

Coordination of leaf, stem and root traits in determining seedling mortality in a subtropical forest



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ABSTRACT

Plant traits from different organs are thought to be coordinated to achieve main vital functions. However, evidence on how the coordination of traits affect plant vital rates (e.g. mortality rates) is rare due to the poor representation of root traits, which play important roles in water and soil nutrients uptake. In this study, we collected plant traits from 13,733 seedlings of 57 species across 10-year monitoring in a subtropical forest in Southern China, asking whether traits from root and aboveground organs are coordinated, and whether they have consistent effects on seedling mortality (e.g. all fast resource-acquisitive traits reduce mortality). We performed phylogenetic principal component analysis (PPCA) to test trait coordination and used generalized linear mixed models (GLMMs) to examine trait-mortality relationships. We found that some of the root and aboveground traits were highly correlated. PPCA of traits separated species to the strategy of resource acquisition or conservation, supporting the plant economics spectrum. Traits from root, stem and leaf showed coordinated effects on seedling mortality, in which species with conservative traits tended to have lower mortality rates than species with acquisitive traits. Root traits, such as root nitrogen content, tissue density and specific root length significantly related to seedling mortality. We concluded that traits from different organs were coordinated describing an acquisitive-conservative continuum of strategies and have consistent effects on seedling mortality, providing the first evidence for the plant economics spectrum and for the root trait-mortality relationships in subtropical seedling communities. Our results emphasized that besides aboveground traits, key root traits significantly impact seedling mortality. Integrating root traits is necessary to gain further understanding in the relationships between plant performance and traits.

1. Introduction

Understanding the link between vital rates and plant functional traits is one of the key goals in community ecology and essential for predicting forest dynamics and community structure (HilleRisLambers et al., 2012; Paine et al., 2015; Record et al., 2016). However, despite the increasing number of studies examining the trait-performance relationship, most of the previous researches focused on commonly measured aboveground traits, such as leaf and stem traits (Iida et al., 2014, 2012; Paine et al., 2015; Poorter et al., 2008; Visser et al., 2016; Wright et al., 2010), while often ignoring belowground traits. Thus, how root traits correlate with vital rates is largely unknown, especially for tropical and subtropical regions. Roots are the most important organs responsible for soil water and nutrient acquisition (Fort et al.,

2014; Kong et al., 2014), and may play important roles in determining vital rates of plant individuals, yet the number of studies including root traits have been relatively scarce. It is expected that root traits may be coordinated with traits of other organs (e.g., leaf and stem) in a single or multiple dimension(s). The coordination of traits from multiple organs can produce complex impact on vital rates of plant individuals.

Traits of root and other organs may be coordinated in a single or multiple dimension(s), but our knowledge on the main trade-offs determining root trait variation have been poorly described. The hypothesis of one-dimensional root economics spectrum (RES) suggests that roots traits are coordinated in a one dimensional trade-off between strategies associated with a range of ecological strategies in resource use that expand from conservative to acquisitive (Chen et al., 2013; Comas and Eissenstat, 2004, 2009; Kong et al., 2014; Liu et al., 2015;

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McCormack et al., 2012; Withington et al., 2006), and that would be analogous to the one-dimensional leaf economic spectrum (LES). For example, species with high specific root length (SRL) and area (SRA) can efficiently explore larger soil volumes, and therefore have higher soil resource uptake rates per unit of root mass, while species with low SRL and SRA would reflect more conservative strategies (Hajek et al., 2013; Mommer et al., 2011). Similarly, species with high root nitrogen (RN) and phosphorus (RP) content would reflect more acquisitive strategies than species with low RN and RP content, playing an analogous role to the leaf nitrogen and phosphorus content related to carbon gain. It is therefore expected that root traits, if assembled under this one-dimensional trade-off, would be analogous to the leaf economics spectrum (LES). In other words, traits from different organs should be coordinated (Reich, 2014). Although some few studies have examined trait coordination integrating root traits, Freschet et al. (2010) and more recently, de la Riva et al. (2016) found coordination for root and leaf traits along a single dimension of plant economics spectrum in a subarctic flora and Mediterranean forests.

Despite of the predicted analogy between root traits and leaf traits describing a single trade-off, a recent review suggested the existence of a multidimensional root economics spectrum because roots face a more complex environment than leaves (Weemstra et al., 2016). For example, soil texture and chemistry may present additional limits to root traits that are not present aboveground. Moreover, soil nutrients uptake is not solely determined by root traits, but also rely heavily on the mycorrhizal pathway, which may counteract the selection for one-dimensional RES (Weemstra et al., 2016). Therefore, more empirical evidence on this topic is needed to fully elucidate the phenotypic structure of the root traits.

