High phosphorus availability and low light intensity resist the invasiveness of alien plant Chromolaena odorata on tropical coral islands

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Abstract

The vegetation and ecosystems of the Paracel Islands are extremely fragile and very difficult to restore after destruction. *Chromolaena odorata* is one of the most common invasive plants as guano phosphorus input constantly decreasing for islands, which has caused substantial harm to native vegetation on the Paracel Islands in recent years. In the current study, we investigated the growth and interspecific competition of *C. odorata* with the native species *Pisonia grandis* and *Scaevola taccada* as affected by light intensity and soil P content. The experiment, which was conducted in greenhouse, had two light intensities (full light or 10% light) and three levels of soil available phosphorus (P) content (53.89 $mg \cdot kg^{-1}$ low P, 253.89 $mg \cdot kg^{-1}$ medium P, and 1053.89 $mg \cdot kg^{-1}$ high P). The results showed that low light intensity significantly inhibited the growth of *P. grandis*, *S. taccada*, and *C. odorata*. However, compared with the low P treatment, the high P treatment significantly inhibited the growth of *C. odorata* and *P. grandis*, and significantly increased the growth of *S. taccada* under full-light conditions. The effect of soil P content on the interspecific competition between *C. odorata*, *P. grandis*, and *S. taccada* was affected by light intensity and plant species. Compared with the low and medium P treatments, the high P treatment significantly reduced the competitive advantage of *C. odorata* over *P. grandis*. The results demonstrate that shaded habitats with high soil P content could restrict invasion by *C. odorata.* This suggests that the invasion on tropical coral islands by *C. odorata* can be reduced by protecting the native vegetation (to increase shade) and seabirds (to increase soil P content).

Introduction

Biological invasion results in severe socioeconomic and environmental damage worldwide (Vilà et al. 2011; Rani et al. 2020). Despite being far from continental ecosystems and despite having clear oceanic boundaries, island ecosystems are still damaged by invasive plant species (Fenouillas et al. 2021). Research on preventing alien flora from invading tropical coral islands is quite limited, in part because studying plant communities on such islands is difficult (Li et al. 2018) and sampling from these areas might be the major limiting factors (Li et al. 2018).

Chromolaena odorata, a perennial plant that originated in Central and South America, has invaded many ecosystems worldwide (Yu 2010). In 1934, *C. odorata* was first found in mountainous areas in Yunnan and Hainan provinces, China; it then quickly spread and became one of the most destructive invasive plants in South China (Xu et al. 2020). The introduced genotype of *C. odorata*, which was characterized by a rapid growth rate and a strong reproduction ability (Yu et al. 2014), has inhibited the growth of native plants and caused serious damage to tropical island ecosystems (Cai et al. 2020). Little is known about how to prevent and control invasions of tropical islands by *C. odorata*.

Successful invasion by exotic plants depends on many factors including light intensity and soil nutrient levels. Chen (2020) found that increased soil phosphorus (P) content significantly reduced the competitive advantage of the invasive plants *Bidens pilosa* and *Eupatorium catarium*. By altering a plant's N/P ratio and its composition, concentration, and inorganic nitrogen (N) utilization efficiency, soil

nutrients affect the growth of invasive and native plants (Yu and He 2021; Geng and He 2021). Differences between invasive and native plants in response to low light intensity is another important factor affecting the successful establishment and expansion of invasive plants (Feng et al. 2007; Martin et al. 2009). Shi et al. (2020) found that strong photosynthetic resistance to irradiance damage may facilitate the invasion of the understory of the planted forest by *C. odorata*. Paudel and Battaglia (2021) also reported that some invasive plants were more tolerant of shade than native plants in the coastal region of the southeastern USA. Although the relationship between invasiveness and the plasticity of a specific trait in response to irradiance has a complex dependence on the level of irradiance (Zheng et al. 2012), low light intensity reduces the invasiveness of *Sonneratia apetala* in native communities (Chen et al. 2013). Research is now needed on how to prevent or control invasions of tropical coral islands by *C. odorata*.

Tropical coral islands, such as the Paracel Islands in the South China Sea, are formed mostly by coral sands and guano and plant residues (Xu et al. 2011). The establishment of plant communities on the Paracel Islands is closely related to the activities of seabirds, who deposit large amounts of P and other nutrients on the island in their feces and thereby promote the development of phospho-calc soils (Gong 2013).

Pisonia grandis is a native and widespread tree on atolls and islands that are heavily influenced by guano additions (Hayward and Horton 2012). *Scaevola taccada* is a native and dominant shrub species in coastal strand plant communities (Goldstein et al. 1996). Both plants are native and common in the Paracel Islands. *P. grandis* grows in the centers of the islands where soil P content is highest, and *S. taccada* grows closer to the coastline where P content is relatively lower. Protecting these two native species is important to the ecology and socioeconomic of the Parcel Islands (Wang et al. 2019).

The number of seabirds in the Paracel Islands has decreased due to anthropogenic disturbance (Cao et al. 2007), and this decrease has greatly reduced the input of guano-derived organic matter to the islands (Wu 2017). In addition, the anthropogenic disturbance has severely altered the original ecosystems and thereby increased the possibility of invasion (Rodgers and Parker 2003). However, no study has yet assessed the effects of guano reduction on biological invasions.

In this study, we conducted a greenhouse experiment with different light intensities and soil available phosphorus content (P), aiming to explore the effects of light intensity and soil P content on the growth and interspecific competition between the invasive species *C. odorata* and the native species *P. grandis* and *S. taccada*.

Methods

2.1 Seeds, soil, and pots

The experiment was conducted in a greenhouse at the South China Botanical Garden, the Chinese Academy of Sciences, Guangzhou, China (23°10' N, 113°21' E).

The seeds of the native species *P. grandis* and *S. taccada* and of the invasive species *C. odorata* were collected from Yongxing Island (16°49' N, 112°20' E) in the Paracel Islands in December 2019.

In order to reduce soil heterogeneity and simulate the soil conditions of the Paracel Islands, we collected soil of 0–20 cm depth from the native communities of *P. grandis* and *S. taccada* on the Paracel Islands. The soils were mixed evenly at a mass ratio of 1:1 and then mixed with coral sand at a mass ratio of soil to the sand of 1:5.

The contents of total P, available P, and total nitrogen (N) in the final soil were 12.08 $g \cdot kg^{-1}$, 53.89 $mg \cdot kg^{-1}$, and 4.26 $g \cdot kg^{-1}$, respectively. The soil was placed in pots (18 cm bottom inner diameter, 32 cm top inner diameter, and 21 cm height). Because the seedlings differed in germination and growth rates, we sowed the seeds of *P. grandis* and *S. taccada* in January 2020, and the seeds of *C. odorata* in June 2020. The seeds were sown in germination trays in a glasshouse.

2.2 Treatments

According to the light intensity and available P in the forest and open land of the original community of the the Parasel Islands, we conducted the experiment with two light intensities (full light and 10% light) and three levels of available P: low P (53.89 $mg \cdot kg^{-1}$), medium P (253.89 $mg \cdot kg^{-1}$), and high P (1053.89 $mg \cdot kg^{-1}$). A sunshade net that blocked 90% of the light was used to obtain 10% light. $NaH_2PO_4 \cdot 2H_2O$ (Analytical Pure, Guangzhou Chemical Reagent Factory) was used to obtain the three levels of available P.

In June 2020, we selected healthy seedlings of similar size and transplanted the seedlings into pots in five polyculture patterns: two *C. odorata* seedlings per pot (CC); two *P. grandis* seedlings per pot (PP); two *S. taccada* seedlings per pot (SS); one *C. odorata* seedling and one *P. grandis* seedling per pot (CP / PC); and *C. odorata* seedling and one *S. taccada* seedling per pot (CS / SC).

