ratios (0:4 or 0:16, 1:3 or 4:12, 2:2 or 8:8, 3:1 or 12:4) of combination of humidicola or Rhodes grass with Navua sedge. The graphs also show RGR of Navua sedge under grazing and nongrazing treatments. Bars represent two standard error of the mean calculated with six replicates at each replacement ratio. “\*” indicates significant difference ( $p < 0.05$ ) between treatments at a given replacement ratio. “Overall” refers to mean plant performance, irrespective of replacement ratio. The significance of differences at the overall level can be found in Table 1.

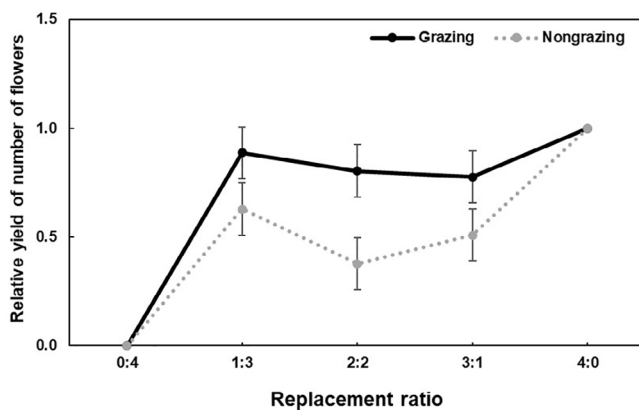
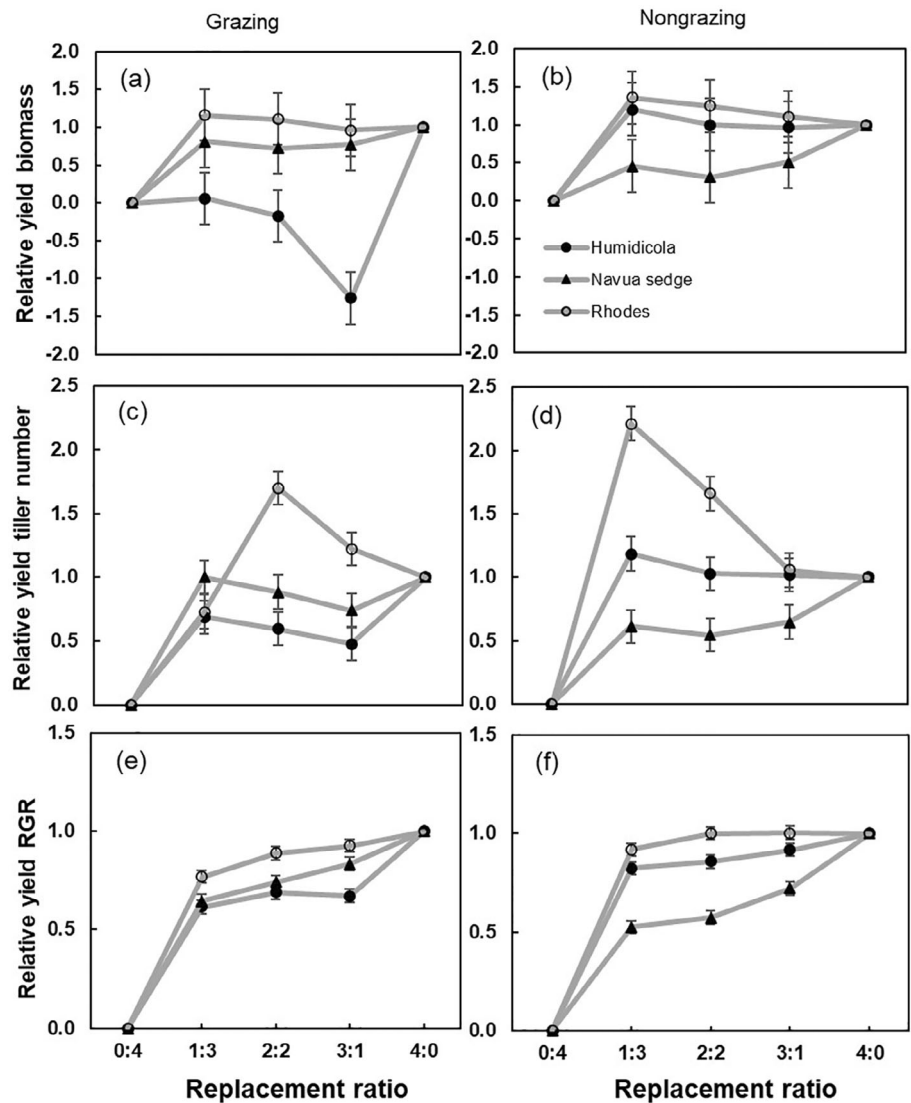
irrespective of the grazing condition, humidicola produced lower RY biomass (RY ratio  $< 1$ ) than Navua sedge; both species (i.e., humidicola or Navua sedge) yields were much lower (RY ratio mostly  $< 1$ ) than that exhibited by Rhodes grass (RY ratio mostly  $> 1$ ), confirming that Rhodes grass tend to perform better in mixtures of hetero-specific plants than when in monoculture, and hence may be a far-better competitor than humidicola in the field (Figure 8). The RY response of flowers production of Navua sedge was more under grazed (concave in shape) than nongrazed conditions (nearly linear) (Figure 9), suggesting that grazing of co-occurring humidicola or Rhodes grass has a stimulating effect on flower production in the invasive Navua sedge.

