

THE COASTAL DISTANCES AND TENDING OPERATIONS INFLUENCE THE LEAF TRAITS AND LEAF ALLOMETRY OF BAMBOO *DENDROCALAMUS MINOR* VAR. *AMOENUS*

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Abstract. Exploring the variation of functional traits and leaf allometry under different tending operations and distances to seashore would aid in understanding the plant's response and adaptation to the environment as well as provide a suggestion for windbreak construction. As a result, communities of *Dendrocalamus minor* var. *amoenus* were selected in Chishan forestry farm, Dongshan Island, China, to determine their leaf traits and leaf allometry under different tending operations, at various distances to the seashore. The results showed that leaf area, length, width, calorific value, C and N contents in the plot under tending operations were significantly higher than that in the plot near to seashore without tending operations and the plot far away to seashore without tending operations ($P < 0.05$). Tending operations and distance to seashore had effects on the leaf traits and leaf allometry. There was a trade-off between leaf morphological traits and leaf dry weight due to the changes in the allocation of resources and energy, caused by tending operations and distances to the seashore. We conclude that tending operations and distances to the seashore have a high impact on leaf morphological, functional traits by balancing the relationship between energy and growth.

Keywords: functional traits, distance to seashores, tending operations, allometric growth, bamboo, sandy coast

Introduction

China has a length of ca. 5948 km, of which the length of the sandy coastline is about 312 km (Department of Natural Resources, 2018). Plants growing on sandy coasts have to tolerate coastal stresses, such as salt spray, poor soil nutrients, and sand burial (Griffiths and Orians, 2004; Lin et al., 2017). Blowing wind and salt spray in the coastal area are prone to affect the morphological and physiological traits of plants (Griffiths and Orians, 2004; Pompeiano et al., 2016). Wind speed, salinity, and salt spray show a decreasing trend with increasing distance to the seashore (Lin et al., 2017; Huang et al., 2020). Different distances from the seashore have a significant effect on plant functional traits; For instance, plants near the coast are shorter (Todo et al., 2019) and have higher branching wood density (Lin et al., 2017). Environmental gradients have resulted in a large amount of intraspecific trait variation in species (Kumordzi et al., 2019).

Plant functional traits refer to traits that can easily respond to the environment and indicate plant growth, development, and reproduction (Cornelissen et al., 2003). Plant evolution and the environment have jointly shaped its growth and development (Chitwood and Sinha, 2016). The leaf is a representative organ that is quite sensitive to environmental changes and can generate phenotypic plasticity in response to abiotic stresses (Xu et al., 2009). Leaf functional traits can explain plants' response to past and future climate change (Heilmeyer, 2019). Therefore, the leaves have been selected as a study object in most studies. The intensity of human disturbance affects the functional

traits (Carreño-Rocabado et al., 2012; Yamashina et al., 2021). The response of communities to disturbances (direct human disturbances, biological pressure, environmental changes) can be predicted and quantified through leaf functional traits (Mouillot et al., 2013). The leaf construction cost is used to evaluate plant energy allocation, which indicates the adaptation strategy of the plant to the environment (Penning et al., 1974; Villar and Merino, 2001). Besides, morphological indexes and functional traits would change with the gradient environment (Guo et al., 2018). Therefore, functional traits, morphological indexes, and construction cost would be selected as indicators that evaluate the adaptation of plants in previous studies.

Some scholars believe that appropriate forest management practices or cultural operations can mitigate the effects of coastal stress on plants, such as watering (Boch et al., 2020). In the recent past, the effects of altitudes, topography, climatic regions and distance from the seashore on the leaf functional traits have been reported (Guo et al., 2018; Pardos et al., 2021; Zhang et al., 2021; Zheng et al., 2021b), but there have been relatively few studies on the effects of various distances from the seashore and tending operations on the leaf functional traits.

The genetic and environmental factors influence the relationships between leaf traits (Granier and Vile, 2014). Evidence suggests that allometric growth relationships among traits can reveal plant adaptive strategies to the environment and forecast future climate responses (Zhang et al., 2021). The altitudinal patterns of leaf characteristics indicate an allometric growth relationship, but a trade-off between branch diameter and length by adjusting the allometric growth relationship to match the gradient distance to the seashore needs further investigation.

