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ORIGINAL ARTICLE



Ecological response of *Casuarina equisetifolia* to environmental stress in coastal dunes in China

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ABSTRACT

Seasonal variations in *Casuarina equisetifolia* branchlet diameter, branchlet internode length, and branchlet length were investigated in plants at various distances from the coast in a *Casuarina* forest, using field studies and laboratory analysis. The branchlet traits of *C. equisetifolia* exhibited approximately linear change with increasing distance from the coast: the branchlet diameter became thinner, while the internode and branchlet lengths became longer. The change in branchlet traits was most evident at 0–20 m from the coast. There was little change in the distance from 40 m to 80 m. The branchlets on trees in favorable habitats showed an increase in internode length and reduced diameter, whereas the branchlets in unfavorable habitats had reduced internode length but increased diameter in limited branchlet length. The spatial changes in *C. equisetifolia* branchlet traits appear to be an adaptation to the environment, in response to the effects of blown sand in the coastal front area. The results suggest that to maintain growth this species shows marked adaptability to the effect of blown sand.

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KEYWORDS

Casuarina; branchlet traits; seasonal change; effect of blown sand

Introduction

Plant traits are readily observed and measured, including leaf size and longevity, dispersal patterns, canopy height, and other factors (Diaz and Cabido 2001). These traits usually reflect the ability of the plant to acquire, preserve, and utilize resources, and have an important impact on plant survival. They reflect the interaction between the plant and its environment in developmental and evolutionary processes. Certain changes in plant traits reflect adaptability to the external environment, and the evolution and balance between various functions within the plant also reflect functional attributes of the plant ecosystem (Wu et al. 2012).

Leaves are an important plant organ for manufacturing organic nutrients for seed plants. Leaf size affects the ability of the plant to obtain light and carbon, which directly affects the photosynthetic yield, highlighting that the relationship between morphology and function directly affects plant production. The leaf area greatly varies among plant species and is affected by prevailing environmental stress conditions including low temperature, drought, and high light intensity. Consequently, changes in leaf area are an adaptation strategy to environmental stress (Milla and Reich 2007).

For *Casuarina* the branchlets are the main photosynthetic organs rather than leaves, and their characteristics directly affect the basic activity and function of these plants (Diemer 2004), thereby influencing the ecosystem function of *Casuarina*, a terminal young branch (including internodes and leaves) representing the current season's growth of a woody plant, is considered important for exploring functional strategies of plant growth because of its main carbon assimilation function (Yang et al. 2015) (Yang et al. 2015). At

the branchlet level, inter-specific comparison studies have shown that branchlet number, diameter, or cross-sectional area are strongly related to leaf size (e.g. Givnish 1987; Westoby and Wright 2003; Eideh and Elkarmi 2005; Sterck et al. 2006). Branchlets of *Casuarina* are among the most sensitive organs to environmental change, which is closely related to the growth strategy of the plant and its ability to utilize resources. The maximum uptake of carbon is affected by changes in the morphological structure and physiological function of branchlets, which reflects a strategy for adapting to the environment (Jiang and Li 2008). The ability to respond to environmental changes reflects plasticity in adaptation to external conditions, and reflects the ability of the plant to adapt to its environment, its evolution, and the balance between various functions within the plant.

Casuarina trees were introduced to the tropical and subtropical zones of China in 1897 (Zhong et al. 2010), and currently cover about 300,000 ha, mostly in the coastal area of South China. *Casuarina* has proven widely adaptable to China's soil types, and can grow on clay to coarse sand, and in saline to calcareous and dry to water-logged soils. This adaptability is essential in the context of global climate change, which is resulting in longer periods of drought and soil salinization (Wang et al. 2003; Chaves et al. 2009). *Casuarina* is one of the preferred plants for forming shelter forests in coastal areas in China, as it acts to stabilize moving sand. It is also useful in agroforestry systems and for wood and fuel production (Zhong et al. 2005). It provides ecological benefits including land reclamation, wind breaks, stabilizing coastal sand, vegetating coasts, and protecting croplands. *Casuarina* is valued as pioneer trees for

degraded sites and for soil improvement, restoration, and maintenance of the ecosystem (Wang and Xiao 2011).

As an alien woody species, *Casuarina* poses ecological risk. For example, it produces large amounts of litter that accumulates as a deep layer under its canopy (Hata et al. 2010), so the density and species richness of saplings of native woody species in forests dominated by *Casuarina* are much lower than those in forests dominated by native species (Hata et al. 2009). Furthermore, hybridization between different *Casuarina* species could potentially enhance the evolution of invasiveness (Lee 2002; Schierenbeck and Ellstrand 2009). However, due to the special geographical environment of the south subtropical zones of China, no other species can replace casuarinas on the foreshores (Zhong et al. 2010). In saline environments, *Casuarina* has proven to have great potential for N_2 fixation, which facilitates its growth in these areas (Reddell et al. 1986; Diagne et al. 2013).

Several physiological studies have been performed to investigate how *Casuarina* species respond and adapt to low temperatures and drought (He et al. 2011; Zhang et al. 2012). These adaptations have reinforced its capacity to control basal metabolism and survive in harsh environments. However, the relationship between branchlet characteristics and environment in terms of functional characteristics has received little attention, and there are no studies of whether the *Casuarina* branchlet characteristics change or remain constant in relation to environmental stress. Because of the large existing and potential planting areas in China and other parts of the world, study of seasonal variations in the characteristics of *Casuarina* at different distances from the coastline will aid our understanding of the mechanisms of adaptation in *Casuarina* to habitat heterogeneity. It will also enable re-evaluation of the value of phenotypic traits in classification, assessment of the use of this species in restoration and reconstruction, and its ecosystem function in coastal frontier areas. The measurement approach we used provides a more precise method for assessing the nature (e.g. isometric vs. allometric relationship) of the trade-off between the characteristics. The objectives of this study were to assess whether the scaling relationship among branchlet characteristics varies with distance from the coast, and if so, whether the scaling relationship is isometric or allometric, and whether *Casuarina equisetifolia* has a shorter branchlet internode length and a thicker branchlet for a limited branchlet length with increasing environmental stress (e.g. strong wind-sand action).