Beyond the coordination between above and belowground traits, it is important to determine how both RES and LES link to vital rates. One hypothesis predicts that the trait-vital rate relationships should be similar across organs if economics spectrum is prevalent across different organs (Reich 2014). Species with acquisitive leaves should have high photosynthetic and growth rates, which would require acquisitive roots that ensure enough water and nutrients to maintain main metabolic processes and growth (Givnish, 1988; Grime, 1977; Reich, 2014). For example, species with high carbon acquisition strategies, should have acquisitive leaf and root traits such as high specific leaf area (SLA), leaf nitrogen content (LN), SRL, RN, low leaf dry matter content (LDMC), and root tissue density (RTD), corresponding to high photosynthetic rate, high water and nutrients transport ability. In other words, all organs should be “fast” or “slow” simultaneously at acquiring all resources, otherwise plants will possess excess capacity, it is wasteful and costly (Reich, 2014). Therefore, species with acquisitive traits at all organs should have high growth and mortality rates. However, traits from different organs could be multidimensional (Kramer-Walter et al., 2016; Weemstra et al., 2016), hence its relationships with vital rates might not be consistent, particularly for roots, which may weaken the relationships between traits and vital rates, results in insignificant or inconsistent relationships (e.g. fast resource-acquisitive traits reduce mortality), yet evidences are largely lacking.

In this study, we examined the coordination of belowground and aboveground traits and their impacts on seedling mortality. We combined information on woody plant censuses of 13,733 seedlings of 57 common species with seedling functional traits of root, stem and leaf in a subtropical forest. We asked the following questions:

- (1) Are aboveground and belowground traits coordinated in a single or multiple dimension(s)?
- (2) Do root traits and aboveground traits have consistent impacts either negative or positive effects on seedling mortality (e.g. SRL and SLA are positively correlated with mortality, and RTD and LDMC are negatively correlated with mortality)?

2. Material and methods

2.1. Study site

Our study site is located in Heishiding Nature Reserve (23°27' N, 111°53' E) in Guangdong Province, Southern China. It is a subtropical evergreen broad-leaved forest with a subtropical moist monsoon climate, dominated by *Lauraceae*, *Fagaceae* and *Theaceae* families. The altitude of the study site ranges from 150 to 930 m and the mean annual precipitation is 1743.8 mm, most of which occurs between April and September. The average annual temperature is 19.6 °C and the average monthly temperature ranges from 10.6 °C in January to 28.4 °C in July (Liang et al., 2015). This information was obtained from a weather station in the Administration of Heishiding Nature Reserve (about 200 m a.s.l.). We established six 1-ha permanent plots during winter 2007 to spring 2008. Three plots are located at relatively high altitude (600 m a.s.l.), and the other three at lower altitude (340 m a.s.l.). All woody individuals with diameter at breast height (DBH) ≥ 1 cm were measured, mapped, tagged and identified to species.

2.2. Seedling surveys

We established 1200 1 m² seedling plots across the six 1-ha permanent plots in the spring of 2008. In each 1-ha plot, 200 seedling plots were regularly located at alternate 10 × 10 m quadrats, each target quadrat has four 1 × 1 m seedling plots (see Fig. S1 for details). All seedlings of woody plants (DBH < 1 cm) have been surveyed from March to April for 2008–2017 (Liu et al., 2012). New recruits have been added to the census every year as they appear. We measured canopy openness and soil properties in 2017 (Table S1).

2.3. Plant traits measurement

In October 2017, we collected 4–5 intact and healthy seedlings (including roots and soil at the base) for each species outside the permanent plots in the Heishiding Nature Reserve, to measure plant traits (Tables 1 and S2). After collection, seedlings were put in a moist sealed plastic bag and stored in a cool box to keep leaves water-saturated until they were processed. Samples were processed as soon as possible (generally within 4 h) in our labs at study site. Seedlings from the same species had at least 20 m away from each other. Their heights range between 20 and 50 cm. We selected 57 species with total abundance ≥ 10 across 10-years seedling monitoring (Table S3).

Three relatively young, healthy and fully expanded leaves were selected for each seedling to measure leaf traits (Cornelissen et al., 2003). Leaves were scanned by an ordinary scanner (EPSON V370, China), and leaf area (LA, cm²) was determined using the ImageJ (version 1.43u, USA) software. Leaf thickness (T, cm) was measured once on each side of the main vein at the widest part of each leaf using a micrometer, and avoiding large secondary veins. After measuring for fresh mass, all leaves were placed in an oven at 60 °C for at least 48 h, and then re-weighed to determine leaf dry mass. Specific leaf area (SLA, cm² g⁻¹) was calculated by dividing leaf area by dried mass. Leaf dry matter content (LDMC, g g⁻¹) was calculated as the ratio of leaf dry mass to leaf fresh mass (Shen et al., 2014, 2016a, 2016b). Finally, the dry leaves were used to measure the nitrogen content (LN, g kg⁻¹, indophenol blue colorimetric method) and phosphorus content (LP, g kg⁻¹, molybdenum blue colorimetric method) (Chen et al., 2016).

Biomass allocation traits including leaf area ratio (LAR, cm² g⁻¹) and stem specific length (SSL, cm g⁻¹) were determined by the ratio of total leaf area to biomass of a seedling and the ratio of stem length to stem dry weight (Poorter et al., 2012), respectively. Leaf and biomass allocation traits were combined and named as “aboveground traits” hereafter.

We sampled 1–3 fine root branches (diameter < 2 mm) with intact terminal branch orders from each seedling (Kubisch et al., 2015; Liese

Table 1

The definition, abbreviation and unit for each functional trait.