Bamboo species with highly ornamental value have high phenotypic plasticity and can improve soil quality compared to bare land (Zheng et al., 2020, 2021a). Bamboo plants have complex branching characteristics and have a good potential to adapt to coastal environments (Bamboo Phylogeny Group, 2012). More than 20 years ago, a large number of bamboo species were introduced to the sandy coast of Dongshan Island in Fujian Province, China for windbreak and landscape greening. Among them, *Dendrocalamus minor* var. *amoenus* is a typical bamboo species suitable for the sandy coast. This species grows well and is widely planted with strong adaptive ability. In this study, we evaluated the leaf traits and allometric growth relationship of *Dendrocalamus minor* var. *amoenus* under the various distance to the seashore and tending operations conditions, revealing the response of *Dendrocalamus minor* var. *amoenus* to diverse conditions, and providing a scientific basis for windbreak construction and tending operations.

Material and Methods

Study area

The study site is located at 23°40'N, 118°18'E, Dongshan Island, Fujian Province, China. The climate of the study site is a subtropical maritime monsoon climate. The mean annual precipitation and evaporation are 1113.9 mm and 2013.2 mm, respectively. The annual temperature ranges from 3.8 °C to 36.6 °C (Mean value is 20.8 °C) (Kong, 1999). The age of bamboo stands is similar, which is planted in 2016~2018. Three sample plots were selected with various distance and tending operations (*Table 1*). The DMY plot (near to seashore with tending operations) was established with NPK compound fertilizer (0.2 kg·m⁻²), and usual practices like weeding, cleaning, and

irrigation were also performed. However, the HB plot (near to seashore without tending operations) and LM plot (far away to seashore without tending operations) plots were not nurturing. Each sample plot was divided into three sub-sample plots (20 m×20 m) where the morphological traits (base diameter, height, density) of *Dendrocalamus minor* var. *amoenus* and distance from the seashore were determined (Table 1).

Table 1. The situations of *Dendrocalamus minor* var. *amoenus*

Sample plot	Base diameter/(cm)	Height/(m)	Density/(Int/cluster)	Tending operations	Distance to seashore/(m)
DMY	3.24±0.43	7.43±0.73	19.80±6.16	Yes	50~80
HB	2.92±0.49	9.31±2.05	8.38±3.29	No	80~100
LM	3.26±0.89	10.31±1.33	39.25±45.42	No	500~800

Determination of functional traits

The 5~10 plants were randomly selected from each sub-sample plot (20 m×20 m) from July to August 2019. The healthy, fully expanded, unshaded leaves were collected from different directions and positions of the crown layer to determine their fresh weight and thickness. The area, length, and width of leaves were measured using Image J. The leaves were immersed in distilled water for 12 h under dark conditions and their saturated fresh weight was determined. The leaves were dried in an oven at 105 °C for 0.5 h and then placed in an oven at 80 °C for about 72 h until constant weight. The equations used to assess the specific leaf area (SLA, cm²·g⁻¹) and Leaf dry-matter content (LDMC, g·g⁻¹) have been described in Pérez-Harguindeguy et al. (2013).

The 1.0 g leaf powder was ashed at 700 °C for 6 h. The mass of ash was measured after cooling. The caloric value per gram was determined using a PC bomb calorimeter (HWR-15E, China). The ash-free caloric value(AFCV), CC_{mass} (Leaf construction cost per unit mass), and CC_{area} (Leaf construction cost per unit area) were calculated according to Williams et al. (1987).

$$\text{Ash content (\%)} = \text{Ash}_{\text{mass}} / \text{Sample}_{\text{mass}} \times 100\% \quad (\text{Eq.1})$$

$$\text{AFCV (kJ} \cdot \text{g}^{-1}) = \text{CV} / (1 - \text{AC}) \quad (\text{Eq.2})$$

$$\text{CC}_{\text{mass}} = [(0.06968\text{AFCV} - 0.065)(1 - \text{AC})] + 7.5 \times (\text{kN}_{\text{mass}} / 14.0067) / \text{EG} \quad (\text{Eq.3})$$

$$\text{CC}_{\text{area}} = \text{CC}_{\text{mass}} / \text{SLA} \quad (\text{Eq.4})$$

where AC: Ash content; AFCV: Ash-free caloric value; EG: The deviation of growth efficiency. The value of EG was estimated to be 0.87 (Penning et al., 1974); N_{mass}: Nitrogen content per unit mass; k: the oxidation state of the nitrogen content. The value of k was estimated to be 5 for the oxidation.