Material and methods

Study sites and sample plots

As shown in Figure 1, the study area is located at the Chihu Forestry Center in Huian County, Fujian Province, China (118°55'E, 23°45'N). From the beginning of the 1960s, the Chihu Forestry Center planted a large area of coastal shelterbelts that gradually formed a relatively stable coastal protection forest system. This area is affected by subtropical oceanic monsoons, has an average annual temperature of 19.8°C (maximum and minimum temperatures: 37 and 2.2°C, respectively), an annual frost-free season of 320 days, and average annual precipitation and evaporation of 1029 mm and 2000 mm, respectively. Evaporation exceeds precipitation, and there are distinct dry and wet seasons. The vegetation community in the woodland is dominated by *C. equisetifolia* L., while *Sageretia thea* (Osbeck) Johnst., *Lantana montevidensis* Briq., *Urena lobata* L., *Breynia officinalis* Hemsl., and other species occur in the shrub layer. The stand age is ~30 years, and water-cultured seedlings were used to establish the plantation. The initial planting density was 4500 plants hm^{-2} in the coastal front area and 2500 plants hm^{-2} in the landward area, and the total plantation area was ~400 ha.

Sand sources

The study area is characterized by sediments reflecting the complex and dynamic oceanic environment; most of the coastal area is derived from Yanshanian granite and Quaternary sandy strata (Wu et al. 1995). Under the prevailing humid subtropical climate, the granite has weathered and been leached extensively, and the weathering crust is relatively thick. Such coastal areas are vulnerable to storm and wave erosion. Large amounts of sediment have formed from water and wave erosion, and large amounts of material have eroded into the sea, especially during typhoons and strong storm events; the resulting sediments constitute the main sand source for the coastal beaches (Wang 2011). There are also many rivers in this area, which provide an important source of sediment for coastal aeolian transport processes that have formed a broad sandy beach and sea plains, and for dispersal by sandstorms (Wang 2011). In addition, large amounts of sand have been carried to the beach by tidal waves and currents.

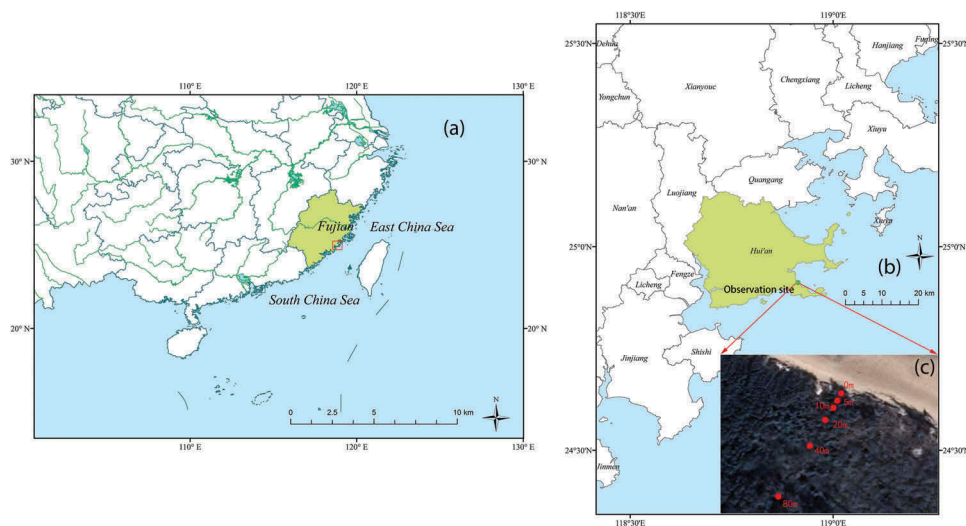


Figure 1. (a) Map of the study area. (b) Enlargement showing the location of the observation site. (c) Aerial photo of the sampling sites, red point mean the sampling site in different distance.

Soil

The soil in the study plot is aeolian sand that is 60–80 cm thick and has loose structure, high permeability, low water-holding capacity, and little organic matter. The pH value of the soil was 5.0, and the total cation exchange capacity, available phosphorus, available potassium, total nitrogen, and total carbon were $4.51 \text{ cmol kg}^{-1}$, 0.25 mg kg^{-1} , 13.27 mg kg^{-1} , 0.24 g kg^{-1} , and 2.48 g kg^{-1} , respectively (Ye et al. 2007). Geological sections show that the mobile dune and semi-mobile dune soils are thick, and there is no obvious difference between soil profiles in the area.

The water table at the outer edge of the beach is relatively high, but the soil salt content is relatively high because of the impact of subsurface tidal seawater that invades the soil water and causes physiological drought conditions. The soil physical properties at various distances from the coast are listed in Table 1. The bulk density decreased with increasing distance from the coast, while the noncapillary porosity, capillary porosity, and total porosity increased. The moisture content generally increased with increasing distance from the coast and reached a peak value at 40 m. The values for physical properties were greater in the subsoil than in the topsoil.

Methods

Field sampling and measurements

The study plot is located in a clearing in the center of the Chihu forest. The high tide level was set as the starting sampling point (0 m), and additional sampling points were established at distances of 5, 10, 20, 40, and 80 m along a transect perpendicular to the coastline (Table 2). Five healthy and mature plants of *C. equisetifolia* fully exposed to sunshine were marked at each sampling point. On 13 March, 15 June, 17 September, and 15 December 2016, 30 branchlets were collected from the canopy of each *C. equisetifolia* specimen using extended branchlet

scissors; if the trees were too high they were climbed to collect branchlets from the middle height of the tree. The branchlet length was measured using a ruler, and the branchlet diameter and internode length were measured using an electronic digital meter (precision: 0.01 mm). The branchlet diameter was defined as the thickness at the mid-point of the branchlet. The internode length was measured five times at different locations for each individual branchlet, and the average value was taken as the individual branchlet internode length. The sand collection device was placed next to the sampling point, and the sand was collected and measured once a month.

Data analysis

Allometry is a discipline in which alternatives to linear regression are routinely required (Warton et al. 2006). When there are two variables, the standardized major axis (SMA) can be used to describe some axis or line of best fit. The purpose of line-fitting is not to predict Y from X, but rather to summarize the relationship between the two variables, such a line that a single dimension can be used to describe two-dimensional data, enabling variation to be quantified and its implications understood.

The measured branchlet parameters (branchlet length, branchlet internode length, and branchlet diameter) for each *C. equisetifolia* specimen were averaged, and $\log_{10}$ transformed to fit a normal distribution. For any two functional characteristics in the study, the relation $y = bx^a$ was linearly converted to $\log(y) = \log(b) + a \log(x)$, where x and y represent the two characteristics, b represents the intercept of the characteristics relation, and a represents the slope of the correlation, which corresponds to the allometric parameter or relative growth index. When $a = 1$ the two characteristics are in an isokinetic relationship, when $a > 1$ the increase in y is greater than that in x , and when $a < 1$ the increase in y is less than that in x . The data analysis was mainly based on the standard principal axis estimation (SMA) method (Warton et al. 2006), and the software

Table 1. Soil physical properties at various distances from the coast.