After 2 weeks of acclimatization in the greenhouse, the seedlings were divided into two groups for full light and 10% light treatments. The pots were placed on a flat well-drained soil with 20 cm between adjacent pots. Half the area occupied by the pots was covered with the sunshade net (at 200 cm above the soil surface). An LI-6800 portable photosynthesis system (Li-Cor, Lincoln, NE, USA) was used for 3 consecutive days to define the full light treatment and the low light treatment at 9 am, 12 noon, and 3 pm. For the full and low light treatments, the measured light intensities were 232.45 ± 6.39 $umol \cdot m^{-2}s^{-1}$ and 21.8 ± 0.78 $umol \cdot m^{-2}s^{-1}$ at 9 am, 1012.46 ± 24.95 $umol \cdot m^{-2}s^{-1}$ and 96 ± 7.30 $umol \cdot m^{-2}s^{-1}$ at 12 noon, and 727.33 ± 11.79 $umol \cdot m^{-2}s^{-1}$ and 73.73 ± 3.49 $umol \cdot m^{-2}s^{-1}$ at 3 pm.

The pots were fertilized with 500 mL of P-free Hoagland solution every month; each liter of solution contained 945 mg $Ca(NO_3)_2 \cdot 4H_2O$, 607 mg KNO_3, 20 mg NH_4NO_3, 493 mg $MgSO_4 \cdot 7H_2O$, 40 mg $[CH_2N(CH_2COONa)CH_2COO]_2Fe$, 2.86 mg H_3BO_3, 2.13 mg $MnSO_4 \cdot 7H_2O$, 0.22 mg $ZeSO_4 \cdot 7H_2O$, 0.08 mg $CuSO \cdot 5H_2O$, and 0.02 mg $H_8MoN_2O_4$.

Within the shaded or unshaded area, the pots were randomly moved every week to avoid a position effect. Each of the 30 treatments (2 light levels, 3 P levels, and 5 plant combinations) was represented by 5 pots, giving a total of 150 pots (Fig. 1).

2.3 Growth measurements

After 3 months, we used a tapeline to measure the height of each plant and collected all the leaves of each plant. We then measured the leaf area of each plant leaf through a portable leaf area meter (LI-3000A, Li-Cor, Lincoln, NE, USA).

The roots in each pot were carefully removed with the aid of running water and were then washed with water. The roots, stems, and leaves were then separately dried at 105 ℃ for 1 h followed by 65 ℃ until they reached a constant dry weight.

At the beginning of the experiment (T_0), the initial total biomass (W_1) of the seedlings and their height were determined. After 90 days (T_1), the total biomass (W_2) of each plant was measured. The following formula was used to calculate the relative growth rate (RGR) (Yamashita 2002):

$$RGR = (lnW_2 - lnW_1) \,/\, (T_1 - T_0)$$

2.4 Photosynthesis measurement

Before plants were harvested as described in the previous section, an LI-6800 portable photosynthesis system equipped with a red/blue LED light source was used to determine the maximum net photosynthetic rate of healthy mature leaves at the top of each plant on clear days. All measurements were repeated three times with a small CO_2 cylinder to ensure the stability of the airflow for each plant. The measurements were carried out with a photo flux density of 1500 μmol·m^{-2} s^{-1} and an ambient CO_2 concentration of 400 μmol·mol^{-1}.

2.5 Relative yield and aggressivity coefficient

The mean total biomasses of the invasive species and the native species were calculated for each treatment, and relative yield (RY) and the aggressivity coefficient (AG) were used to measure the competitiveness of the species. RY per plant was calculated for each species in each replicate using the following equation (Keddy 1988):

$$RY_c = Y_{cn} \,/\, (1/2Y_c)$$

$$RY_n = Y_{nc} \,/\, (1/2Y_n)$$

where RY_c is the relative yield of *C. odorata*; RY_n is the relative yield of native species; Y_{cn} is the biomass of a single *C. odorata* growing with a native species; Y_c is the biomass of two plants of *C. odorata* in monoculture; Y_{nc} is the biomass of a single plant of a native species growing with *C. odorata*, and Y_n is the biomass of two plants of the native species growing in monoculture.

RY values < 1 indicate that interspecies competition was greater than the intraspecies competition. RY values equal to 1 indicate that interspecies competition was equal to the intraspecies competition. RY values > 1 indicate that intraspecies competition was greater than the interspecies competition.

The aggressivity coefficient (AG) represented the competitive strength of *C. odorata* vs. native plants and was calculated by the following equation (Mcgilchrist and Trenbath 1971):

$$AG = 1/2\left(RY_{ab} - RY_{ba}\right)$$

AG values > 0 indicate that *C. odorata* was more competitive than the native plants. AG values equal to 0 indicate equal competitiveness between *C. odorata* and the native plants. AG values < 0 indicate that the native plants were more competitive than *C. odorata*.

2.6 Statistical analysis

Three-way analyses of variance (ANOVA) were used to compare the effects of soil P content, light intensity, and their interaction on growth indicators and the maximum net photosynthesis rate. The effects of soil P content, light intensity, and their interaction on RY and AG were tested with two-way ANOVAs. Independent samples *t*-tests were used to compare the differences between RY and 1, and between AG and 0. LSD tests were used for *post hoc* determination at p 0.05 of statistically significant differences between means for all variables of interest. All statistical analyses were conducted with Origin 2021.

Results

3.1 Effects of P level, light intensity, and competition on plant height

Under full light and with the increase in P content, the height of PP and PC decreased, but the other plants changed not obvious. The plant height of PP was significantly higher with low and medium P than with high P (p 0.05) (Fig. 2d). With 10% light intensity, the height of *C. odorata* plants increased with the increase of P in all polyculture patterns (CC, CP, and CS). The height of CS plants was significantly higher with high P than with low or medium P (p 0.05) (Figs. 2a, 2c). However, the growth of PP plants was inhibited but that of PC plants tended to be increased with the increase in P level (Fig. 2d), but no significance was detected (Fig. 2b).

Light intensity significantly affected the heights of *C. odorata*, *S. sericea*, and *P. grandis* plants (p 0.05). The height of *P. grandis* plants was also significantly affected by competition (p 0.05). The height of CS was significantly affected by P level, and the interaction between light intensity and competition affected *C. odorata* growth in different polyculture patterns. (p 0.05) (Table 1).

3.2 Effects of phosphorus level, light intensity, and competition on leaf area

With full light intensity, C. odorata leaf area was largest with medium P regardless of the polyculture pattern; C. odorata leaf area in CC and CP pots was smallest with high P; and C. odorata leaf area in CS

pots was smallest with low P (Figs. 3a, 3c). As the P content of the soil increased, the leaf area increased for *S. taccada* and decreased for *P. grandis* in spite of monoculture or interplanting. The leaf area of *P. grandis* was significantly smaller with high P than with low or medium P ($p < 0.05$) (Figs. 3b, 3d). However, the leaf area of all plants was reduced by the low light intensity. Interestingly, the leaf area of *C. odorata* tended to increase with the increase in P level and was significantly larger with high P than with low P ($p < 0.05$) (Figs. 3a, 3c). The leaf area of PC was significantly greater with high P than with low P ($p < 0.05$) (Fig. 3d). Under the low light intensity, the leaf area of *S. taccada* did not significantly differ among P levels (Fig. 3b).

Leaf surface area was significantly affected by light intensity and also by competition. The P content of the soil significantly affected the leaf area of *C. odorata* in CC, CP, and CS pots (Table 1). The leaf area of CC, CP, and CS were also significantly influenced by the interaction between P level and light intensity ($p < 0.05$). The interaction between light intensity and competition significantly affected the leaf area of CS and SC ($p < 0.05$) (Table 1).