Allometric growth analysis

The allometric growth analysis was performed to test the relationship between the allocation of functional traits under the different distances and tending operations. Before allometric growth analysis, the log-transformation of all data values was

conducted. The log-transformation is useful for testing the proportional relationships in allometric scaling. The standardized major axis (SMA) was performed to calculate the slope and elevation of the relationship between leaf traits.

$$\log Y = \log \beta + \alpha \log X \quad (\text{Eq.5})$$

where Y refers to the dependent variable, X refers to the independent variable; β represents the elevation and α is the slope of the allometric scaling. If the slope of these relationships were not significantly different from |1.00|, they would be isometric. If the slope of these relationships were significantly different from |1.00|, they would be allometric.

Data analyses

The data presented in the current study is Mean \pm SD. One-way ANOVA and pairwise comparison tests (Tukey's method) were performed to test the difference of leaf morphology, functional traits and construction cost among these sample plots. All the statistical analyses were performed using R v3.6.1 and allometric growth analysis was conducted using the Smatr package (Warton et al., 2012). The graphical illustration was done by using Origin 2013 (Origin Lab, USA).

Results

Leaf morphological traits under different conditions

Leaf area, length, and width were significantly higher in the DMY plot than that of the HB plot and LM plot ($P < 0.05$, Fig. 1). There was no significant difference in leaf area, leaf length, leaf width, and L:W between HB and LM plot ($P > 0.05$). Leaf thickness in the DMY plot was significantly higher than that in the HB plot ($P < 0.05$).

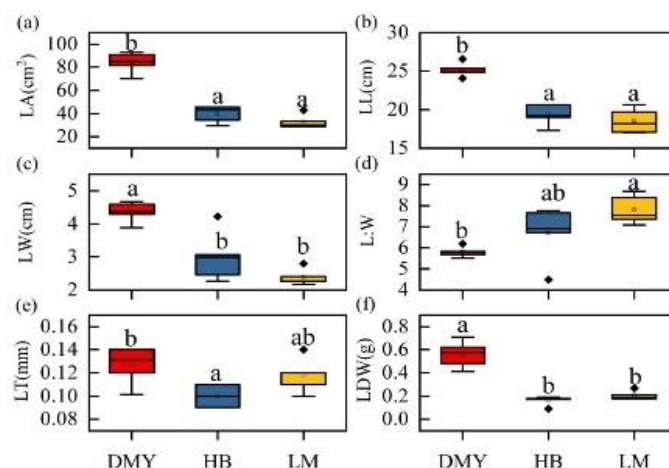


Figure 1. The morphological traits under different conditions. Where DMY represents the plot near to seashore with tending operations; HM represents the plot near to seashore without tending operations; LM represents the plot far away to seashore without tending operations. (a) LA: leaf area; (b) LL: leaf length; (c) LW: leaf width; (d) L:W represents leaf length: leaf width; (e) LT: leaf thickness; (f) LDW: leaf dry weight. Different letters indicate the significant differences between different conditions ($P > 0.05$)

Functional traits under different conditions

In terms of functional traits, no significant differences in leaf dry matter contents (LDMC) were observed among the three sample plots ($P>0.05$). However, SLA and ash contents in the HB plot were significantly ($P<0.05$) higher ($253.25 \text{ cm}^2 \cdot \text{g}^{-1}$ and 7.57% , respectively) relative to other sample plots. Besides, the leaf calorific value in the DMY plot was significantly higher ($18.62 \text{ kJ} \cdot \text{g}^{-1}$) than that of the HB and LM plot ($P<0.05$, Fig. 2).

