Structured and unstructured intraspecific propagule trait variation across environmental gradients in a widespread mangrove

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Abstract

Increasing studies have shown the importance of intraspecific trait variation (ITV) on the ecological process. However, the patterns and sources of ITV are still unclear, especially in the propagule of coastal vegetation. Here, we measured fresh weight (FW), fresh length (FL), maximum transverse diameter (TDmax), minimum transverse diameter (TDmin) and the ratio of TDmax to TDmin (RTD) of the hypocotyl (propagule) of Kandelia obovata for 66 genealogies across 26 sites. By combining multiple factors of climate, ocean and maternal tree to analyze their effects on the intraspecific trait variation of mangrove hypocotyl. The results showed that value of establishment traits (FW, FL, TDmax and TDmin which are related to mass) decreased along increasing latitudinal gradients and they were directly positively regulated by temperature. ITV of dispersal trait (RTD) was unstructured along latitudinal gradients, which was constrained by fitness tradeoff. Our findings indicate that establishment traits mainly varied between populations, whereas dispersal traits mainly varied between individuals. This study provides insights into the ITV of propagule in different functional dimensions on a broad scale and that may help integrate ITV into future analyses of mangrove protection.

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Running Head: Variation of mangrove propagule traits

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Abstract

Increasing studies have shown the importance of intraspecific trait variation (ITV) on the ecological process. However, the patterns and sources of ITV are still unclear, especially in the propagule of coastal vegetation. Here, we measured fresh weight (FW), fresh length (FL), maximum transverse diameter (TD_{max}), minimum transverse diameter (TD_{min}) and the ratio of $TD_{max}$to TD_{min} (RTD) of the hypocotyl (propagule) of*Kandelia obovata* for 66 genealogies across 26 sites. By combining multiple factors of climate, ocean and maternal tree to analyze their effects on the intraspecific trait variation of mangrove hypocotyl. The results showed that value of establishment traits (FW, FL, TD_{max} and TD_{min} which are related to mass) decreased along increasing latitudinal gradients and they were directly positively regulated by temperature. ITV of dispersal trait (RTD) was unstructured along latitudinal gradients, which was constrained by fitness tradeoff. Our findings indicate that establishment traits mainly varied between populations, whereas dispersal traits mainly varied between individuals. This study provides insights into the ITV of propagule in different functional dimensions on a broad scale and that may help integrate ITV into future analyses of mangrove protection.

Keywords

dispersal, intraspecific trait variation, *Kandelia obovate* , mangrove, propagule, tradeoff

1 Introduction

Despite being recognized as a foundation for the theory of evolution by natural selection, the importance of intraspecific trait variation (ITV) has been neglected over time in ecology (Bolnick et al., 2011). Recently, there has been a resurgence of ecological interest in ITV, stimulated by the proliferating studies that underline the tremendous effects of ITV on community assembly and ecosystem functioning (Violle et al., 2012; Cardou et al., 2022). However, the patterns and sources of ITV in themselves are still unclear (Cope et al., 2022). For example, ITV can be structured at various spatial scales in relation to different drivers. Between-population ITV tends to be shaped by large-scale environmental gradients, whereas within-population ITV is more likely the consequence of heritable differences and/or plastic responses to the local environment (Albert et al. 2010; Martin et al., 2017). Alternatively, ITV can be unstructured if the trait is mainly determined by stochastic processes or constrained by fitness tradeoffs (Kendall & Fox, 2003; Moran et al., 2016). Elucidating ITV distribution across multiple scales is yet crucial for understanding and predicting ecological responses to global changes (Cochrane et al., 2015; Moran et al., 2016).

Trait-based plant studies to date have largely focused on vegetative traits (e.g., leaf and root functional traits), with less attention placed on seed traits despite the significance of seed traits for plant regeneration and long-term persistence (Saatkamp et al., 2019). Knowledge of seed traits is particularly urgent for mangroves, which once covered over 200,000 km^2 of sheltered tropical and subtropical coastlines but nowadays has been disappearing worldwide for decades at an extremely high rate (Duke et al., 2007; Friess et al., 2019; Giri et al., 2015). Due to the property of low species richness and redundancy, mangrove degradation is always followed by pronounced losses of ecological multifunctionality (Arifanti et al., 2022; Donato et al., 2011; Feller et al., 2010). Such situation emphasizes mangrove recruitment and thereby calls for characterizing seed/propagule traits that represent key dimensions of the 'regeneration niche' (*sensu*Grubb, 1977) in mangroves (Feller et al., 2010; Peterson & Bell, 2012).