## 4 | DISCUSSION

In replacement series experimental design, the growth dynamics of plants in mixtures may strongly be

influenced by the total density (Jolliffe, 2000; Rodríguez, 1997; Szymura et al., 2018; Taylor & Aarssen, 1989), and hence experiments conducted at a single density may be inadequate. Other biases that may affect the outcome of competition in a glasshouse setting are pot size, nutrient level applied and duration of experiment. To minimize these biases, we used two densities and did not apply additional nutrients (i.e., fertilizer) during the 4 month experiment (during which the focal weed initiated flowering/fruitlet)—thus ensuring that resource demands for both space and nutrients are most likely to exceed their supply, especially under the higher density of 16 plants per pot. To counteract the obscuring impact of differential seedling emergence and vigor on overall competition of the test species, a germination test was conducted prior to experimental setup to evaluate the seedling emergence time of all three species (Swanton et al., 2015). This allowed us to select the seedlings of similar size. The results from these replacement series experiments (Table 1) indicated that though density on its own significantly

**FIGURE 8** Relative yield (RY) of total biomass (a and b), tiller numbers (c and d) and relative growth rate (RGR; e and f) for Rhodes grass (○), Navua sedge (▲) and humidicola (●) after 16 weeks of plant growth under grazing and nongrazing competitions. Error bars display 95% confidence intervals for six replications of Navua sedge, Rhodes grass and humidicola grass at each replacement ratios. Data have been pooled across densities as trends were fairly similar. RY >1 implies that the plant species grew more in mixed culture than in monoculture.



**FIGURE 9** Relative yield (RY) of number of flowers produced by Navua sedge after 16 weeks of plant growth under grazing (black) and nongrazing (gray) conditions of co-occurring Rhodes grass or humidicola. Error bars display 95% confidence intervals for six replications of Navua sedge plants at each replacement ratio.

affected the growth responses and indices, the interactions of this factor (i.e., density) with competition (i.e.,  $C \times D$ ) or with grazing (i.e.,  $C \times G$ ) were largely nonsignificant. These imply consistency of results irrespective of density used, and hence one can be confident of the results obtained (especially the outcome of competitive interactions between the invasive Navua sedge and tested pasture species).

Weeds emerging after crops can be less destructive in terms of reduced yield loss, and results can be misrepresented (Swanton et al., 2015). Hence, our preliminary germination tests were necessary to ensure even emergence time across all focal species and to estimate how much seeds were needed to generate sufficient seedlings of each species. Thus, the time of seedling emergence as well as the knowledge of growth and flowering phenology of Navua sedge that were observed in this study are vital information that should be incorporated into the weed's management strategies.