Position	Distance	Bulk density (g cm^{-3})	Noncapillary porosity (%)	Capillary porosity (%)	Total porosity (%)	Moisture content (%)
Topsoil (0~15 cm)	0	1.42 ± 0.03^b	1.90 ± 0.22^a	40.50 ± 1.80^a	42.40 ± 2.02^a	1.32 ± 0.40^a
	5	1.39 ± 0.05^{ab}	2.10 ± 0.33^a	41.00 ± 1.40^a	43.10 ± 1.73^a	1.53 ± 0.40^a
	10	1.36 ± 0.03^a	2.20 ± 0.21^a	41.00 ± 1.20^a	43.20 ± 0.99^a	3.05 ± 0.40^c
	20	1.35 ± 0.02^a	4.40 ± 0.64^b	39.90 ± 2.00^a	44.30 ± 2.34^{ab}	4.85 ± 0.40^{de}
	40	1.32 ± 0.04^a	5.20 ± 0.40^c	44.90 ± 1.51^a	50.10 ± 1.18^c	5.55 ± 0.50^{ef}
	80	1.31 ± 0.04^a	6.50 ± 0.58^d	42.60 ± 1.50^a	49.10 ± 2.12^{bc}	4.39 ± 0.60^d
Subsoil (15~30 cm)	0	1.41 ± 0.04^b	2.50 ± 0.25^a	41.20 ± 2.80^a	43.70 ± 2.02^a	2.09 ± 0.40^b
	5	1.40 ± 0.02^b	2.30 ± 0.30^a	41.60 ± 2.10^a	43.90 ± 2.33^a	2.90 ± 0.40^c
	10	1.40 ± 0.03^b	3.11 ± 0.25^a	41.02 ± 2.80^a	44.13 ± 2.39^a	4.74 ± 0.50^{de}
	20	1.39 ± 0.02^b	6.16 ± 0.37^b	40.10 ± 3.10^a	46.26 ± 2.34^{ab}	5.82 ± 0.50^f
	40	1.34 ± 0.02^a	7.03 ± 0.72^{bc}	41.80 ± 2.70^a	48.83 ± 2.18^b	7.66 ± 0.80^g
	80	1.34 ± 0.02^a	7.40 ± 0.82^c	40.90 ± 2.80^a	48.30 ± 2.12^b	4.64 ± 0.40^d

The data are the means $\pm$ standard derivation of five separate measurements. Different small letters within columns indicate significant difference ($p < 0.05$).

Table 2. *Casuarina equisetifolia* plots and sampling characteristics.

Distance (m)	Vegetation cover (%)	Canopy density (%)	Stand density (plants hm^{-2})	Height (m)	DBH (cm)	Crown width (m $\times$ m)	Wind damage
0	60	50	4210	1.54 ± 0.12	3.50 ± 0.80	0.8×0.8	67% of branches turned and withered
5	65	60	4350	2.23 ± 0.41	4.12 ± 0.54	1.0×1.0	50% of branches turned and withered
10	70	60	3450	2.70 ± 0.52	5.62 ± 0.34	1.5×1.5	25% of branches turned and withered
20	75	70	2470	3.57 ± 0.47	6.43 ± 1.33	2.0×2.0	Few branches turned and withered
40	72	60	2430	7.22 ± 0.62	9.50 ± 0.65	3.0×3.0	Withered branches not seen
80	70	65	2100	8.79 ± 0.81	12.50 ± 0.46	3.5×3.5	Withered branches not seen

Intervals calculated for height and diameter at breast height based on the default 95% reliability.

(S) MATR version 2.0 (Falster et al. 2006) was used for computations. The confidence interval (CI) for each regression slope was calculated according to the Pitman method (Pitman 1939), and the heterogeneity of the regression slope was determined using the Warton and Weber's method (Warton and Weber 2002). SPSS software was used to analyze the average data for branchlets as a function of distance from the coast. The differences between different data sets were compared using one-way ANOVA and the least significant difference method.

Results

Variation in wind-sand action with distance from the coast

Wind-sand action requires strong wind, a sand source, and a smooth transportation path. As shown in Figure 2, wind from the northeast prevailed throughout the year, accounting for 45.92% of the annual wind direction, while northerly winds were next most prevalent, accounting for 15.8%. The strongest wind was also from the northeast, accounting for 65.97% of wind speeds exceeding 15 m^{-1} . In summer, the main wind direction was northeast (27.75%) followed by southerly winds (23.75%), while southwest and northerly winds were lower in wind speed and less common. In winter, the northeast wind remained dominant, accounting for 63.12% of the wind direction, followed by north winds (18.44%). The region is mainly affected by the northeast monsoon.

The seasonal dynamics of wind speed at varying heights from the ground (0.5, 1.5, and 2.0 m) at various distances from the coast are summarized in Table 3. The order of decreasing seasonal wind speed was winter, autumn, spring, then summer. The wind speed decreased with increasing distance from the coast. For example, in winter at 0 m, the wind speed

decreased by 48.24%, 52.83%, 85.06%, 91.46%, and 95.73%, respectively, with distance from the coast.

The seasonal variation in total sand accumulation is shown in Figure 3. The sand accumulation generally decreased with increasing distance from the coast except in winter, and the order of decreasing seasonal total sand accumulation was winter, followed by summer, autumn, and spring.

The sand accumulation from 40 m to 80 m, as a proportion of the total monthly sand accumulation, is shown in Figure 4. A typical power function relationship is evident, with a lower proportion accumulating in this distance range with increasing total monthly sand accumulation.

Seasonal changes in *Casuarina* branchlet characteristics with distance from the coast

The seasonal change in branchlet diameter and internode and branchlet lengths with distance from the coast is listed in Table 4. The diameter generally decreased with increasing distance from the coast, while the branchlet increased. The internode length generally increased with increasing distance from the coast in spring and summer, but there were no significant changes ($p < 0.05$) in autumn and winter. The seasonal change (decrease) in branchlet diameter thickness was summer, spring, autumn, and winter. The discrete degree of branchlet diameter was highest in winter, and the coefficient of variation was 4.55%–11.59%. The internode length changed little in autumn and winter, and the discrete degree of internode length was highest in summer (coefficient of variation: 7.02%–13.19%). The order of decreasing seasonal change in branchlet length was winter, then summer, autumn, and spring. The branchlet length was greatest in winter, and the coefficient of variation was 4.37%–10.96%.