Trait	Definition	Abbreviation	Unit
Leaf area	Leaf surface area	LA	cm ²
Leaf area ratio	The ratio of total leaf area to biomass of an individual	LAR	cm ² g ⁻¹
Leaf carbon content	Leaf carbon content per mass	LC	%
Leaf dry matter content	The ratio of leaf dry mass to leaf fresh mass	LDMC	g g ⁻¹
Leaf nitrogen content	Leaf nitrogen content per mass	LN	g kg ⁻¹
Leaf phosphorus content	Leaf phosphorus content per mass	LP	g kg ⁻¹
Specific leaf area	Dividing leaf area by dried mass	SLA	cm ² g ⁻¹
Specific stem length	The ratio of stem length to stem dry weight	SSL	cm g ⁻¹
Leaf thickness	Leaf thickness at the widest part of each leaf	T	cm
Fine-root diameter	Average fine root diameter	DIAM	mm
Root branching intensity	Number of root tips per fine-root length	RBI	tips cm ⁻¹
Root nitrogen content	Root nitrogen content per mass	RN	g kg ⁻¹
Root phosphorus content	Root phosphorus content per mass	RP	g kg ⁻¹
Root tissue density	The ratio of root dry mass to its volume	RTD	g cm ⁻³
Specific root area	The root surface area per dry mass	SRA	cm ² g ⁻¹
Specific root length	The root length divided by its dry mass	SRL	cm g ⁻¹

et al., 2017). Next, roots were washed carefully, spread out in a purified water bath and scanned (EPSON STD4800, USA) to obtain the sample images. We obtained root average diameter (DIAM, mm), total root length, surface area, volume and number of root tips (Erktan et al., 2016; Kubisch et al., 2015; Liese et al., 2017; Weemstra et al., 2017) from root images by WinRhizo 2013e software (Régent Instruments Inc., Canada). After scanning, roots were placed in an oven at 70 °C for at least 72 h until constant weight to determine dry mass. Root tissue density (RTD, g cm⁻³) was calculated as the ratio of root dry mass to its volume assuming that a root was a cylinder. Specific root length (SRL, cm g⁻¹) was calculated as the root length divided by its dry mass (Kong et al., 2014). Specific root area (SRA, cm² g⁻¹) was calculated as root surface area per dry mass (Hajek et al., 2013). Root branching intensity (RBI, tips cm⁻¹) was calculated as number of root tips per root length (Liese et al., 2017). Finally, the dry roots were used to measure the nitrogen content (RN, g kg⁻¹) and phosphorus content (RP, g kg⁻¹) by the same methods for leaf.

2.4. Data analysis

In this study, we examined the trait coordination, and the relationships between mortality and traits from different organs for seedling species. We used multiple census years ranging from 2008 to 2017 including data for 13,733 seedlings representing 57 species (Table S3). For the analyses we selected seedlings that were recorded as new recruits after 2008 (for determining seedling age) and species with abundance ≥ 10 seedlings. Overall our data represents the 90.52% of the total recorded seedlings.

In order to examine the coordination of traits from different organs (question 1 in Introduction), we first tested pair-wise trait correlations by univariate phylogenetic least squares models (PGLS) using the function “ppls” in “caper” package (Orme, 2013) in R 3.4.0 (R Development Core Team, 2017). We then used phylogenetic principal component analysis (PPCA) with the whole set of functional traits to assess whether traits of different organs are coordinated along a single or multiple dimension(s) (de la Riva et al., 2016). The PPCA accounted for the phylogenetic effects between plant species when performed principal components analysis, and it is therefore appropriate to avoid phylogenetic dependency between plant species due to shared evolutionary history (Gerz et al., 2018; Martinez-Vilalta et al., 2010). PPCA was performed by “phyl.pca” function in “phytools” packages (Revell, 2012). We used Phylomatic (ver. 3) to construct the phylogenetic tree of the plant species (Fig. S2), phylocom (ver. 4.2) to add branch lengths (Pivovarov et al., 2014). Traits were standardized before fitting the models.

To assess the effects of traits on seedling mortality (question 2 in Introduction), we used generalized linear mixed models (logistic

GLMMs with binomial error) to evaluate how traits affect seedling mortality. We used the seedling census data from 2008 to 2017. The data included 29,106 observations of 13,733 individuals from 57 common species with at least 10 individuals. We added seedling age as a fixed effect to account for the age dependence of mortality. Given that our seedling plots were distributed in two levels of elevation (three plots at high elevation and the other three at low elevation) and this could strongly affect the mortality rates, we also included elevation (two groups: low was assigned to -1 and high was 1) as a fixed effect. In addition, we included census interval and seedling plot as random effects (intercept specified) to account for temporal and spatial variation. Species and individuals were considered as random effects to account for basal differences in species and individual in mortality (Zhu et al., 2015). The model had the following form:

$$y = \beta_0 + \beta_1 \text{trait} + \beta_2 \text{age} + \beta_3 \text{elevation} + \epsilon_{\text{year}} + \epsilon_{\text{species}} + \epsilon_{\text{plot}} + \epsilon_{\text{individual}} + \epsilon_{\text{residual}}$$