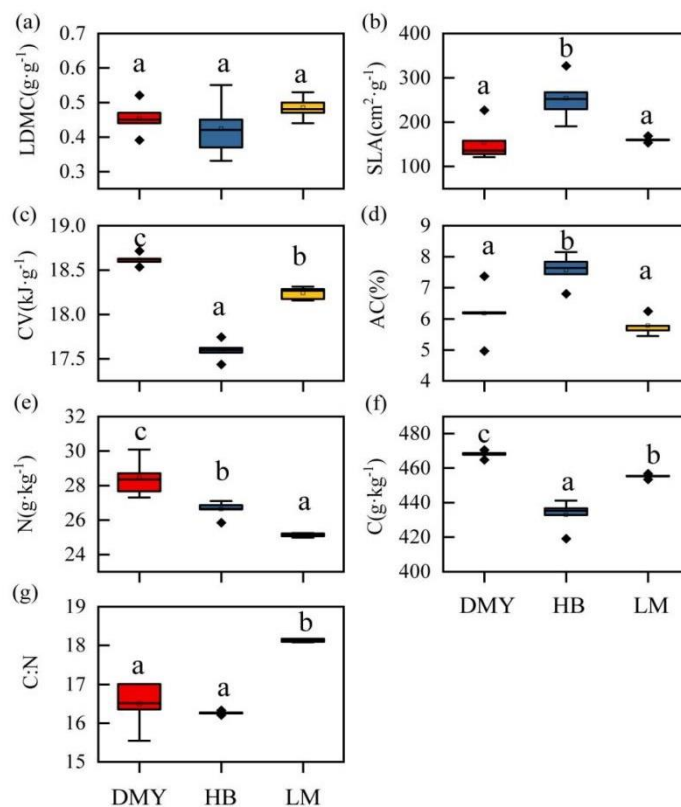


Figure 2. Leaf C and N contents and C: N under different conditions. Where DMY represents the plot near to seashore with tending operations; HM represents the plot near to seashore without tending operations; LM represents the plot far away to seashore without tending operations. (a) LDMC: leaf dry matter content; (b) SLA: specific leaf area; (c) CV: calorific value; (d) AC: ash content; (e) N: nitrogen content; (f) C: carbon content; (g) C:N: carbon content: nitrogen content. Different letters indicate the significant differences between different conditions ($P>0.05$)

Leaf C and N contents in the DMY plot were significantly higher than that of the HB and LM plot ($P<0.05$, Fig. 3). Leaf C contents in HB plot reduced significantly compared to LM plot ($P<0.05$), whereas leaf N contents in HB plot were significantly higher than that of LM plot ($P<0.05$). In addition, the C: N in the LM plot was the highest (18.13).

The construction cost under different conditions

The CC_{mass} in the DMY plot was the highest, reaching up to $10.20 \text{ g glucose}\cdot\text{g}^{-1}$, while CC_{mass} in the LM plot was the lowest ($9.15 \text{ g glucose}\cdot\text{g}^{-1}$, Figure 3). Furthermore, the CC_{area} in the HB plot was the lowest ($389.68 \text{ g glucose}\cdot\text{m}^{-2}$).

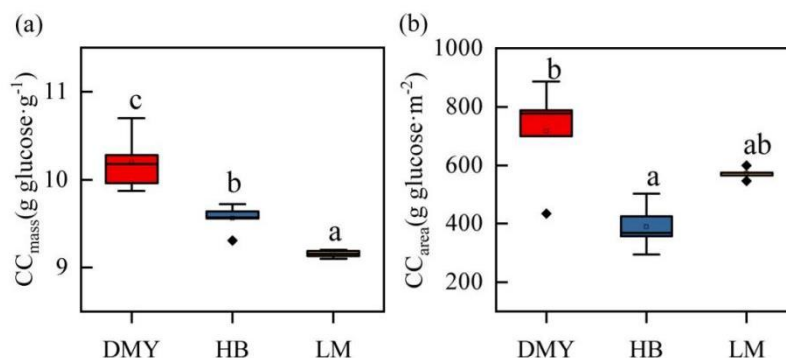


Figure 3. The leaf construction cost under different conditions. Where DMY represents the plot near to seashore with tending operations; HM represents the plot near to seashore without tending operations; LM represents the plot far away to seashore without tending operations. (a) CC_{mass} : Leaf construction cost per unit mass; (b) CC_{area} : Leaf construction cost per unit area

The allometric growth relationship

There was a significant allometric growth relationship between leaf area and leaf width in the three sample plots ($P < 0.05$, $P_{1.0} < 0.05$, see Table 2). Leaf area was significantly related to length, width, and L: W in HB and LM plot with allometric growth ($P < 0.05$, $P_{1.0} < 0.05$). Leaf area was not correlated with leaf thickness ($P < 0.05$). The relationship between leaf area and thickness was isometric growth ($P_{1.0} > 0.05$), which suggests the relationship will not change with different conditions.