Many mangroves (e.g., Rhizophoraceae, Avicenniaceae) have evolved a special reproductive strategy of viviparous seeds (germinating precociously while attached to the maternal plant), probably reflecting an adaptation to the salty and flooding intertidal environments (Feller et al., 2010). Due to the lack of seed dormancy, mangrove forests destroyed by severe disturbances such as hurricanes and tsunamis may not have local seed reserves, necessitating recolonization through long-distance seed dispersal from relatively undisturbed populations (Nettel & Dodd, 2007). This is particularly the case for Rhizophoraceae forests, as Rhizophoraceae species lack the capacity of resprouting from damaged trees as Avicenniaceae species (Baldwin et al., 2001). Therefore, dispersal/retention is a key dimension of propagule functions where focal traits should be targeted for mangroves (Van der Stocken et al., 2019). Whether dispersed or retained, establishment is a prerequisite for any propagules to contribute to the regeneration, representing another critical dimension of seed trait (Krauss et al., 2008).

Most ITV studies in mangroves, though few in absolute number, have investigated propagule traits (e.g., size and weight) in relation to establishment, rarely considering the dispersal/retention dimension (Saenger & West, 2018; Yang et al., 2020; Zhu et al., 2021). These studies showed that temperature and/or precipitation may have given rise to structured ITV in mangroves across geographical gradients (Saenger & West, 2018; Yang et al., 2020; Zhu et al., 2021), a pattern commonly reported in terrestrial forests (Kumordzi et al., 2019). Nevertheless, as mangroves are coastal vegetation, their trait variation may also be shaped by oceanic factors including salinity and tidal currents (Richards et al., 2021; Sousa et al., 2007). Additionally, maternal plants can also affect propagule traits, both through genetically fixed differences and environmentally induced transgenerational plasticity (Alam et al., 2018; Cochrane et al., 2015). However, the relative importance of these abiotic and biotic factors in shaping the distribution of ITV across multiple scales, and whether the patterns differ between the propagule function dimensions (establishment vs. dispersal/retention) are still poorly understood.

Here we use *Kandelia obovata* as the model species to investigate the issues. *Kandelia obovata* (Rhizophoraceae) is the most cold-tolerant true-mangrove species and has a wide latitudinal distribution along the southeast coast of China (Sheue et al., 2003; Wang et al., 2011), providing an ideal system for studying the ITV of mangroves. Using a stratified sampling design across a 9° latitudinal gradient, we analyzed the structure of intraspecific variability for five hypocotyl functional traits in relation to propagule dispersal/retention and establishment. The stratified sampling design and contrasting environmental conditions allowed us to address the following questions: (i) How is ITV structured spatially (between populations, maternal trees, hypocotyls)? (ii) What is the major driver (climatic, oceanic, or maternal factors) shaping the distribution of ITV? Based on the results from previous studies (Saenger & West, 2018; Zhu et al., 2021), the variability of traits on the establishment axis is expected to be higher between populations than within populations and predominantly shaped by abiotic factors. By contrast, the trait on the dispersal/retention axis, likely more reflecting a tradeoff between post-disturbance recolonization and local recruitment (Sousa et al., 2007; Van der Stocken et al., 2019), may be less structured or even unstructured with regard to particular environmental gradients.

2 Materials and methods

2.1 Species, study sites and sample collection

Kandelia obovata was first reported by Sheue, Liu, & Yong (2003), which was mainly different from the relative species *K. candel* (L.) Druce in leaf shape and cold tolerance. The two species are well-differentiated sets of geographical populations separated by the South China Sea. In China, *K. obovata* ranges from Hainan, Guangxi, Guangdong, Fujian, Zhejiang and Taiwan. Mature hypocotyls of*K. obovata* were collected during 2020–2021 from 26 sites along the coastline of southern China, spanning from 19°37'N to 28deg41'N in latitude and from 108deg05'E to 121deg24'E in longitude (Fig. 1A). This geographic range provides wide climatic gradients in annual average precipitation (1102–2373 mm, mean 1578 mm), annual mean temperature (14.7–24.7 , mean 21.1), and surface seawater salinity (13mean 21.8Supplementary Material Table S1. We sampled 1–6 maternal trees from each site (66 trees in total), depending on the population size. To ensure genetic independence, the sampled trees were spaced at least 30 m apart according to Geng et al. (2008). Each maternal tree was thus considered as a single genealogy. We randomly collected 30 hypocotyls from each tree for the study.

2.2 Trait measurement forhypocotyls and maternal trees

We measured traits including fresh weight, fresh length, maximum transverse diameter, and minimum transverse diameter for each hypocotyl (Fig. 1B). We also calculated the shape index of hypocotyl as the ratio of maximum transverse diameter to the minimum (RTD). This index describes the position of barycenter, and is thus a crucial parameter determining the balance between propagule stranding (retention) and buoyancy (dispersal) (Figs. 1B, 1C; Van der Stocken et al., 2019a). We measured height (H) and diameter at breast height (DBH) for maternal trees, and transformed them into aboveground biomass (AGB) using an allometric model of tropical wood tree: AGB = 0.0673 x ($\rho \times \mathrm{DBH}^2 \times \mathrm{H})^{0.976}$ (Chave et al., 2014), where wood density ρ is set as 0.57 g/cm^3 (Jiang, 2021). The aboveground biomass is a comprehensive outcome of the interaction between the genotype and the environment experienced by maternal trees, thereby capturing multiple facets of how maternal trees can affect the progeny. We thus used AGB as a synthesis indicator to predict potential effects of maternal performance on hypocotyl traits.