where y is logit mortality, β_0 is intercept, and β_1 , β_2 and β_3 are coefficients for trait, age and elevation. The random effects of census year, species, seedling plot and individual are denoted by ϵ_{year} , $\epsilon_{\text{species}}$, ϵ_{plot} and $\epsilon_{\text{individual}}$, respectively, and $\epsilon_{\text{residual}}$ represents the residual error. We fit four sets of models based on different trait combinations: (1) individual trait; (2) all traits; (3) aboveground traits; (4) root traits, and calculated marginal and conditional R^2 values for models (Nakagawa and Schielzeth, 2013). Traits were often highly correlated, in order to eliminate multicollinearity in multivariate models (2, 3 and 4), we first checked for multicollinearity between traits using variance inflation factor (VIF) analysis. VIF < 10 was considered that multicollinearity is low and can be generally accepted to establish models (Ohlemuller et al., 2006). Therefore, we stepwise removed a predictor with highest VIF, until all predictors had VIF values < 10, and these remaining predictors were used to establish optimal models. We established an optimal model for each multivariate model (2, 3 and 4) by model selection based on Akaike information criterion (AIC) value. GLMMs were conducted by “glmer” function in “lme4” package, VIF analysis was performed using “vif” function in “car” package, and model selection were conducted by “dredge” function in “MuMIn” package in R.

3. Results

Overall, traits from different organs were highly correlated and coordinated, according to the univariate PGLS (Table 2). For example, SRL was significantly positively correlated with LN, SLA, but significantly negatively correlated with LDMC and RTD. In the PPCA, trait coordination was clearer, indicating the existence of plant economics

Table 2
Coefficient of univariate phylogenetic generalized least squares models (PGLS) for trait pairs.

Trait	LAR	LC	LDMC	LN	LP	SLA	SSL	T	DIAM	RBI	RN	RP	RTD	SRA	SRL
LA	-0.15	-0.11	-0.17	0.03	0.25[*]	-0.1	-0.44^{***}	0.19	0.21^{**}	0.1	0.14	0.09	-0.04	0.06	0.1
LAR		-0.09	-0.34^{**}	0.27^{**}	0.25[*]	0.49^{***}	0.63^{***}	-0.52^{***}	-0.01	-0.03	0.23[*]	0.46^{***}	-0.42^{***}	0.61^{***}	0.42^{***}
LC			0.40^{**}	0.19	0.13	-0.09	0.08	-0.31[*]	0.24[*]	-0.19	0.13	0.21	-0.02	-0.1	-0.24
LDMC				-0.41^{**}	-0.12	-0.67^{***}	-0.04	0.2	0.13	-0.1	-0.23	-0.26	0.36^{**}	-0.46^{***}	-0.38^{**}
LN					0.51^{***}	0.66^{***}	0.24	-0.57^{***}	-0.03	-0.03	0.47^{***}	0.28[*]	-0.46^{***}	0.48^{***}	0.42^{**}
LP						0.35^{**}	0.25	-0.44^{***}	-0.07	0.16	0.32^{**}	0.25	-0.35^{**}	0.44^{***}	0.25
SLA							0.38^{**}	-0.80^{***}	-0.03	0.1	0.26[*]	0.35[*]	-0.39^{**}	0.48^{***}	0.35[*]
SSL								-0.45^{***}	0.05	-0.06	0.13	0.27[*]	-0.26[*]	0.37^{**}	0.27[*]
T									-0.03	-0.03	-0.18	-0.29[*]	0.2	-0.31[*]	-0.17
DIAM										-0.67^{***}	0.36[*]	0.13	-0.57^{***}	-0.28	-0.78^{***}
RBI											-0.21	-0.19	0.45^{***}	-0.06	0.32[*]
RN												0.62^{***}	-0.69^{***}	0.41^{**}	0.15
RP													-0.33^{**}	0.33[*]	0.23
RTD														-0.79^{***}	-0.40^{**}
SRA															0.81^{***}

Significant relationship (P < 0.05) was highlighted in bold. See Table 1 for trait abbreviations.

* P < 0.05.

** P < 0.01.

*** P < 0.001.

Table 3
Factor loadings of the first four components of phylogenetic principal component analysis (PPCA) on traits, explaining 69.62% variation in all traits.

Trait	PC1 (34.09%)	PC2 (14.91%)	PC3 (12.02%)	PC4 (8.60%)
LA	0.07	-0.17	0.82	-0.21
LAR	-0.81	-0.08	-0.20	0.24
LC	-0.04	0.55	-0.17	-0.46
LDMC	0.55	0.22	-0.32	-0.20
LN	-0.71	0.16	0.05	-0.40
LP	-0.55	0.04	0.16	-0.53
SLA	-0.80	-0.04	-0.14	-0.21
SSL	-0.54	-0.01	-0.61	0.29
T	0.64	-0.11	0.41	0.39
DIAM	0.00	0.89	0.11	0.14
RBI	0.12	-0.68	-0.18	-0.43
RN	-0.59	0.49	0.31	-0.01
RP	-0.56	0.21	0.21	0.16
RTD	0.73	-0.37	-0.28	-0.26
SRA	-0.78	-0.32	0.23	0.16
SRL	-0.58	-0.70	0.08	0.07

See Table 1 for trait abbreviations.

spectrum (Table 3, Fig. 1). The first PPCA axis accounted for 34.09% of overall variation in all traits, most of traits from different organs were coordinated and represented a variation along the whole-plant economics spectrum: species on the low end of this axis (left side) had high LAR, LN, LP, SLA, SSL, RN, RP, SRA, SRL and low LDMC, T, RTD, representing fast resources acquisition strategy of species, and species at the right side tended to be resource conservation. However, the second principal component (explained 14.91% variation in traits) represented covariation between LC, DIAM and LA, RBI (Table 3, Fig. 1), and these traits tended to be independent from the whole-plant economics spectrum, because they were strongly correlated with each other, but had weak relationships with any of the traits that loaded on the first principal component (Table 2). The third and fourth PPCA axes explained 12.02% and 8.60% variation in traits, respectively (Table 3).