Table 2. The allometric relationship between leaf area and other leaf functional traits at different conditions

Y	X	Conditions	df	R ²	Slope	5% CI	95% CI	Elevation	P _{1.0} -value	P-value
Leaf area	Length	DMY	62	0.16	1.19	0.95	1.50	0.24	0.133	0.001
		HB	101	0.72	1.99	1.80	2.21	-0.98	0.000	0.000
		LM	151	0.66	1.94	1.77	2.14	-0.96	0.000	0.000
	Width	DMY	62	0.89	1.80	1.66	1.96	0.76	0.000	0.000
		HB	101	0.80	1.59	1.45	1.73	0.89	0.000	0.000
		LM	151	0.72	1.57	1.44	1.71	0.91	0.000	0.000
	L:W	DMY	62	0.05	-1.16	-1.48	-0.90	2.77	0.245	0.078
		HB	101	0.07	-1.89	-2.28	-1.56	3.18	0.000	0.009
		LM	151	0.04	-1.57	-1.84	-1.34	2.89	0.000	0.015
Leaf thickness	DMY	62	0.01	2.77	2.15	3.56	4.34	0.000	0.576	
	HB	101	0.00	-1.93	-2.35	-1.58	-0.38	0.000	0.816	
	LM	151	0.00	-3.21	-3.76	-2.73	-1.59	0.000	0.857	

Where DMY represents the plot near to seashore with tending operations; HM represents the plot near to seashore without tending operations; LM represents the plot far away to seashore without tending operations. *df* represents degrees of freedom; R² represents determination coefficient; Slope represents scaling slope. 5% CI represent 5% confidence intervals; 95% CI represent 95% confidence intervals. *p*_{1.0}- value means the significance of the SMA slope value being different from |1.00|

There was a significant allometric growth relationship between leaf dry weight and leaf length at DMY plot ($P < 0.05$, $P_{1.0} < 0.05$); leaf dry weight and leaf width, leaf dry weight, and leaf area in HB plot ($P < 0.05$, $P_{1.0} < 0.05$, see *Table 3*). Leaf dry weight has a significant allometric growth relationship with leaf thickness in all plots ($P < 0.05$, $P_{1.0} < 0.05$).

Table 3. The allometric relationship between leaf dry biomass and other leaf functional traits at different conditions

Y	X	Conditions	df	R ²	Slope	5% CI	95% CI	Elevation	P _{1.0} -value	P-value
Leaf dry weight	Length	DMY	62	0.07	1.59	1.24	2.02	-2.41	0.000	0.040
		HB	101	0.01	2.45	2.02	2.98	-3.85	0.000	0.221
		LM	151	0.00	-2.20	-2.58	-1.87	2.07	0.000	0.565
	Width	DMY	62	0.00	-2.40	-3.08	-1.86	1.30	0.000	0.959
		HB	101	0.04	1.95	1.61	2.37	-1.55	0.000	0.049
		LM	151	0.00	-1.77	-2.08	-1.51	-0.05	0.000	0.977
	L:W	DMY	62	0.06	1.54	1.21	1.96	-1.38	0.001	0.043
		HB	101	0.01	-2.32	-2.82	-1.91	1.26	0.000	0.245
		LM	151	0.00	-1.78	-2.09	-1.52	0.89	0.000	0.662
	Leaf thickness	DMY	62	0.25	3.68	2.96	4.58	3.04	0.000	0.000
		HB	101	0.04	2.37	1.96	2.88	1.69	0.000	0.046
		LM	151	0.05	3.63	3.10	4.24	2.78	0.000	0.007
	Leaf area	DMY	62	0.00	1.33	1.03	1.71	-2.74	0.026	0.886
		HB	101	0.04	1.23	1.02	1.49	-2.65	0.034	0.043
		LM	151	0.00	-1.13	-1.33	-0.96	0.98	0.132	0.674