Simoes and Baruch (1991) described that grazing has a stimulating effect on the growth of plants in terms of high photosynthetic rate and nutrient availability. Grasses after grazing could potentially be more competitive against nongrazed grasses, although if the grazing is undertaken too frequently (as in this present study—being twice during the experiment), it is also possible that the opposite effect could occur (Yuan et al., 2020). If grazing can make pasture grasses less vigorous, then they may not be able to act as a competitor against weeds such as Navua sedge. Previous studies have shown that several grasses were negatively affected by simulated grazing for survival, growth and reproduction (Hagenah et al., 2008; Mabry & Wayne, 1997). This trend was exhibited by our focal grasses in terms of reduced tiller number, biomass gained and crown diameter, with *humidicola* being the more negatively affected species (Figure 3). Compensation against grazing is dependent on extrinsic factors (e.g., soil nutritional resources, space, competition) and intrinsic factors including physiological and developmental processes (nutrient uptake, photosynthetic rate and food storage of the plant itself) (Rosenthal & Kotanen, 1994; Wang et al., 2019; Yuan et al., 2020). Our study found a comparatively lower impact of grazing on Rhodes grass, irrespective of density and competition with Navua sedge. This implies that the physiology of Rhodes grass is capable of coping more with the grazing regimes imposed compared to *humidicola* and is thus worth exploring in future studies.

Tiller production, biomass accumulation and partitioning patterns, RGR and intensity of flowering are major and direct components of plant life history traits (Harper, 1977; Osunkoya et al., 2010), and hence might give some clue as to the mechanism of plant growth when faced with competition from neighbors. Among the three focal species, Navua sedge produced highest number of tillers under grazing or nongrazing conditions and at different densities (Figure 3), thus underscoring the role of this trait (i.e., tiller production) in Navua sedge for space pre-emption, vegetative growth, spread and hence invasiveness (Baker & Hunt, 1961; Yuan et al., 2020). The biomass of Navua sedge significantly increased when grasses were grazed possibly because of enhanced light availability to the weed (Chirara et al., 1998; Hao & He, 2019). Rhodes grass produced maximum biomass in both high and low densities under both grazed and nongrazed conditions, whereas the least biomass and tiller production were observed for *humidicola* in similar regimes (Figures 3 and 4). Navua sedge produced less biomass as the neighboring grass composition increased due to an increasing effect of density-dependent competition experienced by the Navua sedge, although mixed culture with *humidicola* had comparatively less competitive effects on

Navua sedge (Figure 4). Interestingly, feather fingergrass (*Chloris virgata*) which is in the same genus and hence a very similar species to Rhodes grass (*Ch. gayana*) is regarded as a weed requiring management attentions in Australia (Boutsalis et al., 2017; Chauhan & Manalil, 2022). An additional or alternative explanation for the growth trend observed is that the competition effect of the grasses (especially that invoked by Rhodes grass) on the weedy sedge can also be caused by excessive plant root metabolites and concentrations (such as methylated carboxylic acids, glucosinolate, monoterpene) from grasses under high competition (Eilers & Heger, 2019). These metabolites including allelochemicals can have negative impacts on the morphology and physiology of co-occurring species (Bajwa et al., 2016; Eilers & Heger, 2019). Nonetheless, irrespective of proximate cause of competitive dominance or suppression, there is a need to subject the test species to field trials to validate the impact of Rhodes grass (which naturally exhibits an erect growth form in its posture) and *humidicola* (which naturally exhibits a prostrate growth habit) on the growth dynamics and fitness components of Navua sedge for the weed's long-term management.

Though shoot/root biomass ratio of varied between the tested species, within species the various treatments imposed (density, competition or grazing) had minimal to no effect on shoot/root ratio (Tables 1 and Table S1). Reported effect of environmental factors on biomass allometry are not consistent: increase, decrease and no change have all been documents (Goldberg & Fleetwood, 1987; Pattison et al., 1998; Rehling et al., 2021). It is also not inconceivable that plant traits not measured in this study, such as components of root or shoot masses (e.g., root hair density, leaf rather total above ground biomass or leaf investments per unit area [specific leaf area]) (Osunkoya et al., 2010) may be the traits that are more plastic and hence will change with treatment applications. Equally, the fact that the three tested species are of the same life form—all being monocotyledons (two grasses and a sedge) and hence of similar functional group—may predispose them to similar biomass partition patterns in response to abiotic factors imposed (Boot & Mensink, 1990; Rehling et al., 2021). In summary, the lack of significant shift in shoot/root ratio with environmental factors echoes the assertions by Rehling et al. (2021) that growth condition, species characteristics, including life forms and their interactions influence patterns of biomass allocation and plant morphology.