For the models based on individual trait, we found LDMC (negative) and SLA (positive) had significant effects on seedling mortality (Table 4), and SRL was marginally significantly correlated with mortality rates (positive). Seedlings of species with high LDMC and low SLA tended to have low mortality risk, which were consistent with the expectations that traits positively associated with resource acquisition strategy (SLA, SRL) tended to increase mortality, but traits positively associated with resource conservation strategy (LDMC) tended to reduce mortality.

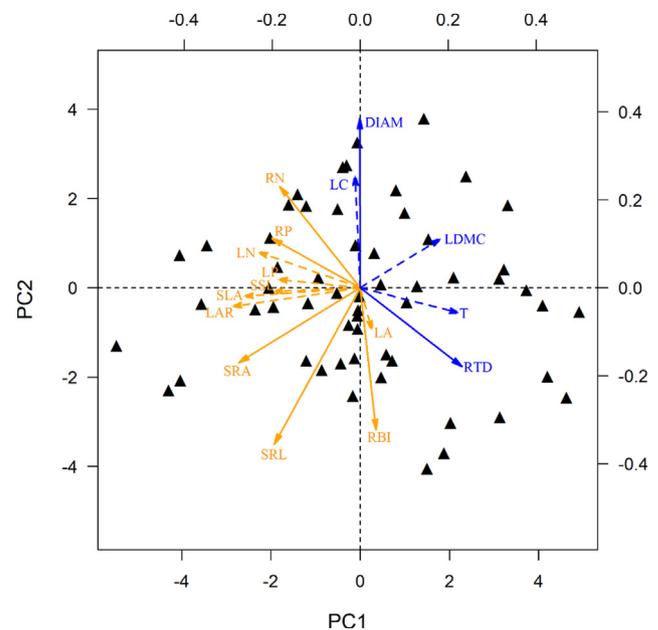


Fig. 1. Trait loadings biplot illustrating the resource-acquisition and resource-conservation strategy derived from phylogenetic principal components analysis (PPCA). Triangles represent species. Orange and blue arrows indicated traits expected to be positively associated with resource acquisition or conservation, respectively. Dashed and solid lines showed aboveground and root traits, respectively. Species at the left region tended to have traits associated with fast resource acquisition. Species at the right region tended to have traits associated with slow resource acquisition. See Table 1 for trait abbreviations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

For the optimal multivariate trait models, we found several key traits significantly contributed to seedling mortality (Table S6). In order to eliminate multicollinearity in multivariate models, DIAM and SLA were stepwise removed first in the all-trait model until all VIF values of predictors < 10; no predictors were removed in the aboveground-trait model; and DIAM and SRA were removed before establishing optimal root-trait model. LDMC, LP, and leaf thickness (T) had relative importance in affecting seedling mortality in the all-trait model (Fig. 2), and LP and SLA were relatively important in the aboveground trait model (Fig. 3). Interestingly, we found that root traits also had important effects on seedling mortality. For example, root nitrogen (RN)

Table 4
Summary information from generalized linear mixed-effects models (GLMM) based on each trait separately. We expected that mortality rates increased with traits associated with resource acquisitive strategy, but decreased with traits associated with conservative strategy. The last two columns showed the expected relationship between trait and mortality, and the consistency between the results and the expectations.

trait	Estimate	P value	Expected relationship with mortality	Consistency
LA	0.04	0.82	+	Consistent
LAR	0.25	0.17	+	Consistent
LC	0.18	0.31	–	Inconsistent
LDMC	-0.38	0.02	–	Consistent
LN	0.18	0.31	+	Consistent
LP	-0.02	0.90	+	Inconsistent
SLA	0.44	0.01	+	Consistent
SSL	-0.02	0.91	+	Inconsistent
T	-0.26	0.16	–	Consistent
DIAM	-0.20	0.25	–	Consistent
RBI	0.14	0.43	+	Consistent
RN	-0.22	0.23	+	Inconsistent
RP	-0.03	0.84	+	Inconsistent
RTD	-0.10	0.58	–	Consistent
SRA	0.23	0.19	+	Consistent
SRL	0.30	0.08	+	Consistent

The fixed effect of age and elevation were always significantly negatively correlated with mortality (not showed in this table), seedlings in lower elevation had higher mortality rates. Significant trait-mortality relationships ($P < 0.05$) were highlighted in bold. See Table 1 for trait abbreviations.