Where DMY represents the plot near to seashore with tending operations; HB represents the plot near to seashore without tending operations; LM represents the plot far away to seashore without tending operations. *df* represents degrees of freedom; R² represents determination coefficient; Slope represents scaling slope. 5% CI represent 5% confidence intervals; 95% CI represent 95% confidence intervals. P_{1.0}-value means the significance of the SMA slope value being different from |1.00|

Discussion

Effect of tending operations on leaf morphology, functional traits, and construction cost

The current research was designed to assess the impacts of various distances and tending operations on the plant communities around the coastal line. We hypothesized that the tending operations would affect leaf morphology, functional traits, and construction cost. In this study, various traits such as leaf area, length, width, leaf thickness, leaf dry weight, leaf C and N content, calorific value, CC_{mass}, and CC_{area} in DMY plot were significantly higher than that observed in the HB plot ($P < 0.05$), which indicates that tending operations have prompted larger leaves with higher carbon fixation capacity, calorific value and nutrient content. The thicker and higher N contents under tending operations facilitate resistance to physical damage and high water use efficiency (Wright et al., 1993). On the contrary, previous studies have reported that the thicker leaves reduce the N content (Pérez-Harguindeguy et al., 2013). Tending operations alters the correlation of traits by coupling coordination or combination (Baraloto et al., 2010; Freschet et al., 2010), It has been evident in previous reports that tending operations affect the functional traits of the vegetation (Carreño-Rocabado et al., 2012; Yamashina et al., 2021), and the soil organic matter has been the main factor

influencing the variation in functional traits under different tending operations (Chen et al., 2018). Consequently, tending operations would supply nutrients to the soil, resulting in C and N content in leaves increased, photosynthesis, and carbon fixation increased.

SLA reflects the ability of plants to absorb resources from the environment, and it is positively correlated with the potential reproduction rate (Pérez-Harguindeguy et al., 2013). SLA and ash content in the DMY plot were significantly lower than that observed in the HB plot ($P < 0.05$). The thicker and lower SLA would reduce water evaporation from the leaves, alleviate the damage caused by high temperatures, and drought stress in this research in this research in this research (Comstock and Mencuccini, 1998). It's the ecological strategy of *Dendrocalamus minor* var. *amoenus* with thicker leaf and lower SLA under tending operations in the DMY plot. SLA was negatively correlated with leaf longevity (Pérez-Harguindeguy et al., 2013). The high SLA in the HB plot had relatively shorter leaf longevity and lower CC_{mass} than that in the DMY plot. Leaf construction cost is used to evaluate plant energy allocation, which indicates the adaptation strategy of the plant to the environment (Penning et al., 1974; Villar and Merino, 2001). *Dendrocalamus minor* var. *amoenus* under tending operations had thicker leaves, higher CC_{mass} , and lower SLA, which suggest with the tending operations, *Dendrocalamus minor* var. *amoenus* have higher nutrient contents and water use efficiency, while relatively slow potential reproduction rate enhances resistance to physical damage (e.g., wind stress).

Effect of distances to the seashore on leaf morphology, functional traits, and construction cost

The distance to the seashore would affect the plant morphology (Todo et al., 2019). Previous research has shown that different distances to the seashore with gradient coastal stress influence branching functional characteristics (Lin et al., 2017; Zheng et al., 2021b). For instance, leaf C contents of *Pinus thunbergii* decreased with distance to seashore increased, however, C: N would not change with various distances (Sun et al., 2019). On the contrary, the leaf C content, and C: N of *Dendrocalamus minor* var. *amoenus* increased as the distance from the seashore increased. The inequalities in findings may be attributed to the various soil types and conditions. The plant absorbs the C content from the soil and in the current study, the C contents in sandy soil increased as the distance to the seashore increased. It is also possible that plant communities located far from the seashore would attract a large number of seabirds, and owing to their droppings the leaf litter would increase the C content in the soil (Huang et al., 2020).