2.3 Access of climate and tide data

We extracted the data of each site from the WorldClim dataset (Hijmans et al., 2005) for mean annual temperature (MAT) and mean annual precipitation (MAP), and from Global Tidal Forecasting Service (http://global-tide.nmdis.org.cn/) for tide and tidal currents datasets. Specifically, the highest tide, the lowest tide, the fastest tidal current and the slowest tidal current were obtained from the nearest tide station. Since the annual average of the tide data is not available, we used the data of four months (January, April, July and October) to represent the whole year. We calculated the annual highest tide (AHT), annual lowest tide (ALT), annual fastest tide current (AFC) and annual slowest tide current (ASC). We also measured sea surface salinity (SAL) at each site using the Portable Refractometer (Apu, China).

2.4 Data analysis

Bivariate analysis with ordinary least-squares linear regression (OLR) and quadratic regression (QR) were used to quantify how hypocotyl trait values varied with latitudinal gradients and biotic/abiotic factors. Because of high correlations among most hypocotyl traits ($r > 0.36$, $P < 0.001$), we performed a principal component analysis (PCA) with multiple traits using the 'princomp' function in R 4.1.3 (R Core Team 2022), and used the two first PC axes to represent the hypocotyl traits.

To evaluate how environmental factors, maternal plants or inherent factors explained variation in hypocotyl traits, we used a nested analysis of variance (ANOVA) coupled with variance partitioning techniques (Martin et al., 2017). We carried out linear mixed model (LMM) for PC1 and RTD by using the 'lme' function in 'nlme' R package (Pinheiro, Bates, & R Core Team, 2022). In each model, all nested levels (i.e. site > genealogy > within [individual]) were entered as sequential random effects and the intercept was the only estimated fixed effect. We then used the 'varcomp' function in the 'ape' R package (Paradis et al., 2004) to calculate the variance components associated with each nested level.

To quantify how hypocotyl traits were affected by climatic factors, oceanic factors, and maternal performance, we implemented LMMs using the 'lme' function in the R package 'nlme'. The fixed-effect terms included the climatic, oceanic and maternal variables. To account for additional variation potentially caused by some missing site-specific effects (e.g., other environmental factors), and that caused by other maternal effects uncaptured by aboveground biomass, we treated sampling site and tree genealogy as random factors. All variables were standardised before the modelling, such that each variable had a mean of zero and a standard deviation of one. To reduce the adverse influence of multicollinearity, we removed multicollinear variables until the variance inflation factors (VIFs) of all variables in the model were less than three (Ouyang et al., 2019). Both primary and quadratic mixed models were considered, and only the better fitted model was showed (based on the Akike information criteria). We calculated the VIF using the R package 'car' (Fox & Monette, 2019). The pseudo-R^2 was calculated using the function 'r.squaredGLMM' in the R package 'MuMIn' (Bartoń, 2022), to represent the variance explained by the fixed effect in the LMM. The effect sizes of fixed factors were measured by the regression coefficients in the LMM.

Structural equation modelling (SEM) was used to disentangle direct and indirect effects of all predictive factors on hypocotyl traits. After standardising all variables, multicollinear variables were removed based on

VIF. We first considered a full model that included all variables and all reasonable pathways. Non-significant pathways were then sequentially removed, unless the pathways were biologically informative. The removing and adding of pathways were repeated until both$\mathit{\Pi}_{\chi\ \text{2-test}}$ [?] 0.05 (that is, no significant difference between model predictions and the observed data) and root mean square error of approximation (RMSE) < 0.08 were reached (Wu et al., 2022). The SEM was performed using the 'lavaan' R package (Rosseel, 2012).

3 Results

3.1 Patterns of ITV in hypocotyl along latitudinal gradients

The first two PC axes (associated eigenvalues > 1) accounted for 83.6% of the total variation among all these traits, where the first axis (PC1) mainly reflected hypocotyl mass and size, and the second axis was primarily determined by the shape index (RTD; Fig. 2). PC1 (fresh weight, fresh length, maximum transverse diameter, and minimum transverse diameter) decreased significantly with increasing latitudinal gradients ($R^2 = 0.42$, $P < 0.001$). In addition, quadratic regression had a better explanation for their relationship ($R^2 = 0.53$, $P < 0.001$; Fig. 3A). Intriguingly, RTD did not show any significant correlation with latitude ($P > 0.05$; Fig. 3B).

3.2 Sources of ITV in hypocotyl

Variance partitioning showed that site was mainly contributed to variation of PC1 (63.75%; Fig. 4A), while variation of RTD was mainly explained neither by site nor genealogy (69.03% in individual; Fig. 4E).