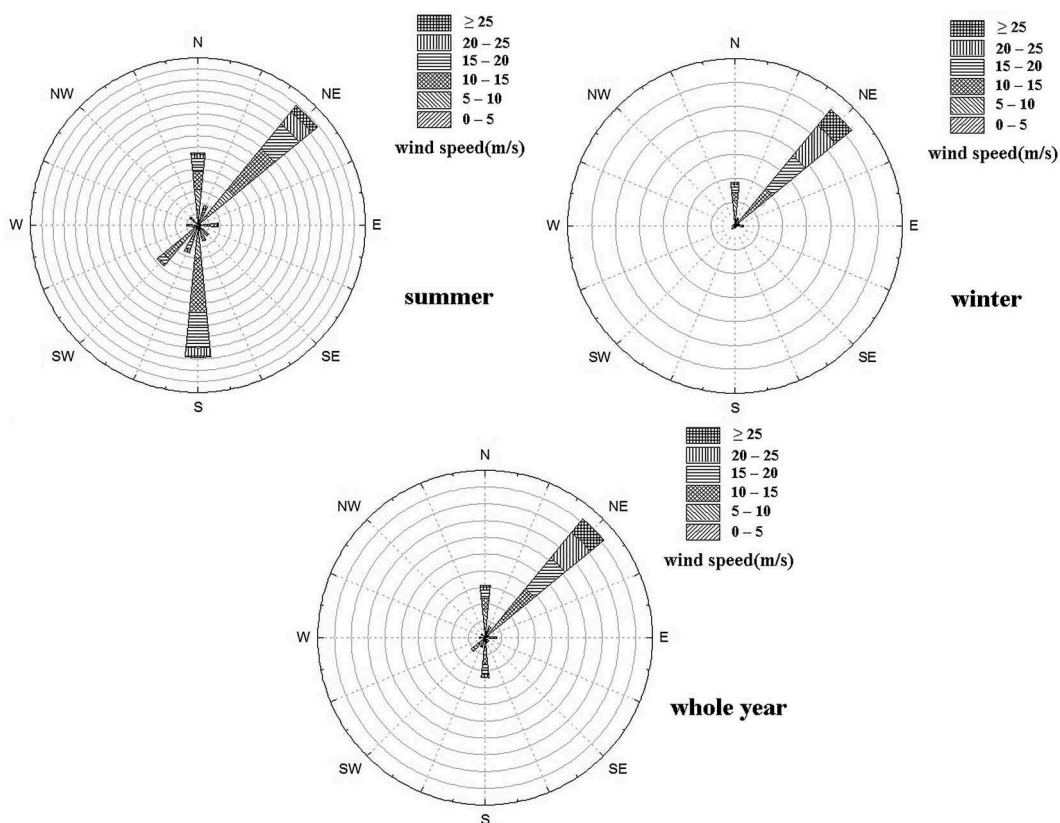
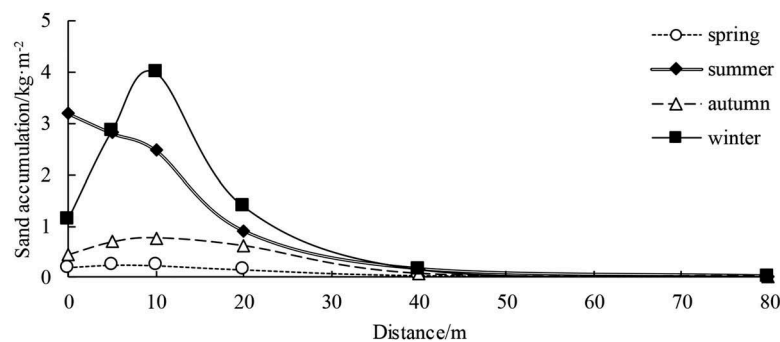
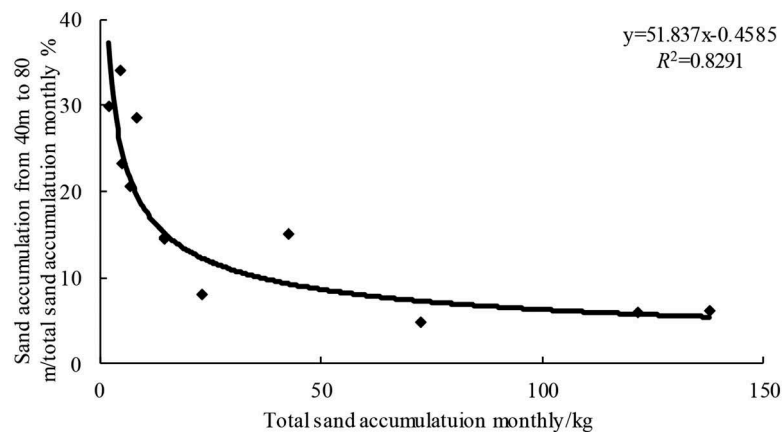


Figure 2. Annual average wind speed and wind direction at Huian.

Table 3. Seasonal dynamics of wind speed at various distances from the coast.

height from the ground (m)	Distance (m)	Spring	Summer	Autumn	Winter
0.5	0	1.80 ± 0.24 ^{aA}	1.07 ± 0.04 ^{aA}	1.80 ± 0.46 ^{aA}	3.72 ± 1.50 ^{aB}
	5	0.83 ± 0.10 ^{bC}	0.57 ± 0.23 ^{cC}	1.20 ± 0.26 ^{aB}	1.83 ± 0.24 ^{abA}
	10	0.50 ± 0.03 ^{bC}	0.23 ± 0.03 ^{cC}	0.63 ± 0.12 ^{bcB}	1.67 ± 0.23 ^{abA}
	20	0.10 ± 0.09 ^{dC}	0.06 ± 0.01 ^{dC}	0.50 ± 0.04 ^{bcB}	1.53 ± 0.26 ^{abA}
	40	0.01 ± 0.00 ^{dC}	0.02 ± 0.01 ^{dC}	0.35 ± 0.03 ^{bcB}	0.40 ± 0.10 ^{bA}
	80	0.00 ± 0.00 ^{dB}	0.00 ± 0.00 ^{dB}	0.00 ± 0.00 ^{cB}	0.30 ± 0.00 ^{cA}
1.5	0	3.39 ± 0.66 ^{aB}	2.38 ± 0.08 ^{aB}	5.33 ± 0.69 ^{aB}	6.30 ± 1.25 ^{aA}
	5	2.40 ± 0.10 ^{bB}	1.47 ± 0.32 ^{bC}	2.63 ± 0.63 ^{bAB}	3.34 ± 0.72 ^{bA}
	10	0.80 ± 0.06 ^{cC}	0.33 ± 0.07 ^{cC}	1.67 ± 0.36 ^{cB}	2.64 ± 0.30 ^{bA}
	20	0.20 ± 0.09 ^{dB}	0.09 ± 0.01 ^{cB}	1.13 ± 0.30 ^{cA}	1.20 ± 0.20 ^{cA}
	40	0.01 ± 0.00 ^{dB}	0.02 ± 0.01 ^{cB}	0.50 ± 0.09 ^{dA}	0.70 ± 0.30 ^{cA}
	80	0.00 ± 0.00 ^{dB}	0.00 ± 0.00 ^{cB}	0.17 ± 0.05 ^{dA}	0.30 ± 0.10 ^{cA}
2	0	5.64 ± 0.36 ^{aB}	3.83 ± 1.81 ^{aC}	6.38 ± 1.98 ^{aB}	9.37 ± 1.33 ^{aA}
	5	3.50 ± 0.10 ^{bB}	2.13 ± 0.17 ^{bC}	4.01 ± 0.67 ^{bB}	4.85 ± 0.74 ^{bA}
	10	0.90 ± 0.08 ^{cC}	0.47 ± 0.10 ^{cC}	2.50 ± 0.43 ^{cB}	4.42 ± 0.50 ^{cA}
	20	0.20 ± 0.09 ^{dB}	0.09 ± 0.01 ^{cB}	1.80 ± 0.35 ^{cA}	1.4 ± 0.20 ^{dA}
	40	0.01 ± 0.00 ^{dB}	0.02 ± 0.01 ^{cB}	0.57 ± 0.08 ^{dA}	0.80 ± 0.40 ^{dA}
	80	0.00 ± 0.00 ^{dC}	0.00 ± 0.00 ^{cC}	0.17 ± 0.03 ^{dB}	0.40 ± 0.10 ^{dA}