3.3 Effects of phosphorus level, light intensity, and competition on photosynthesis

To examine the effects of P level, light intensity, competition, and their interactions on photosynthesis, we measured the maximum net photosynthetic rate (MNPR) of mature leaves of the experimental plants. The MNPR of CS was highest among all plants of *C. odorata* with full light and low P. Interestingly, the MNPR of CS decreased as the P content increased, and was significantly lower with high P than with low or medium P ($p < 0.05$) (Figs. 4a, 4c).

In comparison, the MNPR of SS with low light were significantly lower than those of *S. taccada* with full light regardless of P level, but the MNPR of SC with low P was significantly higher than that of SC with medium or high P under full light intensity ($p < 0.05$) (Fig. 4b). The MNPR of PP was the highest with low P and with full light intensity and decreased with the increase in P level. The MNPR of PC was significantly higher with high P than with low or medium P ($p < 0.05$) (Fig. 4d).

In general, the MNPR was lower for *C. odorata* than for *S. taccada*, but was greater for *C. odorata* than for *P. grandis* under the same conditions. Light intensity, P level, and their interactions significantly affected the MNPR of CS and tended to affect the maximum photosynthetic rate of CP although the effect was not statistically significant in the latter case. The competition had slight effects on the maximum photosynthetic rate of *C. odorata* but had significant effects on *S. taccada* and *P. grandis* (Table 1).

3.4 Effects of phosphorus level, light intensity, and competition on relative growth rates

Among the treatments, the light intensity had the largest effect on the relative growth rates (RGR). The RGR of *C. odorata* and *S. taccada* were significantly greater with full light intensity than with low light intensity, ($p < 0.05$), but were unaffected by P level or polyculture pattern (Figs. 5a, 5b, 5c). The RGR of PP and PC with low or medium P level under full light was also significantly greater than those

under shading light ($p < 0.05$). Interestingly, the RGR of CP was significantly increased by high P in the full light intensity treatment ($p < 0.05$) (Fig. 5d).

However, the RGR was significantly lower for SC than for SS with high P ($p < 0.05$) (Fig. 5b). PP grew faster than PC, and the RGR of both was significantly greater under full light than those under low light with low or medium P ($p < 0.05$). However, the RGR of PC was significantly lower with low and medium P than with high P and with low light intensity ($p < 0.05$) (Fig. 5d).

Comparing the same treatments, the RGR of *C. odorata* was significantly higher than that of *P. grandis* and *S. taccada*, indicating that *C. odorata* had better adaptability to the environment. Light and the interaction of P and light significantly affected the RGR of *C. odorata*, while P had a significant effect on CS. The RGR of *S. taccada* was significantly affected by light and the interaction of light and competition, and *P. grandis* growth was significantly affected by light, competition, and P and their interactions ($p < 0.05$) (Table 1).

3.5 Effects of phosphorus level, light intensity, and competition on relative yield and aggressivity coefficient

The relative competitiveness of *P. grandis*, *S. taccada*, and *C. odorata* was compared using relative yield (RY) and the aggressivity coefficient (AG). Light intensity significantly affected the RY of *C. odorata* and *S. taccada*, and P level only significantly affected the RY of *C. odorata* when competing with *S. taccada* ($p < 0.05$). The AG of *C. odorata* was significantly affected by light intensity and the interaction between light intensity and P level ($p < 0.05$) (Table 2). The RY of *P. grandis* was significantly affected by light intensity, P level, and their interaction, while the RY of *C. odorata* was significantly affected only by light intensity ($p < 0.05$). The AG of *C. odorata* was significantly affected by light intensity, P level, and competition with *P. grandis* ($p < 0.05$) (Table 3).

With full light, the RY of *C. odorata* increased as the P level increased, and was significantly greater with medium and high P than with low P ($p < 0.05$). However, the RY of *S. taccada* decreased with the increase in P level and was significantly greater with low P than with high P ($p < 0.05$). The AG of *C. odorata* increased significantly as the P level increased, and was significantly greater with high P than with medium or low P ($p < 0.05$). Interestingly, under low light, the AG values < 0 indicated that *S. taccada* was more competitive than *C. odorata* (Table 4).

The RY of *P. grandis* was smallest with low P and full light and was significantly greater with high P than with medium or low P under low light ($p < 0.05$). However, the RY of *C. odorata* was the smallest with a high P. The AG of *C. odorata* was significantly higher with high P than with low or medium P under full light ($p < 0.05$). With the increase in P level, the AG of *C. odorata* declined and that indicated the competitiveness was reducing with full or low light (Table 5).

Overall, competition between *C. odorata* and *P. grandis* or *S. taccada* was affected by both light and P level. Especially with low light, increases in the P content of the soil reduced the ability of *C. odorata* to

compete with the native species.

Discussion

4.1 Low light intensity inhibits the invasion of C. odorata on tropical coral islands

Light is the energy source of photosynthesis and a vital factor affecting plant growth. Invasive plants that are heliophiles are limited by light intensity, and the ability to capture, utilize, and tolerate light is important for their successful invasion of native communities (Feng et al. 2007; Zheng et al. 2009). Previous studies found that the tolerance of invasive plants to low light accelerated their invasion (Zavala et al. 2007; Martin et al. 2009). In our study, low light intensity significantly reduced the height, leaf area, biomass, and relative growth rate of *C. odorata*., *P. grandis* and *S. taccada* grow in communities dominated by tall plants on the tropical islands.

Plant growth and biomass accumulation largely depend on the efficiency of light capture and utilization (Okada and Katoh 1998; Meekins and McCarthy 2000). Moreover, plant height and leaf area are considered the main traits that affect plant competition for light resources (Gorchov and Trisel 2003). Both *C. odorata* and *S. taccada* can acquire more light resources under full light than under low light such that their growth was greater under full light. In contrast, the growth of *P. grandis* was not significantly greater with full light than with low light. High light intensities inhibit the growth of *P. grandis* by inducing the production of reactive oxygen species (Niyogi 1999). Consistent with the view that plant growth is often more affected by light intensity than by the levels of soil nutrients (Wei et al. 2017), we found that the growth of *C. odorata, P. grandis*, and *S. taccada* did not significantly vary among P levels when the light intensity was low. Invasive plants with a low tolerance to shade find it difficult to invade communities with high canopy closure (Sharma et al. 2022).

4.2 High soil phosphorus level reduces the competition of C. odorata to native plants

Because nucleic acid synthesis and energy conversion in plants require P, P levels in soil may greatly affect plant communities (Mo et al. 2022; Zhang et al. 2022). Our results indicate a high P level in soil significantly reduces the growth of *C. odorata*, which is consistent with the results obtained for other invasive plants (Cai et al. 2020). In contrast, other studies have found that P addition improves the growth of *C. odorata* (Suding et al. 2004; Quan et al. 2014). This inconsistency may result from differences between the initial P content of the soil. The initial available P content in the soil of the latter two studies may have been sufficiently low so that the addition of P did not result in growth inhibition. The P content, however, is unusually high in soil from the Paracel Islands (Zhao 2006). The high P habitat is suitable only for a few native, dominant plants. Previous studies also found that increases in the availability of soil P weakened the ability of invasive plants to compete with native plants (Brewer and Cralle 2003; Chen et al. 2020).