The linear-mixed model indicated that the predictor variables explained 58% the variation in PC1 (quadratic mixed model). Specifically, MAT^2 had the strongest negative effect on PC1 (effect size = -0.55 ± 0.12 s. e., $P < 0.001$), while MAT had a significant positive effect on PC1 (0.38 ± 0.16, $P < 0.001$). SAL had a significant negative effect on PC1 (-0.21 +- 0.09,$P < 0.05$; Fig. 4B). Bivariate relationships between MAT and PC1 (OLR: $R^2 = 0.42$; QR:$R^2 = 0.54$) were much stronger than SAL and PC1 ($R^2 = 0.01$; Figs. 4C, 4D). In contrast, all these predictive factors together explained only 12% of the variation in the shape index, though significant effects of MAP (-0.30 +- 0.07) and AGB (-0.15 +- 0.07) were indicated by the model (Figs. 4F). Bivariate analysis also showed that MAP and AGB had significant relation with RTD, but the models had low explanation ($R^2 = 0.06$ and$R^2 = 0.02$, respectively; Figs. 4G, 4H).

3.3 Direct and indirect effects on hypocotyl traits

We further used SEM to disentangle the direct and indirect effects of climatic, oceanic, and maternal factors on hypocotyl traits. MAT played the strongest role in directly shaping PC1 (standardized path coefficients, β = 0.75). SAL (-0.22) was the main oceanic factors that directly negatively affected PC1. Tide effects (ALT and AFC) were much weaker than MAT. MAP had no direct effect and AGB had a weak effect on PC1 (Figs. 5A, 5B). All the factors had a weak direct effect on RTD (|β| < 0.15), except for MAP (-0.31). Compared with the effect of climatic factors on PC1, effect of climatic factors was much smaller on RTD (Figs. 5C, 5D). Overall, these variables can explain 64% and 88% of the variations in PC1 and RTD, respectively.

4 Discussion

Increasing studies have showed the importance of ITV on the ecological process. However, the patterns and sources of ITV in themselves are still unclear (Cope et al., 2022). There are large ITVs in mangroves due to the complex environment but are less concerned on propagule which can determine the recruitment or/and distribution (Feller et al., 2010; Petersan & Bell, 2012). It is urgent to study the ITV of mangrove propagule at the background of global changes. We analyzed the relationship between biotic and abiotic factors and hypocotyl traits on a large scale for a typical viviparous mangrove species. We found that PC1 (FW, FL, TD_{max} and TD_{min}) was on the establishment dimension, and ITV of PC1 was mainly structured between populations which was directly shaped by climate. While RTD was mainly structured between hypocotyls, which was constrained by fitness tradeoff between dispersal and retention. Our study provides insights to the ITV mechanism of hypocotyl traits in mangrove plants.

4.1 Structured traits variation of mangrove hypocotyl

Pervious study showed that ITV in propagule size has been observed, especially in the genera *Rhizophora* , *Bruguiera* ,*Kandeli* and *Ceriops* (Tomlinson, 2016). Our results showed that variation of PC1 was significantly negatively correlated with latitude, similar to the results of a previous study (Yang et al., 2020). But there was an inverse relationship in a black mangrove study. The propagule of *Aegiceras corniculatum* was smallest in the northern (low latitude) population, while the largest propagule was in the southern population in Australian (Saenger & West, 2018). The opposite pattern of structured ITV was possibly due to the different strategies for improving fitness between true viviparous and crypto viviparous mangrove species. Moreover, the genetic analysis also suggested that differences evident in populations of *A. corniculatum* at the extremes of its range, are explained as evolutionary adaptations in response to the local physical, climatic or biological characteristics (Maguire et al., 2000). Therefore, ITV of PC1 sources from the local biotic and abiotic factors at different sites.

We found that climate (especially temperature) was the main driver of intra-specific variation in PC1. In general, temperature and precipitation have a negative relation with latitude (Hijmans et al., 2005), while oceanic factors such as salinity and tides have little to do with latitude. Obviously, higher temperature means that more materials can be accumulated in hypocotyl. MAP had little effect on PC1, probably because mangrove plants have adapted to tidal environments and are able to obtain fresh water from seawater (Parida & Jha, 2010).

Although oceanic factors were not found to be the main factors affecting the variation of hypocotyl traits, salinity did have a significant effect on PC1 variation. Salinity has long been considered an important factor limiting the growth and distribution of mangroves (Chen & Ye, 2014; Richards et al., 2021), and study also found that length and weight of propagules of mangrove was negatively correlated with the salinity (Alam et al., 2018). In addition, salt-stress is also a factor in the evolution of vivipary in mangrove plants. The hypocotyl of viviparous seeds contains a large amount of nutrients and water, which are needed for the growth of newly colonized seedlings, thus avoiding the vulnerable life stage (Joshi, 1933; Zhou et al., 2016), that also can keep its vitality even floating in the sea for server months. When salinity is too high, maternal tree will invest more energy to against with salt stress (Alam et al., 2018; Parida et al., 2004), which may reduce the investment on the hypocotyl and eventually lead to variation in its traits. Tide is an important factor to mangrove growth and hypocotyl dispersal process (Clarke et al., 2001; Duke et al., 1998; Van der Stocken et al., 2015; Zhang et al., 2021), however, the effect of tides on the variation of hypocotyl traits was marginal in our study. The possible reason is that previous studies have only considered the influence of tidal effects, rather than the combination of multi biotic and abiotic effects. When count on the climate, the effect of tides may be marginal. In addition, we suggest that PC1 is the variability of traits on the establishment axis (Saatkamp et al., 2019; Moles & Westoby, 2004), which is greatly affected by resource-based factors (such as temperature and nutrients *etc.*), while tides may not be an important factor affecting hypocotyl mass.