The N contents in leaves are used primarily to construct proteins, which has been highly correlated with energy investment and construction cost (Griffin et al., 1996; Zhang et al., 2019). The leaf N contents and CC_{mass} decreased with increasing distance from the seashore. However, the relationship between leaf construction costs and the environment is controversial. Some scholars suggest that leaf construction costs increase when plants are subjected to environmental stress (Villar and Merino, 2001; Fortunel et al., 2012; Matías et al., 2012), and others suggest that plants increase their adaptability to environmental stress by reducing leaf construction costs (Suárez, 2003; Falcão et al., 2017). In this research, we found that when plants were subjected to environmental stress, the cost of leaf construction increased. The distance to the seashore is negative with coastal stress (Lin et al., 2017). The greater the distance from the seashore, the richer the environmental resources, and therefore the lower

construction cost of *Dendrocalamus minor* var. *amoenus*, which needs less energy to develop plant tissues. However, the plant established closer to the seashore, requires more energy to develop tissues and resist environmental stress.

Tending operations and distances to the seashore on the allometric growth of leaf morphology

The mechanism of leaf size and adaptive strategy is generally considered to be highly related to the balance in leaf energy (Niinemets et al., 2006). The study of the allometric growth relationships of leaf morphology under different environmental conditions can help to understand the mechanism of how plants adapt to environmental stress. Plants adapt to environmental patterns by changing the allometric growth relationships of morphological traits (Guo et al., 2018). In this research, there was no correlation between leaf area and leaf thickness even though the environment was altered. Previous studies have suggested the correlations of some traits did not change with the environment, indicating strong covariance relationships of the traits (Chave et al., 2014; Zhang et al., 2015). The changes in leaf morphology indicate the adaptation strategies of plants to environmental resources; the longer and broader leaves are beneficial to resource acquisition and conservation (Xu et al., 2009). To adapt to the poor environment, leaf morphological traits in HB and LM plots adjust allometric growth relationships. The growth relationship between leaf length, width, and L: W with leaf area is significantly allometric in HB and LM plot ($P < 0.05$, $P_{1.0} < 0.05$), and leaf area was increased by adjusting the leaf morphological traits to increase photosynthetic efficiency to adapt to coastal pressure.

The leaf dry weight and leaf thickness exhibited the allometric growth relationships among different conditions. The slopes in the HB plot were low, and the slopes in the DMY plot and LM plot were relatively higher and similar, which suggests that tending operations and distance to seashore have a similar effect on allometric growth relationships between leaf dry weight and leaf thickness. Previously, studies have shown that the allometric growth relationships exist between leaf dry weight and leaf morphology in *Pleioblastus amarus* at different elevation gradients (Guo et al., 2018). Various distances to the seashore cause diversified environments, resulting in significant allometric growth relationships among traits (Zheng et al., 2021b). There were significant positive allometric growth relationships between leaf dry weight and leaf length, L: W, and leaf thickness in the DMY plot ($P < 0.05$, $P_{1.0} < 0.05$), and there were significant positive allometric growth relationships between leaf dry weight and leaf thickness, leaf width, and leaf area in HB plot ($P < 0.05$, $P_{1.0} < 0.05$). There was a significant positive allometric growth relationship between leaf dry weight and leaf thickness in the LM plot ($P < 0.05$, $P_{1.0} < 0.05$). The soil nutrient and water contents can be improved under tending operations, and various distances to the seashore are highly correlated with environmental resources (Lin et al., 2017; Huang et al., 2020). There was a trade-off allocation of resources and energy between leaf morphological traits and leaf dry weight in *Dendrocalamus minor* var. *amoenus*, which would change the allometric growth relationship between traits. Larger leaves will be more efficient for photosynthesis and might fix more carbon assimilation products, which helps the plant to resist abiotic stresses.

Conclusion

Tending operations changed the correlation between traits, supplied more nutrients to the plant, and also increased the plant's resistance to coastal stress. The plant grows in places far away from the seashore with lower coastal pressure and construction costs. Tending operations and distances to the seashore have a high impact on leaf morphological, functional traits of *Dendrocalamus minor* var. *amoenus* by balancing the relationship between energy and growth. Future studies can focus on revealing the determining environmental factors of the functional traits and allometric growth relationships among various distance and tending operations. These findings would provide a reference for windbreak construction, and it also reveals the ecological meaning of plants adapting to the coastal environment.

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