C. odorata has a substantial competitive advantage over *P. grandis*, but this advantage decreases as soil P increases. In contrast, P addition to soil increased the competitive advantage of *C. odorata* over *S. taccada* under full light. This difference perhaps results from the secretion of allelochemicals by invasive plants, which causes the photosynthetic rate of native plants to decrease (Yu et al. 2003; He et al. 2009). Plant photosynthesis is the basis for plant survival, and a higher photosynthetic rate is conducive to the efficient use of resources for plant growth or competition (Baruch and Goldstein 1999). *C. odorata* might have a higher P utilization efficiency than native plants and allocate more P to metabolic P for photosynthesis (Sun et al. 2022). Wan (2018) also found that P addition reduced the competitive advantage of an invasive weed under different nutritional conditions. In other studies, the combined effects P, N, and other soil nutrients affected the growth and distribution of plants (Zhang 2017; Ye 2022), and may also inhibit invasion by *C. odorata.*

4.3 Controlling C. odorata by adjusting the soil phosphorus content and light intensity of understory

Light intensity and soil P content significantly affect plant growth and survival (Holste et al. 2011). The competitive advantage of *C. odorata* over native plants is weak when the native plants have formed a high canopy over the soil with a high P content. It follows that the invasion of *C. odorata* on tropical coral islands may be restricted by healthy native plant communities and healthy seabird populations. Once the native communities, such as those with *P. grandis* or *S. taccada*, are damaged, *C. odorata* may quickly invade and replace the native plants. Therefore, protection of plant communities and ecosystems is crucial for preventing invasion by *C. odorata.* Vegetation also provides a habitat for seabirds, and the guano of seabirds is an important source of soil P on the tropical islands. For partially degraded plant communities on tropical coral islands, we suggest that fast-growing native plants be planted as soon as possible to increase the canopy closure and thereby minimize the probability of invasion by *C. odorata.* If the P content of the soil is low, it can be increased by the addition of guano obtained from guano-rich areas.

In summary, the results of our study suggest that invasion by *C. odorata* may be controlled by increasing the health and vigor of native plant communities and seabird communities.

Conclusion

In this study, we conducted different phosphorus contents and light intensities to reveal the invasion ability of *C. odorata* to native plants on a tropical island. Comparing the photosynthesis of leaves and analyzing the effects of phosphorus content, light intensity, and competition on the plant height, leaf area, maximum net photosynthetic rate and relative growth rate of *C. odorata, P. grandis*, and *S. taccada.* The relative yield and relative competition coefficient were used to reflect the competitiveness of *C. odorata* to *P. grandis* and *S. taccada*. We found that in the habitat of low light and high soil phosphorus content, the invasive ability of *C. odorata* was significantly inhibited in different plant combinations. Therefore, building a suitable vegetation community, protecting the original vegetation, and maintaining

seabirds' continued input phosphorus effectively reduce the invasion of *C. odorata*. This study provided a scientific theory for the subsequent ecological restoration and protection of coral islands.

Declarations

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Author contributions

JSG, LHX, LZF, and LMC contributed to the study conception and design; LMC, HLP, CHY, ZWM, XZH, OYKT, and YWY collected the data; LMC, HLP, and LHX analyzed the data; HLP, LMC, and JSG wrote the manuscript. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Conflict of interest

The authors declare that they have no conflict of interest.

References

1. Baruch Z and Goldstein G (1999) Leaf Construction Cost, Nutrient Concentration, and Net CO Assimilation of Native and Invasive Species in Hawaii. Oecologia 121: 183-192
2. Brewer JS and Cralle SP (2003) Phosphorus addition reduces invasion of a longleaf pine savanna (Southeastern USA) by a non-indigenous grass (Imperata cylindrica). Plant ecology 167: 237-245
3. Cai H, Lu H, Tian Y, *et al.* (2020) Effects of invasive plants on the health of forest ecosystems on small tropical coral islands. Ecological Indicators 117: 106656
4. Cao L, Pan YL and Liu NF (2007) Waterbirds of the Xisha Archipelago, South China Sea. Waterbirds 30: 296-300
5. Chen L, Peng S, Li J, *et al.* (2013) Competitive Control of an Exotic Mangrove Species: Restoration of Native Mangrove Forests by Altering Light Availability. Restoration Ecology 21: 215-223
6. Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration [J]. Annual Review of Ecology Evolution and Systematics, 34: 183-211.
7. Feng Y, Wang J and Sang W (2007) Biomass allocation, morphology and photosynthesis of invasive and noninvasive exotic species grown at four irradiance levels. Acta Oecologica 31: 40-47
8. Fenouillas P, Ah Peng C, Amy E, *et al.* (2021) Quantifying invasion degree by alien plants species in Reunion Island. Austral Ecology 46: 1025-1037

9. Geng X and He W (2021) Success of native and invasive plant congeners depends on inorganic nitrogen compositions and levels. Journal of Plant Ecology 14: 202-212
10. Goldstein G, Drake DR, Alpha C, *et al.* (1996) Growth and photosynthetic responses of Scaevola sericea, a Hawaiian coastal shrub, to substrate salinity and salt spray. International journal of plant sciences 157: 171-179
11. Gong Z, Zhang G,Yang F (2013) Soils and the soil ecosystem in the South China Sea Islands. Ecology and Environmental Sciences 2: 183-188
12. Gorchov DL and Trisel DE (2003) Competitive Effects of the Invasive Shrub, Lonicera maackii (Rupr.) Herder (Caprifoliaceae), on the Growth and Survival of Native Tree Seedlings. Plant ecology 166: 13-24
13. Hayward JA and Horton TR (2012) Edaphic factors do not govern the ectomycorrhizal specificity of Pisonia grandis (Nyctaginaceae). Mycorrhiza 22: 647-652
14. He W, Feng Y, Ridenour WM, *et al.* (2009) Novel weapons and invasion: biogeographic differences in the competitive effects of Centaurea maculosa and its root exudate (±)-catechin. Oecologia 159: 803-815
15. Holste EK, Kobe RK and Vriesendorp CF (2011) Seedling growth responses to soil resources in the understory of a wet tropical forest. Ecology (Durham) 92: 1828-1838
16. Keddy C (1988) A comparative approach to predicting competition ability from plant traits. Nature 334: 242-243
17. Li S, Qian X, Zheng Z, *et al.* (2018) DNA barcoding the flowering plants from the tropical coral islands of Xisha (China). Ecology and Evolution 8: 10587-10593
18. Martin PH, Canham CD and Marks PL (2009) Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. Frontiers in Ecology and the Environment 7: 142-149
19. Mcgilchrist CA, Trenbath BR (1971). A revised analysis of plant competition experiments [J]. Biometrics, 27: 659-671
20. Meekins JF and McCarthy BC (2000) Responses of the Biennial Forest Herb Alliaria petiolata to Variation in Population Density, Nutrient Addition and Light Availability. The Journal of ecology 88: 447-463
21. Mo S, He S, Sang Y, *et al.* (2022) Integration of Microbial Transformation Mechanism of Polyphosphate Accumulation and Sulfur Cycle in Subtropical Marine Mangrove Ecosystems with Spartina alterniflora Invasion. Microbial Ecology 10.1007/s00248-022-01979-w
22. Niyogi KK (1999) PHOTOPROTECTION REVISITED: Genetic and Molecular Approaches. Annual review of plant physiology and plant molecular biology 50: 333-359
23. Okada KTUJ and S K (1998) Two long-term effects of light that control the stability of proteins related to photosynthesis during senescence of rice [Oryza sativa] leaves. Plant and cell physiology 39: 394-404