4.2 Unstructured traits variation of mangrove hypocotyl

We noted that the shape index RTD did not vary with latitude, and it was also less affected by abiotic and biotic factors. There are three possible reasons for ITV of RTD was structured between individuals (hypocotyls): 1) those traits may be constrained by limited genetic variation (Bradshaw 1991). Studies have shown that the genetic diversity of mangrove populations is low (Richards et al., 2021; Ruan et al., 2013) and the complex matrix also limits gene flow between mangrove populations (De Ryck et al., 2012; Van der Stocken et al., 2015); 2) traits are related to plant fitness tradeoffs. Such as costs induce tradeoff, they give rise to covariation between dispersal and other life-history traits at different scales of organismal organization (Bonte et al., 2012). Dispersal event through investments in special morphologies, are facing the risk and opportunity for transfer and settlement; 3) low ITV may also be caused by very sharp contrasts in conditions in space and time (Holt & Gomulkiewicz, 2004), which induce the plant stress. This is exactly what happens in coastal ecosystems where mangroves grow. Plants evolving in stressful environments have less plasticity in making use of resources upon their increased availability (Quadros et al., 2021). However, even the low genetic diversity and stressful environments, there were still large ITV of mangroves (Tomlinson, 2016), or such as the ITV of PC1. Consequently, RTD was related to plant fitness tradeoffs.

Specifically, we inferred that RTD was correlated with dispersal/retention tradeoff, because the center of gravity was important to determine the position relative to the water surface while floating (Van der Stocken et al., 2019; Figs. 1B, 1C). Although dispersal can avoid competition with conspecific species, it also faces the risk of colonization or/and establishment in an unfavorable environment. On the contrary, retention means colonizing in a similar environment to the parent tree, but cannot avoid the between conspecific species and natural enemies (Stump & Comita, 2020). Not all mangrove species recolonize proportionately with the previous generation at the same site (Kamruzzaman et al., 2017). Therefore, mangroves may regulate the RTD to determine more dispersal or retention.*K. obovata* is the most widely distributed species of mangrove (Sheue et al., 2003; Wang et al., 2011), the RTD of *K. obovata* may be relatively small which is facilitated to dispersal. While other Rhizophoraceae spp., like*Bruguiera sexangular* , *B. gymnorrhiza* , *Rhizophora stylosa etc.* are thermophilic species (Wu et al., 2018), the RTD of those species may relatively large which can ensure the settlement/establishment of offspring (propagule) in a suitable place. Based on that strategy of tradeoff, mangroves can maintain a high-level fitness.

Many studies have emphasized the importance of maternal effects in the variation of offspring traits (Alam et al., 2018; Cochrane et al., 2015; Galloway, 2005), but the strength of maternal effect on ITV was minor in this study. As we only recorded the height and DBH of maternal plants, which reflecting the size and age, that may have less to do with morphology than with yield (Hangelbroek & Santamaria, 2004). Rather, heredity may be the major contributor to maternal effects. In general, genetic diversity is low in the natural mangrove population (Hodel et al., 2018; Richards et al., 2021), but researchers discovered that high epigenetic diversity can maintain the high plasticity of traits in mangrove (Mounger et al., 2021). That was possibly why the ITV of RTD was mainly contributed from within individuals. Due to the lack of dormant seed periods, true mangrove species do not have seed banks and are difficult to regenerate after anthropogenic disturbances or natural disasters (Nettel & Dodd, 2007). Therefore, the collection of germplasm resources and artificial cultivation of true-viviparous mangrove species are particularly important, especially under global climate change. Study showed that *K. obovata* had higher regenerative capacity than other viviparous species (Zhang et al., 2021), because *K. obovata* had higher dispersal capacity. We recommend that the RTD of hypocotyl should be considered in germplasm collection and restoration, thus conducive to the regeneration of the population. More studies should be combined those biotic and abiotic factors to help us to have a comprehensive understanding of the trait variation of mangroves and to better protect the mangroves.

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Supplementary Material

Field sites data details are reported in Supplementary Material Table S1.