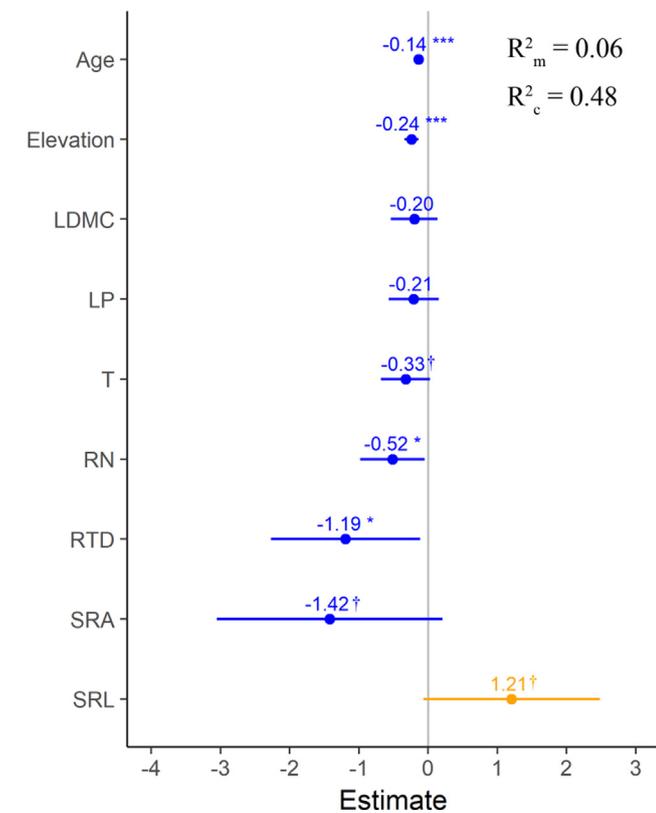


Fig. 2. Estimates of fixed effects for the optimal all trait model. R_m^2 , R_c^2 were marginal and conditional R^2 . * $P < 0.05$, *** $P < 0.001$. Marginally significant relationships were also showed in this figure († $P < 0.1$). Traits included leaf dry matter content (LDMC), leaf phosphorus content (LP), leaf thickness (T), root nitrogen content (RN), root tissue density (RTD), specific root area (SRA), specific root length (SRL).

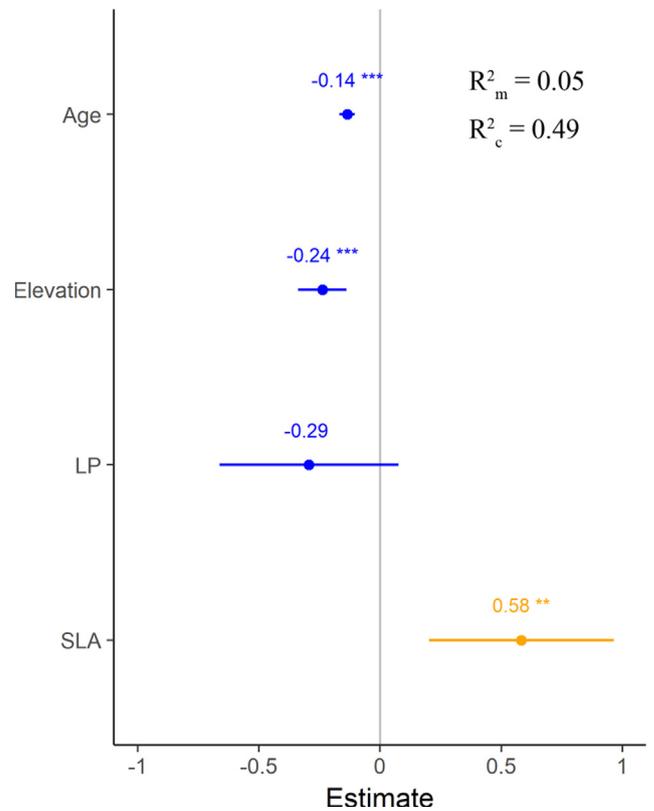


Fig. 3. Estimates of fixed effects for the optimal aboveground trait model. R_m^2 , R_c^2 were marginal and conditional R^2 . ** $P < 0.01$, *** $P < 0.001$. Traits included leaf phosphorus content (LP) and specific leaf area (SLA).

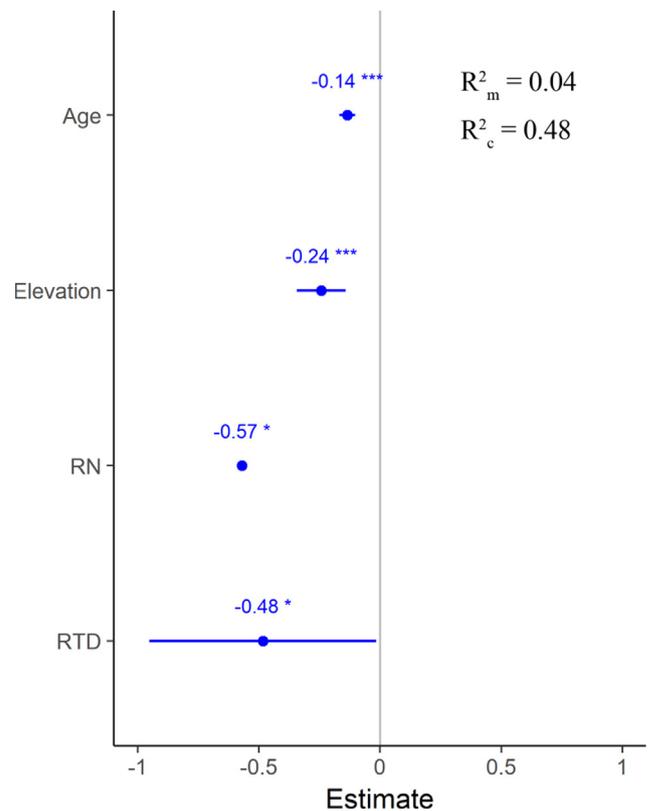


Fig. 4. Estimates of fixed effects for the optimal root trait model. R_m^2 , R_c^2 were marginal and conditional R^2 . * $P < 0.05$, *** $P < 0.001$. Traits included root nitrogen content (RN) and root tissue density (RTD).