The data are the means ± standard derivation of 30 separate measurements. Different small letters within columns indicate significant difference ($p < 0.05$) at each height from the ground, different capital letters within rows indicate significant difference ($p < 0.05$).

**Figure 3.** Seasonal variation of total sand accumulation at various distances from the coast.**Figure 4.** Proportion of sand accumulation from 40 m to 80 m to total monthly sand accumulation.

Relationship between branchlet diameter and length with distance from the coast

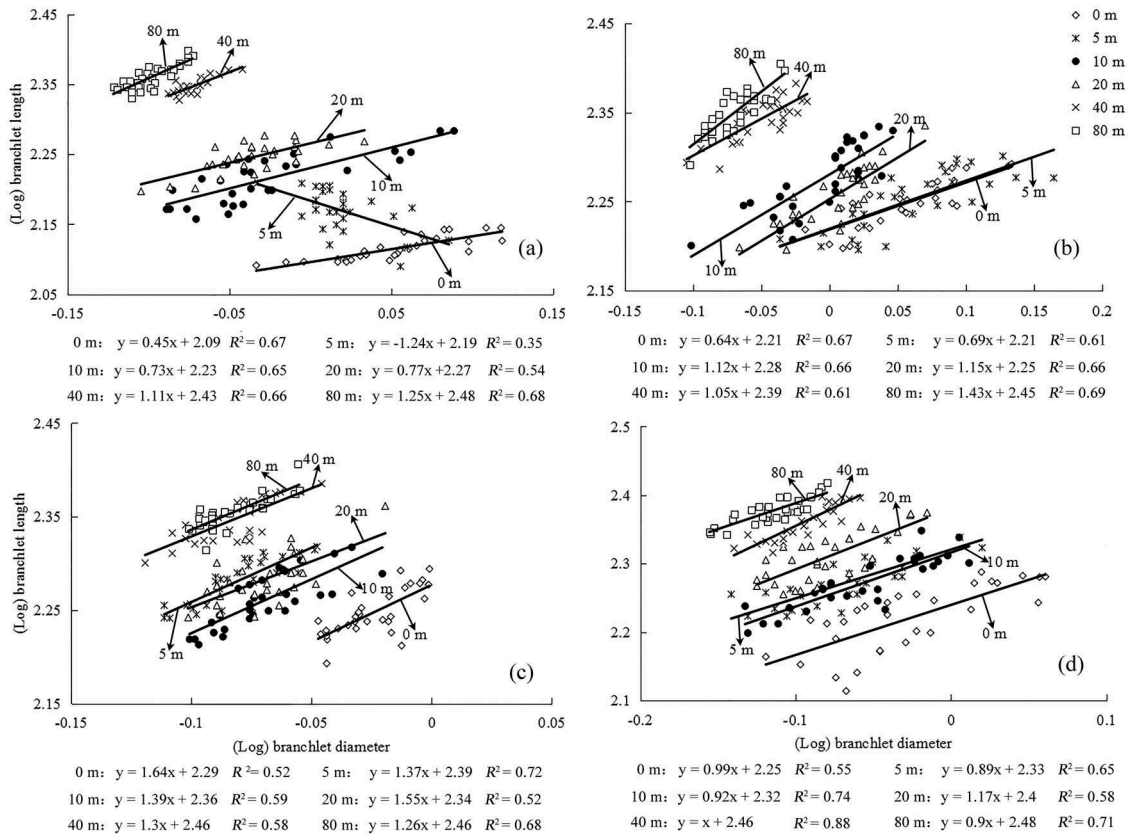
There was a positive correlation between branchlet diameter and branchlet length except at the 5-m site in spring. In spring (Figure 5(a)), the slope at 40 m was 1.11 with the 95% CI being 0.85–1.39 ($p = 0.36$), and at 80 m was 1.25 (95% CI: 0.92–1.55; $p = 0.1$). As there was no significant difference with a slope of 1.0 ($p > 0.05$), this indicates that there was a isokinetic trade-off relationship between branchlet diameter and branchlet length at 40 and 80 m. With increasing distance the slope increased gradually,

which meant that at farther distances there was a greater ratio of branchlet length and branchlet diameter in a limited branchlet length, except at 5 m. In summer (Figure 5(b)), there were three growth relationships evident. Among these, there was a significant difference in the slopes at 0 m (0.64; 95% CI: 0.52–0.8; $p = 0.01$) and 5 m (0.69; 95% CI: 0.54–0.88; $p = 0.01$) compared with the other distances. For these distances, the slopes were significantly different from 1.0 ($p < 0.05$), indicating that the rate of growth in the branchlet diameter was greater than that of the branchlet length. For 10, 20, and 40 m, the slopes were not significantly different from 1.0 ($p > 0.05$). The slope at 80 m was 1.43

Table 4. Seasonal changes in branchlet diameter, internode length, and branchlet length (mm) at various distances from the coast.