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Figure Legends

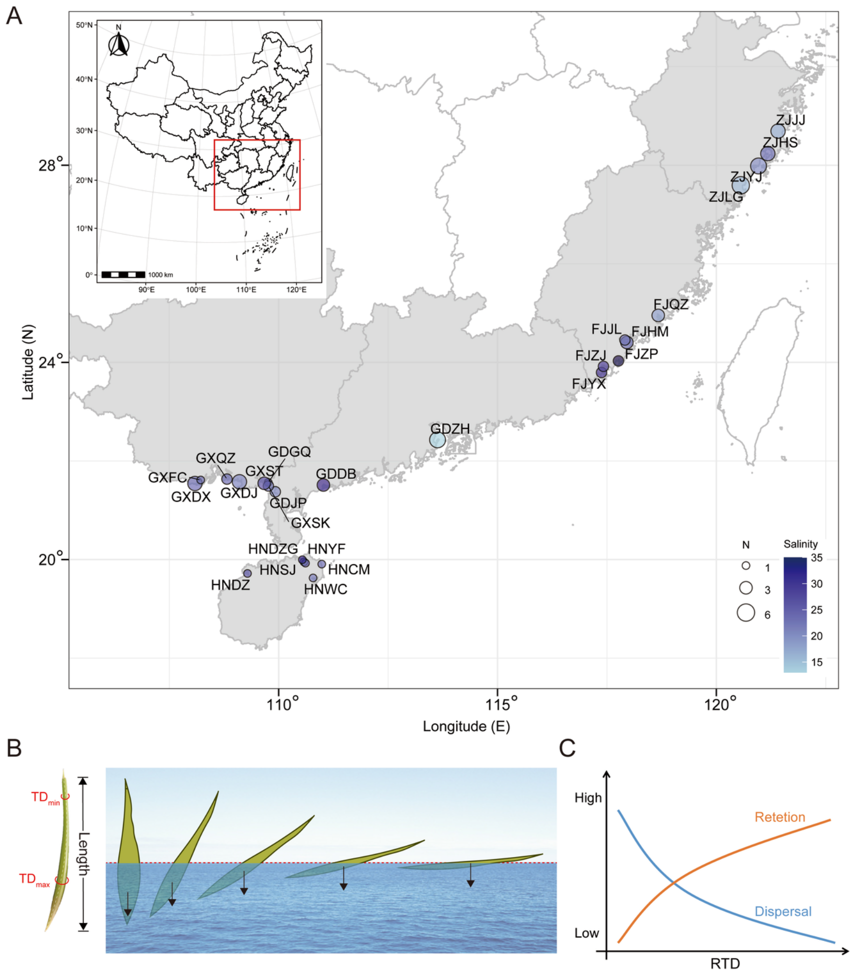
Fig. 1. Distribution of sampling sites and hypothesis of hypocotyl dispersal status. **A,** Sampling sites of *Kandelia obovata* hypocotyl on the south coast of China. The color gradient indicates the salinity (proportional to genealogies size (N). See Table S1 for a detailed description of field sites. **B,** Determination of hypocotyl traits: length, maximum transverse diameter (TD_{max}) and minimum transverse diameter (TD_{min}). **C,** The hypothesis of different ratio of TD_{max} to TD_{min} (RTD) of hypocotyl have different positions relative to the water surface while floating and illustration of the linkage of RTD and tradeoff between dispersal and retention.

Fig. 2. Principal component analysis (PCA) of hypocotyl traits. FW, fresh weight; FL, fresh length; TD_{max}, maximum transverse diameter; TD_{min}, minimum transverse diameter; RTD, ratio of TD_{max} to TD_{min}.

Fig. 3. Patterns of hypocotyl intraspecies traits variations (ITV) along latitudinal gradients.**A,** Relationship between PC1 and latitude. **B,** Relationship between RTD and latitude. Bule line is ordinary least-squares linear regression (OLR), and red line is quadratic regression (QR). Solid line indicates statistical significance ($P < 0.05$), dashed line indicates statistical non-significance ($P> 0.05$). Filled area means SE. PC1, the first principal component. RTD, ratio of TD_{max} to TD_{min}.

Fig. 4. Sources of hypocotyl intraspecies traits variations (ITV). **A, E,** Variance partitioning of PC1 and RTD across three nested levels of organization.**B, F,** Summary of the linear mixed-effect modeling for multiple biotic and abiotic factors on PC1 and RTD. Data are presented as coefficients +- standard errors of the estimated effect sizes.R^2m represents marginalR^2, R^2c represents conditional R^2. *, $P < 0.05$; ***, $P < 0.001$. **C, D, G, H,** The relationships between significant biotic and abiotic factors and PC1 and RTD. Bule line is ordinary least-squares linear regression (OLR), and red line is quadratic regression (QR). Filled area means SE. SAL, sea surface salinity; MAT, mean annual temperature; MAP, mean annual precipitation; AFC, annual fastest tide current; ALT, annual lowest tide; AGB, aboveground biomass. PC1, the first principal component. RTD, ratio of TD_{max} to TD_{min}.

Fig. 5. Direct and indirect effects of biotic and abiotic factors on hypocotyl intraspecies traits variations (ITV). **A, C,** Structural equation models (SEMs) showing the relationships among biotic, abiotic factors and PC1 and RTD.**B, D,** Standardized effects derived from SEMs of PC1 and RTD. Red and black arrows indicate positive and negative relationships, respectively. Solid or dashed lines indicate significant ($P< 0.05$) or non-significant relationships. Numbers near the pathway arrow indicate the standard path coefficients.R^2 represents the proportion of variance explained. The relevant indicators are abbreviated as: PC1, the first principal component; RTD, ratio of TD_{max} to TD_{min}; AGB, aboveground biomass; SAL, sea surface salinity; AFC, annual fastest tide current; ALT, annual lowest tide; MAT, mean annual temperature; MAP, mean annual precipitation.