and phosphorus (RP) content, specific root area and length (SRA and SRL) was significantly or marginally significantly related with seedling mortality in the all trait models (Fig. 2), and RN and RTD had significant effect on seedling mortality (Fig. 4). However, the predictive power of traits for seedling mortality was weak. The proportion of variation in seedling mortality can be explained by these three models were from 48% to 49%, but the fixed effects explained much lower variation in mortality (4–6%).

4. Discussion

In this study, we aimed to examine the coordination of traits and trait-mortality relationships for 13,733 seedlings of 57 species across a 10-year period in a subtropical forest in the Heishiding Nature Reserve, China. We found that traits from different organs were highly correlated with each other (Table 2); most of the traits were coordinated along a single axis (PC1), supporting the plant economics spectrum (Fig. 1). However, few traits tended to be independent from plant economics spectrum. In addition, we found that traits associated with fast resource acquisition tended to increase mortality, while traits associated with resource conservation decreased seedling mortality (Table 4). Several root traits, such as root nitrogen content, tissue density and specific root length, had important impacts on seedling mortality (Figs. 2, 4). To our knowledge, this is the first detailed examination of the plant economics spectrum and root trait-mortality relationships for a subtropical seedling community.

4.1. Traits from different organs are coordinated

A single “fast-slow” plant economics spectrum, which integrates root, leaf, and stem traits, was proposed to explain individual ecological strategies, community structure, and ecosystem function (Reich, 2014). Previous studies have tested the traits coordination for leaf and stem (Baraloto et al., 2010; Santiago et al., 2004), but with little attention to root traits. However, in a subarctic flora, Freschet et al. (2010) found that traits correlated across leaves, stems, and roots for significant pattern of whole-plant integrative resource economy. Similarly, functional coordination among traits belonging to different plant organs (leaf, stem, and root) was found in 38 Mediterranean woody plant species (de la Riva et al., 2016) and between aboveground and belowground traits in a Mediterranean rangeland (Perez-Ramos et al., 2012). However, although some traits from different organs were coordinated describing an axis of conservative-acquisitive strategies, some previous studies found that traits could be multidimensional, particularly for root traits. For example, Kramer-Walter et al. (2016) found that specific root length and root diameter were independent from plant economics spectrum, suggesting that root traits could be multidimensional because roots perform multiple pivotal roles in plant and ecosystem function. Also, Weemstra et al. (2016) suggested that a single acquisition-conservation axis cannot adequately capture the variety of belowground functions and tradeoffs that drive differences in resource acquisition and plant performance across species, because roots are constrained by a more complex soil environment and their functions are different from leaves. Our results presented a similar pattern: strong coordination was observed among traits from different organs (Table 2), and the first PPCA axis showed a clear plant economics spectrum from fast resource acquisition species to resource conservation species, with the same acquisitive or conservative strategy across different plant organs (Fig. 1), but traits of LA, LC, RBI and DIAM were independent from this axis, and they had weak relationships with any of the traits that loaded on the first principal component (Table 2), indicating that some traits may be simultaneously constrained by various environmental drivers not necessarily related to the continuous acquisitive-conservative axis and resource uptake (Weemstra et al., 2016). Therefore, variation in traits should be explained by a multidimensional framework in the future, and this framework should be

established in consideration of some key factors. For example, for root traits, should consider the complexity of the soil environment, root form and function, and multiple belowground resource uptake strategies (such as mycorrhizal pathway) (Weemstra et al., 2016).

4.2. Conservative aboveground traits reduce seedling mortality

Studies proposed that plant traits represent the inherent differences among species that contribute to growth-mortality trade-off (Martinez-Vilalta et al., 2010; Poorter et al., 2008; Wright et al., 2010). Species with acquisitive traits will have high growth and mortality rates, and species with conservative traits will grow slowly but have lower mortality rates, such as the growth-mortality trade-off between light-demanding and shade-tolerant species. Our results also supported this conclusion: slow-growing species with slow resource acquisition and low metabolic rates (e. g. low SLA) and high tissue density (e.g. high LDMC), characterized by conservative strategies had lower mortality rates than species with aboveground-acquisitive traits for tropical seedlings (Table 4). This trade-off may due to the very limited light availability for seedlings, average canopy openness is only 2.83% in our study site (Table S1), that benefit the survival of seedlings with conservative strategies (Paine et al., 2015; Poorter et al., 2008; Visser et al., 2016; Wright et al., 2010).