24. Paudel S, Battaglia L L (2021) Linking responses of native and invasive plants to hurricane disturbances: implications for coastal plant community structure. Plant Ecology, 222: 133-148
25. Rani S, Ahmed MK, Xiongzhi X, *et al.* (2020) Economic valuation and conservation, restoration & management strategies of Saint Martin's coral island, Bangladesh. Ocean & Coastal Management 183: 105024
26. Rodgers JC and Parker KC (2003) Distribution of alien plant species in relation to human disturbance on the Georgia Sea Islands. Diversity & distributions 9: 385-398
27. Sharma LN, Adhikari B, Watson MF, *et al.* (2022) Forest canopy resists plant invasions: a case study of Chromolaena odorata in Sal (Shorea robusta) forests of Nepal. Journal of Tropical Ecology 38: 49-57
28. Shi X, Liu G and Zheng Y (2020) Comparisons of irradiance utilization efficiency by invasive Chromolaena odorata and its three co-occurring species in one planted understory. Flora 271: 151680
29. Suding KN, LeJeune KD and Seastedt TR (2004) Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorus availability. Oecologia 141: 526-535
30. Sun F, Zeng LD, Cai ML, et al (2021) An invasive and native plant differ in their effects on the soil food-web and plant-soil phosphorus cycle. Geoderma 410: 115672
31. Wan LY, Qi SS, Zou CB, *et al.* (2018) Phosphorus addition reduces the competitive ability of the invasive weed Solidago canadensis under high nitrogen conditions. Flora, 240: 68-75
32. Vilà M, Espinar JL, Hejda M, *et al.* (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14: 702-708
33. Wang SH, Zhu YJ, Wang YF, et al. (2019) Effect of Vegetation Types on Soil Physicochemical Property in East Island and Yongxing Island of Xisha Islands. Journal of Tropical and Subtropical Botany 27: 383-390 (in Chinese)
34. Wei H, Yan W, Quan G, *et al.* (2017) Soil microbial carbon utilization, enzyme activities and nutrient availability responses to Bidens pilosa and a non-invasive congener under different irradiances. Scientific Reports 7
35. Wu LB, Liu X, Liqiang XU (2017) Change of organic 13C in ornithogenic sediments of the Xisha Archipelago, South China Sea and its implication for ecological development. Acta Geologica Sinica-English Edition 91: 1119
36. Xu L, Liu X, Sun L, *et al.* (2011) Geochemical evidence for the development of coral island ecosystem in the Xisha Archipelago of South China Sea from four ornithogenic sediment profiles. Chemical Geology 286(3-4): 135-145
37. Xu QY, Wang D, Quan GM, *et al.* (2020) Invasive Chromolaena odorata species specifically affects growth of its co-occurring weeds. Annals of the New York Academy of Sciences 1470: 57-66
38. Yamashita N, Koike N, Ishida A (2002) Leaf ontogenetic dependence of light acclimation in invasive and native subtropical trees of different successional status. Plant Cell and Environment: 1341-1356

39. Ye XQ, Ma RX, Lei ST, *et al.* (2022) Maintained nutrient accumulation in invasive Solidago canadensis in response to competition: Competition tolerance and nutrient accumulation. Flora, 295: 152136
40. Yu H and He W (2021) Congeneric invasive versus native plants utilize similar inorganic nitrogen forms but have disparate use efficiencies. Journal of Plant Ecology 14: 180-190
41. Yu JQ, Ye SF, Zhang MF, *et al.* (2003) Effects of root exudates and aqueous root extracts of cucumber (Cucumis sativus) and allelochemicals, on photosynthesis and antioxidant enzymes in cucumber. Biochemical Systematics and Ecology 31: 129-139
42. Yu X, He T, Zhao J, *et al.* (2014) Invasion genetics of Chromolaena odorata (Asteraceae): extremely low diversity across Asia. Biological Invasions 16: 2351-2366
43. Yu X, Feng Y, Li Q (2010) Review of research advances and prospects of invasive Chromolaena odorata. Chinese Journal of Plant Ecology 34: 591-600
44. Zavala MA, Angulo Ó, Bravo D, *et al.* (2007) An analytical model of stand dynamics as a function of tree growth, mortality and recruitment: The shade tolerance-stand structure hypothesis revisited. Journal of Theoretical Biology 244: 440-450
45. Zhang HJ, Chang RY, Guo X, *et al.* (2017) Shifts in growth and competitive dominance of the invasive plant Alternanthera philoxeroides under different nitrogen and phosphorus supply. Environmental and Experimental Botany 135: 118-125
46. Zhang Y, Leng Z, Wu Y, *et al.* (2022) Interaction between Nitrogen, Phosphorus, and Invasive Alien Plants. Sustainability 14: 746
47. Zhao SP (2006) Evolution of seabird eco-environment on Xisha islands of south China. Disertation, University of Science and Technology of China.
48. Zheng Y, Feng Y, Lei Y, *et al.* (2012) Comparisons of plastic responses to irradiance and physiological traits by invasive Eupatorium adenophorum and its native congeners. Journal of Plant Physiology 169: 884-891
49. Zheng Y, Feng Y, Liu W, *et al.* (2009) Growth, biomass allocation, morphology, and photosynthesis of invasive Eupatorium adenophorum and its native congeners grown at four irradiances. Plant Ecology 203: 263-271

Tables

Tables 1 is available in the Supplementary Files section.

Table 2
Results of two-way ANOVAs for the effects of phosphorus level and light intensity on the relative yield of *C. odorata* and *S. taccada* and the aggressivity coefficient of *C. odorata*

Factor	RYc		RYs		AG	
	F	p	*F*	p	*F*	p
P	**7.667**	**0.003**	0.048	0.953	3.104	0.064
I	**9.656**	**0.005**	**15.865**	**< 0.001**	**33.920**	**< 0.001**
P×I	1.694	0.205	1.249	0.305	**3.884**	**0.035**

Note: RY_c, the relative yield of *C. odorata*; RY_s, the relative yield of *S. taccada*; AG, the aggressivity coefficient of *C. odorata*; P, phosphorus level; I, light intensity. Boldface values are significant at $p < 0.05$.

Table 3
Results of two-way ANOVAs for the effects of phosphorus level and light intensity on relative yield of *C. odorata* and *P. grandis* and competition aggressivity of *C. odorata*

Factor	RYc		RYp		AG	
	F	p	*F*	p	*F*	p
P	2.811	0.080	**5.601**	**0.010**	3.322	0.054
I	**13.011**	**0.001**	**4.873**	**0.037**	**18.334**	**< 0.001**
P×I	0.843	0.442	**9.980**	**< 0.001**	**3.570**	**0.045**

Note: RY_c, the relative yield of *C. odorata*; RY_p, the relative yield of *P. grandis*; AG, the aggressivity coefficient of *C. odorata*; P, phosphorus level; I, light intensity. Boldface text indicates significant effects at $p < 0.05$.

Table 4
The relative yield and aggressivity coefficient between *C. odorata* and *S. taccada*

	light intensity	phosphorus level		
		P_1	P_2	P_3
RYc	F	0.873 ± 0.012B*	1.160 ± 0.025A*	1.215 ± 0.037A*
	L	0.813 ± 0.125A	1.010 ± 0.087A	0.907 ± 0.051A
RYs	F	0.856 ± 0.072A	0.814 ± 0.031AB*	0.687 ± 0.014B*
	L	1.110 ± 0.144A	1.083 ± 0.099A	1.251 ± 0.200A
AG	F	0.008 ± 0.037C	0.173 ± 0.006B*	0.264 ± 0.020A*
	L	-0.134 ± 0.048A	-0.037 ± 0.044A	-0.172 ± 0.108A

Note: RY, the relative yield of *C. odorata*; RY_s, the relative yield of *S. taccada*; AG, the competitive aggressivity of *C. odorata*; F, full light intensity; L, low light intensity; *t*-test was used to compare RY with 1 and AG with 0, * indicates significant differences ($p < 0.05$). Different uppercase letters indicate significant differences ($p < 0.05$) of RY_c, RY_s, and AG among phosphorus levels under the same light intensity.