This study was completed without any chemical input, which means tolerance of Rhodes grass (the better competitor against Navua sedge) can be further explored using fertilizers. Increasing competitive capacity following fertilizer addition has been observed in other grass

competition studies (Chirara et al., 1998; Vadigi & Ward, 2014), including conspecific of Rhodes grass (Boschma et al., 2017; Boutsalis et al., 2017; Manalil et al., 2020). Also, if grasses are clipped/grazed in the dry season, the plant growth dynamics would be different as suggested by a competitive study on grass-shrub competition (Chirara et al., 1998). In a previous study by Moilwa (2018), though of a shorter duration of 8 weeks, Rhodes grass (compared to humidicola) was significantly more competitive against Navua sedge under water-stressed regimes - indicating the growth of Navua sedge may be adversely affected even further when co-occurring Rhodes grasses are grazed under moisture stress (e.g., dry spell) conditions.

#### 4.1 | Management implication

This study has documented that under the tested regimes of simulated herbivory using low and high densities of increasing proportion of heterospecific plants, Rhodes grass can withstand and even outcompete Navua sedge, while humidicola is not able to achieve this fit as well. Other studies (Ellett, 2011; Moilwa, 2018) and anecdotal evidence (Barry McPaul—Cape Tribulation, Queensland, Australia) have also supported this finding. Moilwa (2018) in a similar replacement ratio competition experiments, but of water-stressed in treatments between Navua sedge and the two focal pasture species, also found Rhodes grass to have the greater competitive ability. Other co-occurring grasses in pasture fields that are not tested in this work like Signal grass (*U. decumbens*) and Setaria (*S. sphacelata*) have been shown to be less competitive against Navua sedge, especially under increasing density of the weed (Ellett, 2011; Shane Campbell and Wayne Vogler, unpublished data), and hence the use of Rhodes grass as a winner (choice) species in managing landscape infested with Navua sedge cannot be disputed. The findings also echoed what is known in the field: in cropping situation, Rhodes grass and/or its conspecifics are often regarded as aggressive weeds (Boschma et al., 2017; Boutsalis et al., 2017; Manalil et al., 2020), while in grazing/pasture condition, Rhodes grass is a desirable pasture that responds very well to fertilizer application (a factor not explored in the present study), especially at high plant density (Brima & Abusuwar, 2020; Ehrlich et al., 2003; Ruolo et al., 2022). These field observations indeed confirm Rhodes grass high competitive ability and its desirability by pastoralists. The mechanism of Rhodes grass higher competitive ability is probably linked to its higher compensatory activity of biomass accumulation following grazing and/or changes in allocation to biomass parts with increasing density in the presence of

heterospecific plants like Navua sedge. No doubt, such a shift in biomass allocation strategy (see Table S1) which neither Navua sedge nor humidicola were able to achieve—allows Rhodes grass a greater access to limiting resource like nutrient, water or even space.

As in many studies (Baker & Hunt, 1961; Jones et al., 1969; Rosenthal & Kotanen, 1994), grazing of tested pasture species encouraged growth and reproduction in co-occurring species (i.e., Navua sedge). The findings from Moilwa (2018) suggested that of three co-occurring species tested, Navua sedge was the most adversely affected by water stress. Thus, it is possible to design an intensive grazing period for pastures invaded by the weed to align with the relatively dry season of May–October in North Queensland as the growth fitness of the sedge will be relatively reduced during this phase. In summary, grazing appears to counteract the competitive effect on Navua sedge, and hence grazing management should be prioritized once the pasture replacement with Rhodes grass is initiated. Furthermore, the choice of a competitive pasture plants can be complemented with biological control agents feeding on the sedge weed to enhance further the pasture species competitive ability and offer a better integrated weed management option (Shabbir et al., 2020).

## 5 | CONCLUSIONS

Navua sedge is a severely problematic weed for pastures of the wet tropics of Queensland, with the propensity to expand into other regions in Australia. In a controlled environment, we have shown that grazing of co-occurring pasture grasses can simulate growth and reproduction of Navua sedge, while high density of conspecific and heterospecific plants has the opposite effect. Of the two tested pasture species against Navua sedge, Rhodes grass could compete and hence suppress the weed effectively, irrespective of the grazing regimes. Nonetheless, using competitive pasture species, the field validation and application of these tested factors, along with other abiotic factors not investigated in this work (e.g., moisture and nutrient availabilities, including pH) need to be taken into careful consideration in the adaptive management of the weed.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

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