4.3. Conservative root traits also reduce seedling mortality

If a single “fast-slow” plant economics spectrum is prevalent in tropical forests, it is expected that the leaf, stem and root traits that are related to resource acquisition are also correlated with each other and with mortality rates (Reich, 2014). Root is the primary organ for plant resource acquisition from soils, and very important in carbon and nutrient cycling (Kong et al., 2014; Pregitzer et al., 2002), yet few studies have considered this organ to predict vital rates in plant communities. To our knowledge, this is the first study to examine the role of several key root traits in predicting seedling mortality for subtropical seedling communities. We showed that seedlings with conservative resource acquisition strategies for roots (e.g. low SRL and high RTD) attained lower mortality rates, than species with fast-resource acquisition root traits (Table 4). The relative low concentration of soil nutrients in our study site (Table S1) may be not beneficial for the fast-growing/acquisitive seedlings, and they will suffer high mortality. On the other hand, seedlings with conservative strategy and having thicker roots tend to survive better in limiting environments and have effective defenses against pathogens and herbivory (Holdaway et al., 2011; Kong et al., 2014; Withington et al., 2006). For tropical seedling communities, nutrient has been hypothesized to be one of the most limiting factors in addition to light (Pasquini and Santiago, 2012; Record et al., 2016; Santiago et al., 2012). Previous studies have addressed that soil nutrients, such as N, P, potassium (K) concentration and soil moisture, had crucial effects on seedling growth (Pasquini and Santiago, 2012; Santiago et al., 2012; Umana et al., 2017), survival (Cecon et al., 2003; Record et al., 2016), recruitment (Cecon et al., 2003) and even diversity (Lu et al., 2010) in tropical forests. Our results emphasize the importance of traits related to soil nutrients acquisition in promoting good performance for tropical seedlings, and root traits may have great potential in contributing to growth-mortality trade-off. However, inconsistent effects of root traits (such as RN and RP) on seedling mortality were also observed (Table 4), also emphasizing multidimensional root traits (Kramer-Walter et al., 2016; Weemstra et al., 2016).

4.4. Predictive power of plant traits for seedling mortality is weak

Although a few of studies examined the trait-mortality relationships, large proportion of variation in vital rates remain unexplained (Iida et al., 2014; Poorter et al., 2008; Visser et al., 2016; Wright et al., 2010), especially for early ontogenetic stages (Paine et al., 2015; Visser

et al., 2016). In our study, few trait-mortality relationships were significant in the models of individual trait (Table 4), but we found several key traits in affecting seedling mortality in multivariate models (Figs. 2–4), indicating that combination of traits contribute to achieve the main vital functions of species simultaneously. In addition, our results also showed that plant traits had weak predictive power for seedling mortality (Figs. 2–4), which was found in many previous studies (Martinez-Vilalta et al., 2010; Poorter et al., 2008; Visser et al., 2016; Wright et al., 2010). There are some reasons can explain the weak predictive power. First, variation in vital rates also depends strongly on local environment (Martinez-Vilalta et al., 2010; Paine et al., 2015; Uriarte et al., 2016; Visser et al., 2016). For example, not only plant traits, but also abiotic factors, such as topography, soil water and nutrients could contribute to vital rates (Lin et al., 2017; Martinez-Vilalta et al., 2010; Record et al., 2016); and biotic interactions, such as individual densities, pathogens and herbivory might also have an important impact on seedling demography. Previous studies have found that pathogens and herbivory mediated by negative density dependent effects are key for seedling dynamics in tropical forests (Clark et al., 2012; Liang et al., 2015; Liu et al., 2012; Record et al., 2016; Umana et al., 2018). However, environmental factors were represented by random effects, but not explicitly included as fixed effects in our models. Second, seedling mortality may be more easily caused by stochastic and unpredictable factors in tropical forests, such as falling debris (Paciorek et al., 2000; Poorter et al., 2008). Third, plant traits are multidimensional, and might be involved in multiple trade-offs with contradictory effects on vital rates. As different traits are often associated with different ecological processes which relate to different niche axes (Violle et al., 2007), predictive power may be weakened in multivariate models when traits are associated with opposing niche axes (Cornwell and Ackerly, 2009; Cornwell et al., 2006; Spasojevic and Suding, 2012).

Such weak trait-mortality relationship implies that the predicting power of traits on community composition and dynamics needs to be refined in order to obtain robust results. It has been suggested that combined “hard” traits (e.g. photosynthetic or respiration rates) would improve the predictive power of traits in vital rates (Lavorel and Garnier, 2002); and traits of whole-plant should be considered simultaneously to represent the functional integration of individual level, rather than at the organ level (Craine et al., 2012). Various environmental conditions (e.g. light condition, soil property) should be also taken into account in the future studies, to refine the predictive ability of traits in vital rates, and thus community dynamics (Paine et al., 2015).

5. Conclusions

In this study, we combined a wide arrangement of aboveground and belowground traits to examine plant economics spectrum, and to predict seedling mortality of 10-year period in a subtropical forest. We found that most of the traits from different organs were coordinated, supporting the plant economics spectrum in subtropical seedling communities for the first time. Traits had consistent effects on mortality, in which seedlings with conservative strategy reduced mortality, but seedlings with acquisitive strategy suffered higher mortality. Although predictive power of traits for seedling mortality was weak, several key root traits, including root nitrogen content, tissue density and specific root length, were first discovered had significant impacts on seedling mortality in multivariate models, thus integrating the often-ignored root traits is necessary to gain further understanding in the relationships between plant performance and traits.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.05.032>.

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