A
ZJJJ
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FJQZ
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GXQZ
GDGQ
GXFC
GXST
GDDB
GXDX
GXDJ
GDJP
GXSK
HNDZG
HNYF
HNSJ
HNCM
HNDZ
HNWC
N
1
3
6
Salinity
35
30
25
20
15
28°
24°
20°
Latitude (N)
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B
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Retetion
Dispersal
RTD

Figure 1

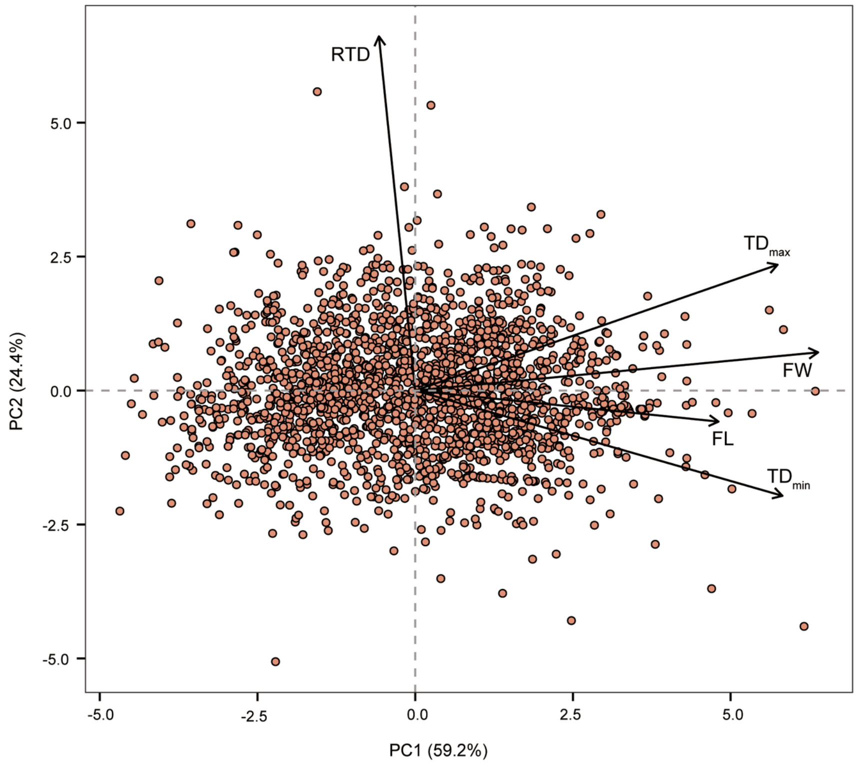


Figure 2

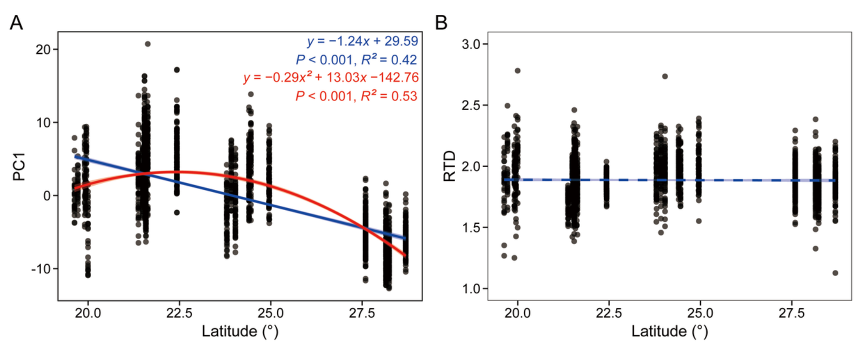
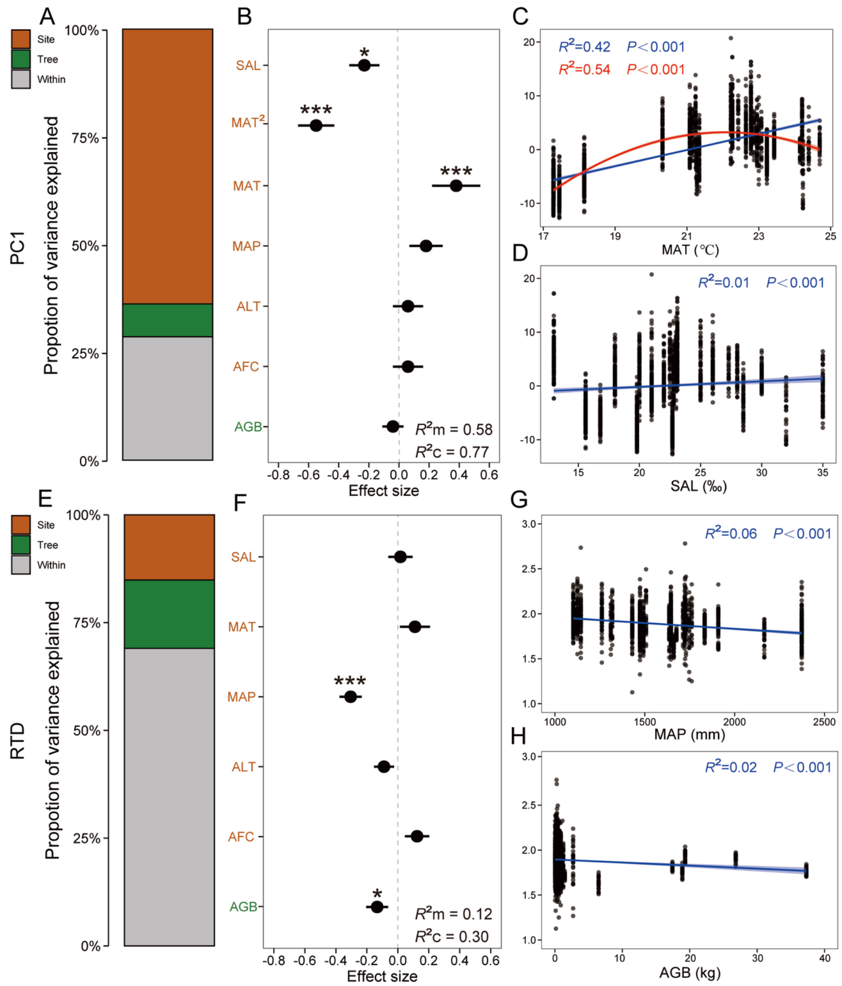
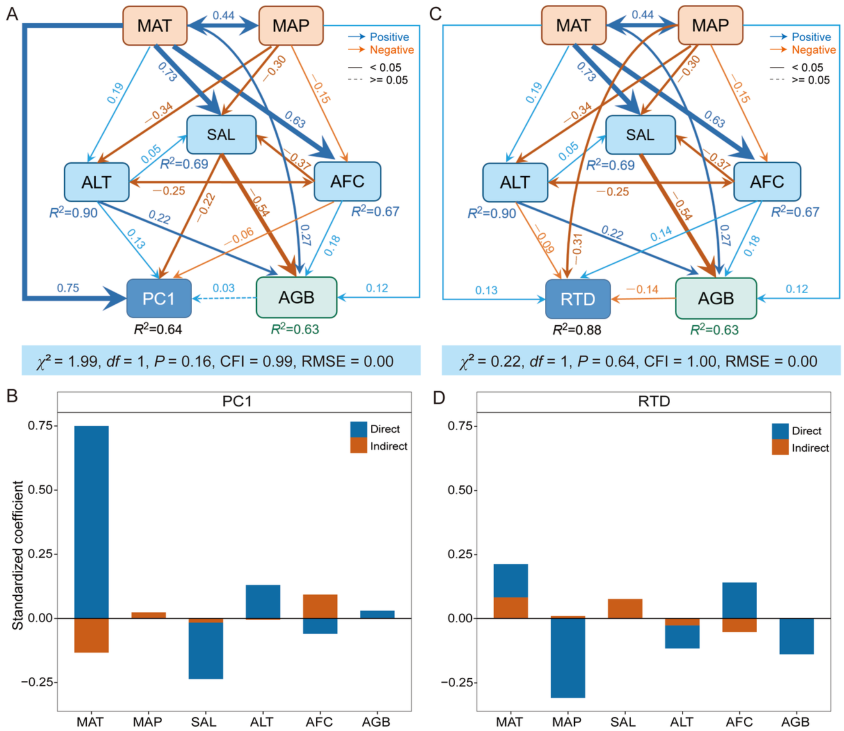


Figure 3



A
B
C
D
E
F
G
H
Site
Tree
Within
PC1
RTD
Propotion of variance explained
100%
75%
50%
25%
0%
SAL
MAT²
MAT
MAP
ALT
AFC
AGB
R^2m = 0.58
R^2c = 0.77
R^2m = 0.12
R^2c = 0.30
Effect size
R^2=0.42 P<0.001
R^2=0.54 P<0.001
MAT (℃)
R^2=0.01 P<0.001
SAL (‰)
R^2=0.06 P<0.001
MAP (mm)
R^2=0.02 P<0.001
AGB (kg)

Figure 4



A
MAT
MAP
0.44
Positive
Negative
< 0.05
>= 0.05
SAL
ALT
AFC
PC1
AGB
R^2=0.69
R^2=0.90
R^2=0.67
R^2=0.64
R^2=0.63
χ^2 = 1.99, df = 1, P = 0.16, CFI = 0.99, RMSE = 0.00
C
RTD
R^2=0.88
χ^2 = 0.22, df = 1, P = 0.64, CFI = 1.00, RMSE = 0.00
B
D
Standardized coefficient
Direct
Indirect

Figure 5