Table 5
The relative yield and aggressivity coefficient between *C. odorata* and *P. grandis*

	light intensity	phosphorus level		
		P_1	P_2	P_3
RYc	F	1.216 ± 0.018AB*	1.313 ± 0.060A*	1.134 ± 0.031B*
	L	0.954 ± 0.051A	1.116 ± 0.088 A	1.035 ± 0.093A
RYp	F	0.432 ± 0.081B*	0.709 ± 0.035A*	0.493 ± 0.053B*
	L	0.544 ± 0.053B*	0.552 ± 0.042B*	0.848 ± 0.068A
AG	F	0.430 ± 0.028A*	0.302 ± 0.019B*	0.321 ± 0.023B*
	L	0.205 ± 0.045AB*	0.282 ± 0.058A*	0.093 ± 0.066B

Note: RY_c, the relative yield of *C. odorata*; RY_p, the relative yield of *P. grandis*; AG, AG, the aggressivity coefficient of *C. odorata*; F, full light intensity; L, low light intensity; *t*-test was used to compare RY with 1 and AG with 0, * indicates significant differences ($p < 0.05$). Different uppercase letters indicate

significant differences ($p < 0.05$) of RY_c, RY_p, and AG among different phosphorus levels under the same light intensity.

Figures

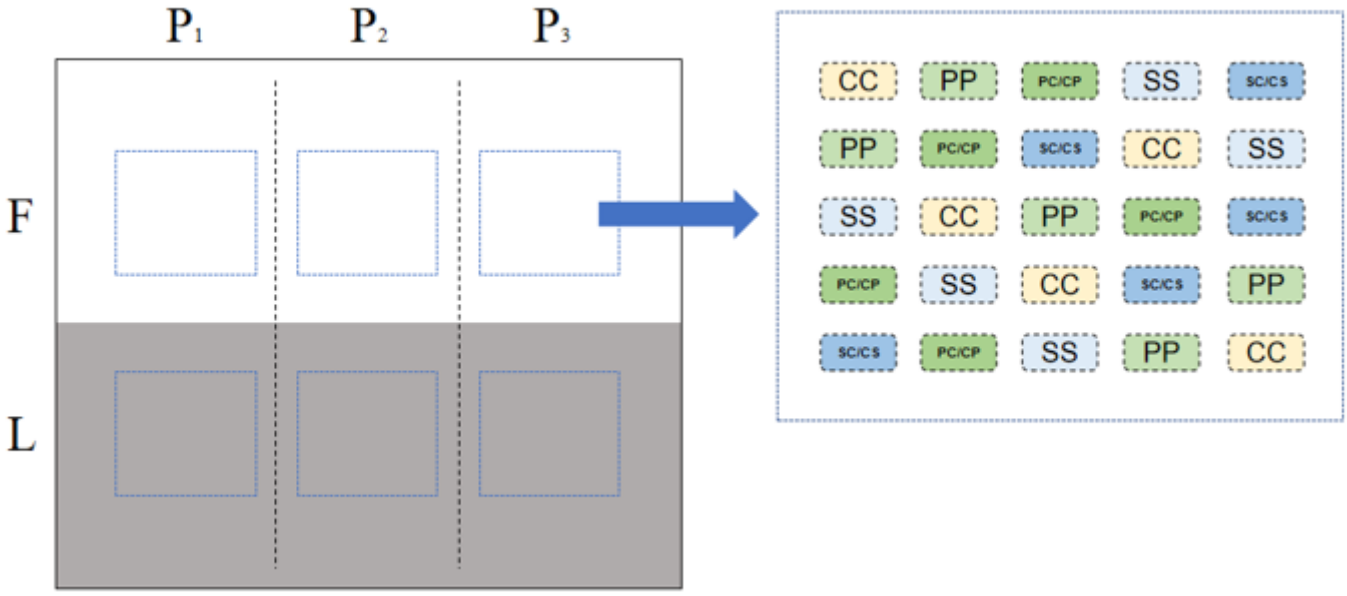

Figure 1

Schematic representation of the experimental design

Note: F, full light intensity; L, 10% light intensity; P_1, P_2, and P_3 refer to low, medium, and high phosphorus levels, respectively; CC, two *C. odorata* seedlings per pot; PP, two *P. grandis* seedlings per pot; SS, two *S. taccada* seedlings per pot; CP, one *C. odorata* seedling (interplanting with *P. grandis*); PC, one *P. grandis* seedling (interplanting with *C. odorata*); CS, one *C. odorata* seedling (interplanting with *S. taccada*); SC, one *S. taccada* seedling (interplanting with *C. odorata*).

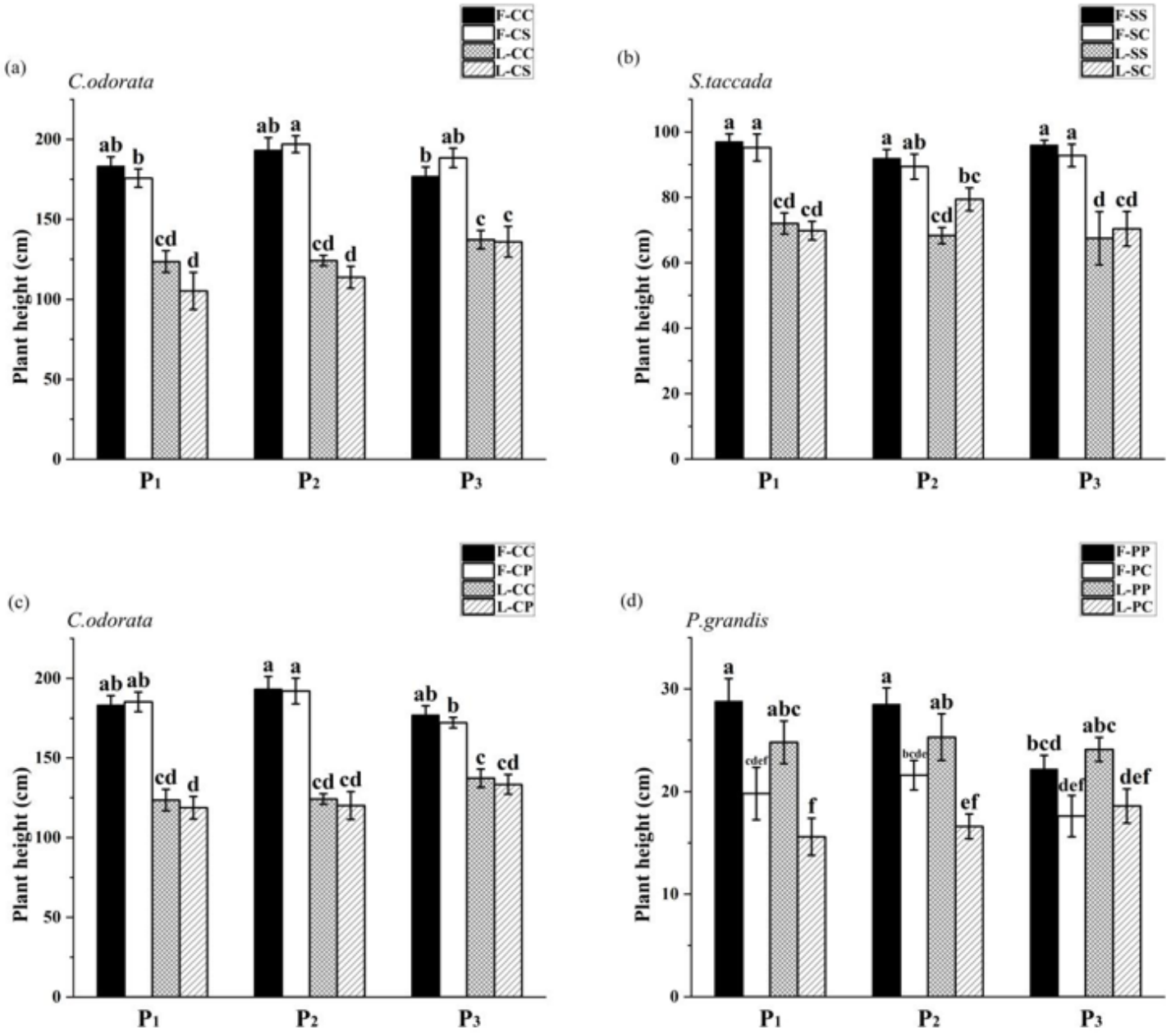

Figure 2

Plant height as affected by different light intensities and soil available phosphorus content