Branchlet characteristic	Distance (m)	Spring	Summer	Autumn	Winter
Diameter	0	1.13 ± 0.10 ^{aA}	1.14 ± 0.11 ^{aA}	0.95 ± 0.03 ^{aB}	0.94 ± 0.11 ^{aB}
	5	1.05 ± 0.06 ^{bB}	1.15 ± 0.13 ^{aA}	0.83 ± 0.03 ^{cdC}	0.86 ± 0.08 ^{bcC}
	10	0.95 ± 0.11 ^{cA}	0.99 ± 0.08 ^{bA}	0.85 ± 0.04 ^{bcB}	0.88 ± 0.08 ^{bb}
	20	0.92 ± 0.06 ^{cB}	1.02 ± 0.07 ^{bA}	0.86 ± 0.04 ^{bc}	0.83 ± 0.06 ^{bcC}
	40	0.85 ± 0.02 ^{dB}	0.89 ± 0.04 ^{cA}	0.82 ± 0.03 ^{dc}	0.81 ± 0.04 ^{cdC}
	80	0.80 ± 0.03 ^{dC}	0.85 ± 0.03 ^{cA}	0.83 ± 0.03 ^{cdB}	0.77 ± 0.04 ^{dD}
Internode length	0	6.97 ± 0.19 ^{cC}	7.57 ± 1.00 ^{bB}	8.35 ± 0.59 ^{aA}	8.14 ± 0.82 ^{aA}
	5	6.91 ± 0.31 ^{cB}	8.04 ± 0.86 ^{abA}	8.16 ± 0.44 ^{aA}	8.04 ± 0.57 ^{aA}
	10	7.08 ± 0.67 ^{bcB}	8.13 ± 0.88 ^{abA}	8.12 ± 0.56 ^{aA}	8.11 ± 0.49 ^{aA}
	20	7.31 ± 0.40 ^{bB}	8.15 ± 1.12 ^{abA}	8.22 ± 0.81 ^{aA}	8.25 ± 0.56 ^{aA}
	40	8.31 ± 0.35 ^{aA}	8.22 ± 0.88 ^{abA}	8.37 ± 0.43 ^{aA}	8.31 ± 0.71 ^{aA}
	80	8.25 ± 0.46 ^{aA}	8.39 ± 0.59 ^{aA}	8.28 ± 0.32 ^{aA}	8.35 ± 0.44 ^{aA}
Branchlet length	0	130.49 ± 5.11 ^{cC}	176.84 ± 10.65 ^{cA}	177.21 ± 10.16 ^{cA}	166.79 ± 18.28 ^{dB}
	5	148.11 ± 9.82 ^{dC}	178.88 ± 13.81 ^{cB}	190.89 ± 10.75 ^{bA}	187.49 ± 15.01 ^{cA}
	10	165.15 ± 13.81 ^{cB}	189.45 ± 16.60 ^{bcA}	182.60 ± 16.60 ^{cA}	188.08 ± 16.45 ^{cA}
	20	176.09 ± 8.63 ^{bc}	181.82 ± 13.76 ^{bc}	193.34 ± 13.80 ^{bB}	204.61 ± 17.03 ^{bA}
	40	222.94 ± 5.94 ^{aB}	220.34 ± 11.60 ^{aB}	222.13 ± 11.31 ^{aB}	230.46 ± 13.38 ^{aA}
	80	229.67 ± 9.29 ^{aB}	223.63 ± 13.06 ^{aC}	226.50 ± 9.23 ^{aBC}	238.23 ± 10.42 ^{aA}

The data are the means ± standard deviation of 30 separate measurements. Different small letters within columns indicate significant difference ($p < 0.05$), different capital letters within rows indicate significant difference ($p < 0.05$).

**Figure 5.** Relationship between branchlet length and diameter with increasing distance from the coast.

(95% CI: 1.14–1.91; $p = 0.01$), indicating that the rate of growth of the branchlet length was greater than that of the branchlet diameter. The slope gradually increased with increasing distance from the coast. In autumn (Figure 5(c)), with significant differences in slope found among all distances from the coast, except between 40 m and 80 m ($p < 0.05$). The slopes for correlations among sites were greater than and significantly different from 1.0 ($p < 0.05$). The slope gradually decreased with increasing distance from the coast. In winter (Figure 5(d)), the slopes for correlations at the various distances from the coast were not significantly different from 1.0 ($p > 0.05$), indicating an isokinetic trade-off relationship between branchlet diameter and branchlet length.

Relationship between internode length and branchlet length with distance from the coast

There was a positive correlation between the internode and branchlet lengths. In spring (Figure 6(a)), there were three growth relationships evident. Among these, there was a significant difference between the slopes at both 0 m (1.4; 95% CI: 1.1–1.78; $p = 0.01$) and 5 m (1.49; 95% CI: 1.14–1.93; $p = 0.01$) and the other sampling sites; the correlation slopes were significantly different from 1.0 ($p < 0.05$). For the 10 and 20 m sites, the slopes were 0.87 (95% CI: 0.7–1.1; $p = 0.24$) and 0.93 (95% CI: 0.74–1.17; $p = 0.52$), respectively. The slopes at 40 m (0.64; 95% CI: 0.51–0.8; $p = 0.01$) and 80 m (0.73; 95% CI: 0.57–0.93; $p = 0.01$). The slopes gradually decreased with increasing