Note: F, full light intensity; L, low intensity; P_1, low phosphorus level; P_2, medium phosphorus level; P_3, high phosphorus level; CC, two *C. odorata* seedlings per pot; PP, two *P. grandis* seedlings per pot; SS, two *S. taccada* seedlings per pot; CP, one *C. odorata* seedling (interplanting with *P. grandis*); PC, one *P. grandis* seedling (interplanting with *C. odorata*); CS, one *C. odorata* seedling (interplanting with *S. taccada*); SC, one *S. taccada* seedling (interplanting with *C. odorata*). Values are means ± SE. Within each panel, means with different letters are significantly different ($p < 0.05$).

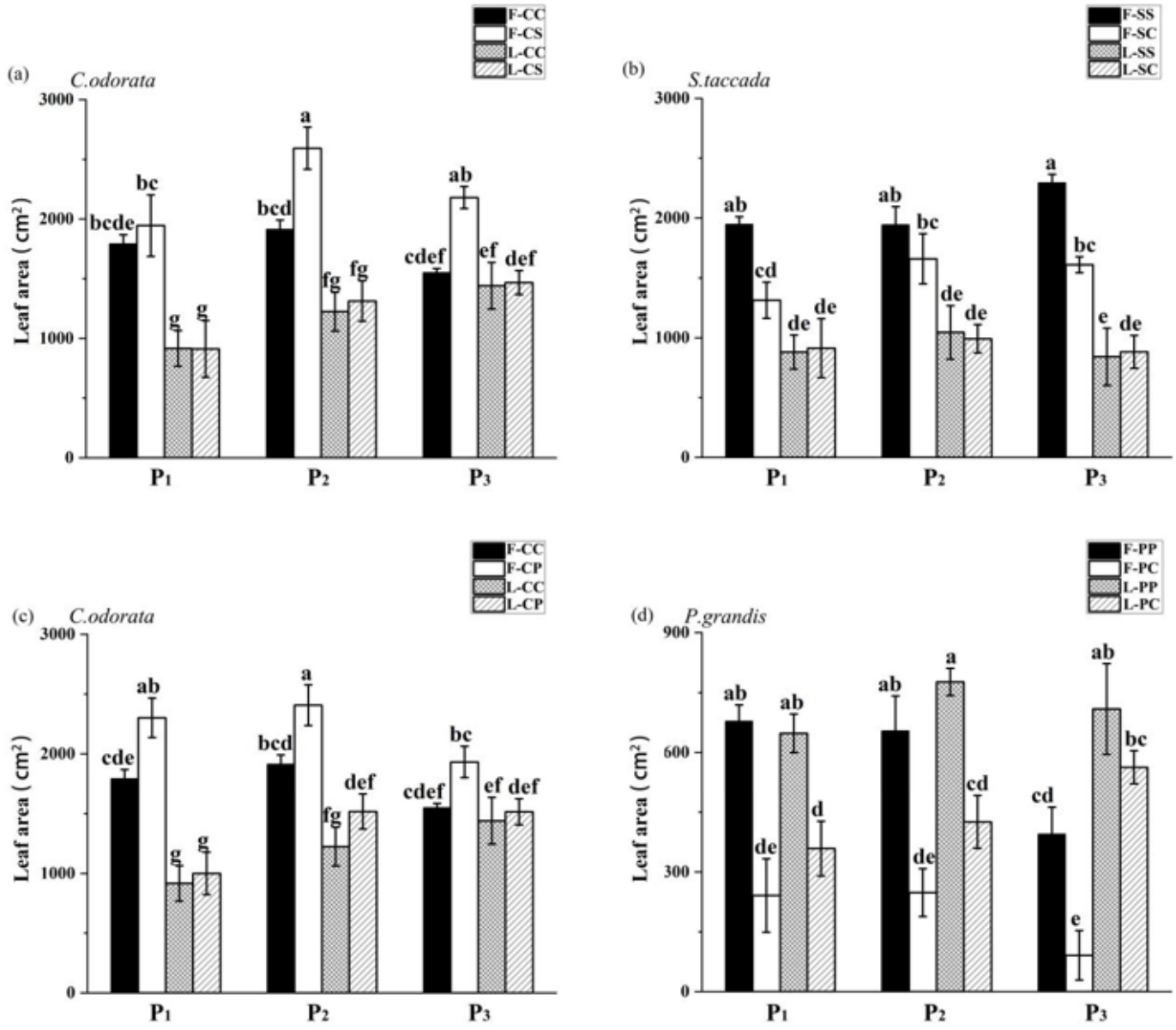

Figure 3

Leaf area as affected by different light intensities and soil available phosphorus content

Note: F, full light intensity; L, low intensity; P1, low phosphorus level; P2, medium phosphorus level; P3, high phosphorus level; CC, two *C. odorata*seedlings per pot; PP, two *P. grandis* seedlings per pot; SS, two S. taccada seedlings per pot; CP, one *C. odorata* seedling (interplanting with *P. grandis*); PC, one *P. grandis* seedling (interplanting with *C. odorata*); CS, one *C. odorata* seedling (interplanting with *S. taccada*); SC, one *S. taccada* seedling (interplanting with *C. odorata*). Values are means + SE. Within each panel, means with different letters are significantly different ($p < 0.05$).

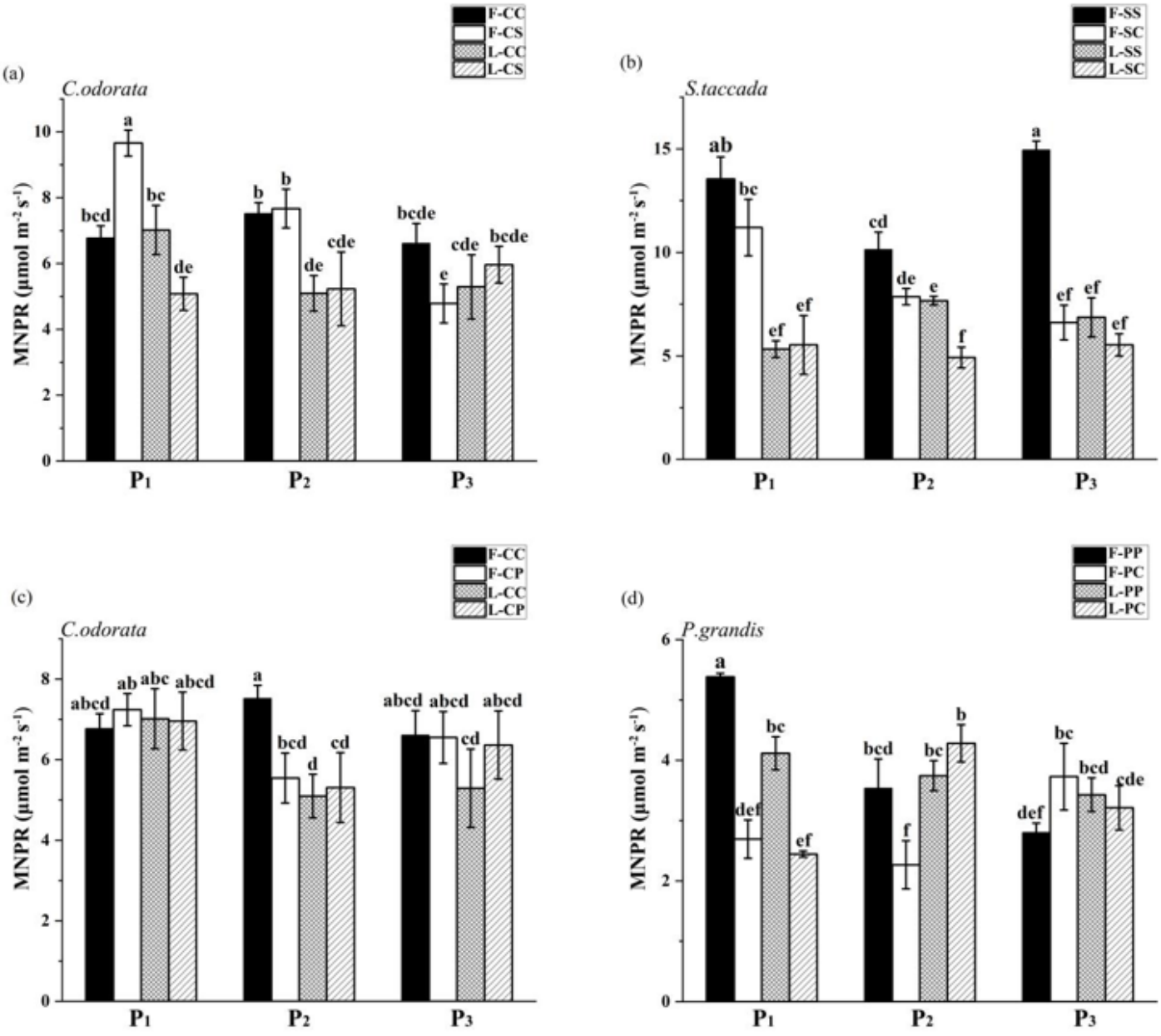

Figure 4

Maximum net photosynthetic rates (MNPR) as affected by different light intensities and soil available phosphorus content

Note: F, full light intensity; L, low intensity; P1, low phosphorus level; P2, medium phosphorus level; P3, high phosphorus level; CC, two *C. odorata* seedlings per pot; PP, two *P. grandis* seedlings per pot; SS, two *S. taccada* seedlings per pot; CP, one *C. odorata* seedling (interplanting with *P. grandis*); PC, one *P. grandis* seedling (interplanting with *C. odorata*); CS, one *C. odorata* seedling (interplanting with *S. taccada*); SC, one *S. taccada* seedling (interplanting with *C. odorata*). Values are means + SE. Within each panel, means with different letters are significantly different ($p < 0.05$).

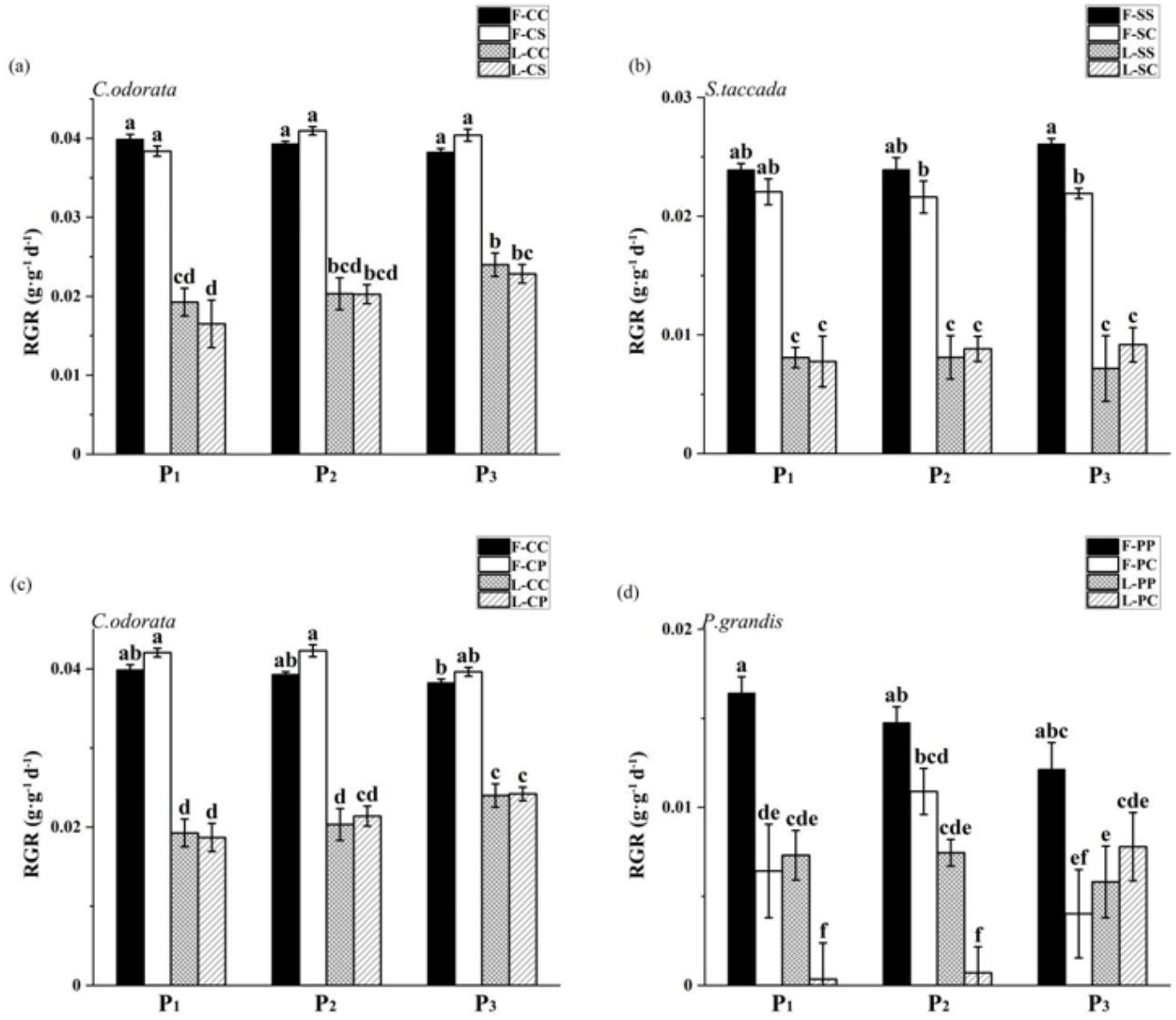

Figure 5

Relative growth rate (RGB) of the plants as affected by different light intensities and soil available phosphorus content

Note: F, full light intensity; L, low intensity; P1, low phosphorus level; P2, medium phosphorus level; P3, high phosphorus level; CC, two *C. odorata* seedlings per pot; PP, two *P. grandis* seedlings per pot; SS, two *S. taccada* seedlings per pot; CP, one *C. odorata* seedling (interplanting with *P. grandis*); PC, one *P. grandis* seedling (interplanting with *C. odorata*); CS, one *C. odorata* seedling (interplanting with *S. taccada*); SC, one *S. taccada* seedling (interplanting with *C. odorata*). Values are means + SE. Within each panel, means with different letters are significantly different ($p < 0.05$).

Supplementary Files

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- Table1.docx