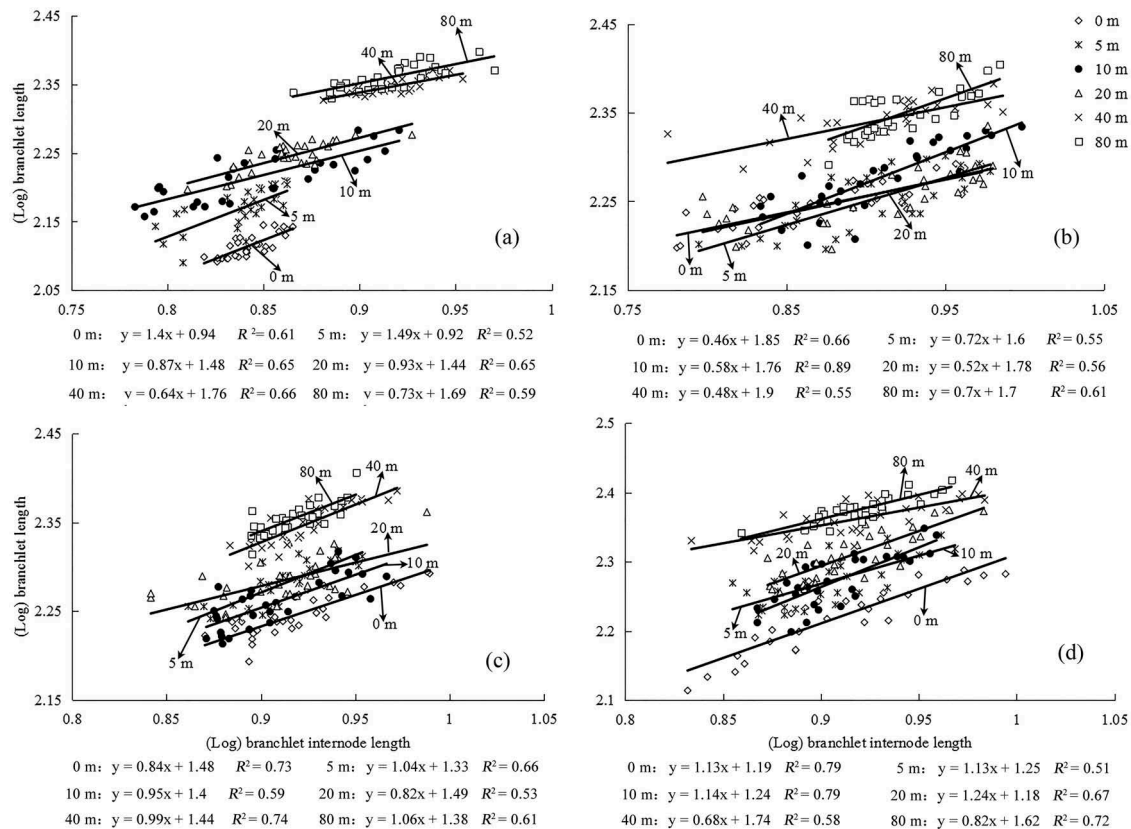


Figure 6. Relationship between branchlet length and internode length with distance from the coast.

distance from the coast. In summer (Figure 6(b)). The correlation slopes for the various distances from the coast were significantly different from 1.0 ($p < 0.05$). In autumn (Figure 6(c)), the correlation slope at 20 m from the coast was 0.82 (95% CI: 0.57–0.96; $p = 0.02$). Only at this distance was the slope significantly different from 1.0 ($p < 0.05$), indicating an isokinetic trade-off relationship between internode length and branchlet length at all distances except 20 m in winter (Figure 6(d)). In the distance range 0–20 m, the correlation slopes were not significantly different from 1.0 ($p > 0.05$). In the distance range 40–80 m, the correlation slopes were less than and significantly different from 1.0.

Discussion

Plants show adaptability and resistance to environmental changes and stresses, which are controlled genetically and by individual physiological and ecological conditions. In this study, it was found that in a coastal sandy environment the branchlet length, branchlet internode length, and branchlet diameter in *C. equisetifolia* changed significantly with season over distances of 0–20 m from the coast, and that branchlet morphology showed developmental plasticity at the individual level. These results indicate that *C. equisetifolia* has a marked potential for adaptation to coastal sandy environments (Vendramini 2002).

Wind-sand action is the main reason for the change in branchlet traits

A co-evolution and adaptation relationship is observed between plant functional traits and the environment (Hou

et al. 2014). The response reflects the distribution of branchlet biomass and the functional requirements in both biochemical and hydrological biology (Normand et al. 2008). With increasing distance from the coast, the internode length increased in spring and summer, the branchlet diameter decreased, and the branchlet length increased. The likely explanation for this finding is wind-sand action. The coastal study site is on the edge of southern China. In winter, the continental climate is influenced by the Siberian High, which brings cold conditions with strong dry cold northeasterly winds. Because of two underlying surfaces properties (thermodynamic and hydraulic characteristics), there is a horizontal temperature gradient near the coastal zone, resulting in the generation of a pressure gradient that increases the wind speed (Lin et al. 2006). Consequently, there is a rapid change in wind speed in the narrow coastal strip, where wind speed contours are approximately parallel to the coastline (Wu et al. 1995). However, the Fujian coastal area is located in the Taiwan Strait, and from October to March the wind speed is greatly increased by the topography of the “neck channel” (Peng 2010), which commonly causes strong winds to occur. The combination of strong and constant northeast winds, the presence of abundant beach sand, and the synchronous dry and windy seasons result in wind-sand action.

The physical damage from strong wind action and salt carried by the wind in these areas are important factors affecting the growth of *Casuarina*. Salt injury occurs when salt accumulates on the leaf surface and is absorbed by the branchlet (Turner and Kelly 1973). The swelling of *Casuarina* branchlets is caused mainly by NaCl and KCl from seawater (Qiu and Liang 1987). It has been reported that the content of chloride and sodium ions in diseased

branchlets in plants located 0–20 m from the coast affected by wind–sand action was twice that in healthy branchlets, and that the growth of *Casuarina* was influenced by Na^+ directly, resulting in the senescence and withering of branchlets (Catherine, 2010). In response to salt the branchlet epidermis thickness and the diameter of sponge tissue cells increase, and the palisade tissue cells enlarge to conserve water. When a large amount of salt accumulates on branchlets because of winds blowing from the sea, the stored water is used to dilute the absorbed salt to a level that is not toxic to the branchlets (Zhao 2002). However, branchlet transpiration increases because of strong winds, the length and thickness of branchlets is limited by water availability, the density and thickness of tissues increases, and the length decreases as an adaptation to drought conditions (Gratani and Bombelli 2000). Thicker branchlets help prevent excessive water loss, reduce moisture loss, and maintain nutrients (Lambrecht and Dawson 2007). Thus, in coastal front areas, shorter and thicker branchlets are an adaptation to the barren and arid environment, and provide greater resource utilization capacity for maintaining *in vivo* nutrition. (Wilson et al. 1999)

Farther landward from the coast, where the stress from blown sand is relatively low (Figure 4), thinner branchlets promote CO_2 and H_2O exchange, and longer branchlets affect the growth rate though their ability to transport more heat, CO_2 , and H_2O , which maximizes the benefits of photosynthesis (Solbrig et al. 1979). However, the lifespan of branchlets is affected by branchlet morphology, and can reflect the plant's ecological adaptability to stress factors including low temperature, low pressure, and low soil-nutrient levels, as well as herbivory and natural disasters (He et al. 2006). Sea winds cause terminal shoots to turn yellow, dry, and die. The production of new branchlets, increased loss of old branchlets, and a reduction in the size of branchlets are responses to adverse condition in coastal front areas. Farther inland the plants grow normally, the branchlet length is longer, and the time required to pay for the initial construction costs of the carbohydrates produced by their own photosynthetic production is longer (Kikuzawa 1991), the plant increased branchlet's lifespan to maintain the consumption of branchlet, it was conducive to nutrient preservation, carbon balance, and nutrient use efficiency (Iii 1980), so it promoted increased branchlet and internode lengths.

The seasonal changes identified in the present study are related to wind–sand action. In winter, the growth of branchlets in the coastal front area is limited by wind–sand action and water. The wind strength and sand accumulation in winter were the highest among the four seasons (Figures 2 and 3). Shorter and thicker branchlets contribute to survival under the harsh environmental conditions. However, the plant response to the environment was not immediate. There was a short time lag, and therefore the morphological changes in branchlets were most obvious in spring. After spring, the wind strength gradually declined and sand accumulation was least, meaning that light intensity and water were the main factors affecting the plasticity of morphological development. Because of the wind–sand action in winter, the vegetation was relatively sparse in the coastal front area, the light was more uniform, and the branchlets grew faster. Consequently, the branchlet length and internode length and diameter increased rapidly in summer, when increased light intensity resulted in accelerated growth. Summer is the main growth period for *Casuarina*. The average branchlet and internode length increased in autumn,

but the average diameter declined significantly. This was related to the rapid growth of new branches, which resulted in reduced average diameter. Some branchlets affected by severe salt injury were unable to photosynthesize effectively, and fell from the plant over time. After autumn the wind strength gradually increased, causing salt injury and water stress, and the average branchlet diameter increased as winter approached.

Ecological significance of variations in branchlet characteristics with distance from the coast

Changes in morphological and growth characteristics are important in plant adaptation to different environmental conditions and resource levels (Maherali and Delucia 2001). Variations in *Casuarina* branchlet characteristics reflect a trade-off in the size of individual branchlets as a by-product of energy exchange efficiency, driven by local environmental conditions. We found differences in branchlet characteristics at different distances from the coast. Beyond 40 m, the rate of growth in branchlet length was greater than that of branchlet diameter, and the rate of growth in internode length was greater than that in branchlet length, except in autumn. This indicates that thinner and longer branchlet internodes developed in this area. In the case of limited branchlet length, the branchlet characteristics in the coastal front area were inconstant with the alternation of seasons: the rate of growth in branchlet diameter was greater than that of branchlet length in spring and summer, whereas the rate of growth in branchlet length was greater than that of branchlet diameter in autumn. There was an isokinetic trade-off relationship between branchlet diameter and branchlet length in winter. For the relationship between branchlet and internode length, in spring the rate of growth in branchlet length was greater than that of the internode length at 0 and 5 m, there was a isokinetic trade-off in the relationship between the internode and branchlet lengths at the 10 and 20 m sites, the rate of increase in internode length was greater than that of branchlet length in summer, and there was an isokinetic trade-off relationship between the internode and branchlet lengths in autumn and winter. In the case of limited branchlet length, the branchlets in the coastal front area were thicker and had a shorter internode length in spring, thicker and longer internode length in summer, thinner and medium length internode length in autumn, and medium sized branchlets in winter. Possible explanations of these results are as follows:

- (1) Light is a key ecological factor that affects the survival and reproduction of plants, and light intensity can restrict photosynthesis and organic matter production (Li et al. 2014). The height and canopy density were higher in the landward area, the plants were more abundant, and there was greater shading. Consequently, photosynthetically active radiation levels were reduced, so to capture more light the branchlets in the landward area tended to be longer and thinner to increase the spatial distribution and reduce shading among branchlets, and so improve light interception efficiency (Brites and Valladares 2005; Pearcy et al. 2005); this is an ecological strategy to survive in low-light environments. As the canopy was low in the coastal front area, the competition for light was not as great as in the landward area, and the limited resources were used to enhance the ability to resist external stimulus.

- (2) Adequate water supply is important for plant growth. Growth in the coastal front area would be affected by a lack of water. Because of the high level of transpiration, the plants experience large water loss that strongly affects metabolism; this limits the division and growth of cells, and consequently growth is retarded. The development of thicker branchlets may help overcome water loss and provide for enhanced development of water transport systems. In cases of resource scarcity, such a practice is conducive to saving the cost of resource transportation, and avoiding the embolism in windy season (McCulloh and Sperry 2005). By reducing branchlet length at the beginning of spring through the formation of thicker and shorter internode length branchlets, the effects of sandstorms on plants in the coastal front area were greatly reduced in summer and autumn, which are the main growth seasons for *Casuarina*. Increased branchlet length and internode length enable more resource acquisition and enhance photosynthesis, so the thinner and longer internode length branchlets develop during summer and autumn in the coastal front area. In the landward area, water availability was less limited, and the water requirements of longer branchlets were met by the relatively adequate soil–water content. To ensure the availability of water, the internode joint was increased to have stronger water transportation ability, and the longer internode length branchlet was formed.
- (3) The investment allocation of branchlet support structure costs was different. Biomass allocation is an important factor driving net carbon acquisition for the whole plant (Korner 1991). In general, the plant growth rate is positively correlated to leaf biomass, and negatively correlated to the biomass of structural support tissues (Wright and Westoby 2001). Previous studies have proposed that mechanical support should scale positively with size to compensate for mechanical damage and gravity, and that larger leaves require proportionally greater investment in support and structure (Howland, 1962; Grubb, 1998). *Casuarina* is a special case because the branchlets are the main organs for photosynthesis (and are therefore central to the ability to acquire resources), but are also an important part of the entire branchlet support structure. In addition to its function in transporting water, the branchlets support the static gravity and resist external dynamic pull, so the branchlets need additional mechanical support. This affects the allometric relationship between internode and branchlet length, and because of the allocation of limited resources the growth in branchlet length is often sacrificed at the expense of branchlet diameter growth. Therefore, *Casuarina* adapts to unfavorable conditions by maximizing the efficiency of branchlets, using a strategy of balancing branchlet biomass allocation in response to the consumption and acquisition of energy. In the coastal front area the branchlets had a short lifespan, the competition between branchlets was low, and the growth rate was high. In the landward area the lifespan was longer, the competition between branchlets was greater, and the growth was slower because more nutrients were used to conserve branchlets. The longer branchlets are usually subjected to greater pull forces, increasing the need for the internode joints to have a

higher support capacity; the resulting investment in energy increased greatly with increasing branchlet size. The increased branchlet support cost is likely to be greater than the increased carbon acquisition capacity of the increased branchlet length. This probably explains the absence of changes in the landward branchlets.

Conclusion

We found that branchlet characteristics varied with distance from the coast. Compared with the coastal front area, the branchlets in plants in the landward area were usually longer, and the branchlet diameter was thinner. Where branch length was reduced, the branchlets in favorable environments had increased internode length and reduced diameter, while those in unfavorable environments had branchlets with reduced internode length and increased diameter. This enabled *Casuarina* to maximize photosynthetic carbon capture, to cope with the changing environmental influences. These results demonstrate the plasticity of functional traits as a plant mechanism to adapt to environmental variation. In this study, the changes in branchlet diameter, internode length, and branchlet length were analyzed only in relation to distance from the coast. The identified relationships may be affected by other factors, including terrain slope and genetic characteristics, thereby indicating the need for further experimental studies.

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