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Seedling growth and survival responses to multiple soil properties in subtropical forests of south China



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ABSTRACT

Soil properties and light availability have been long recognized as fundamental drivers of species distribution and are especially important during the regeneration phase. The role of nutrients such as exchangeable base cations is poorly understood, despite forests facing considerable changes in soil composition due to climatic change and atmospheric acid deposition, including in south China.

With the aim of understanding the response of naturally regenerating seedling communities to a wide range of abiotic conditions, we quantified seedling growth and survival of over 2000 seedlings representing 166 morphospecies within four subtropical forests in south China, for two years. We assessed their responses to canopy openness, and a natural gradient of soil characteristics: moisture, pH, total nitrogen (N), total carbon (C), C:N ratio, available phosphorus (P), available potassium (K), calcium (Ca), iron (Fe), magnesium (Mg), manganese (Mn), and sulfur (S). We conducted our analyses at three levels: landscape (1), forest site (4), and species (7).

We found statistically clear effects of several soil properties on seedling growth and survival, at all levels of analysis, while canopy openness showed a minimal negative effect on survival and none on growth. Seedling growth was positively affected by increasing soil Ca and Mn and negatively by increasing soil Mg at the land-scape level (all four forest sites combined). Seedling survival responded positively to soil Fe and C:N ratio, but negatively to soil Ca, Mg, Mn, N, and S. The observed patterns were forest site- and species-specific. These results are especially relevant in a region experiencing severe changes in soil conditions as well as intense deforestation and land use change. Reforestation programs should consider the site specificity of soil properties with respect to a wide range of soil nutrients when planning restoration activities.

1. Introduction

Abiotic resources contribute to shape forest community structure and composition (Condit et al., 2013; John et al., 2007; Kobe, 1999), with edaphic characteristics affecting species spatial distribution by modulating individual growth and survival (Swaine, 1996). This is especially important at the seedling stage, the most severe bottleneck in plant recruitment (Grubb, 1977; Queenborough et al., 2007), and a pivotal phase influencing species turn-over and community dynamics (Grubb, 1977). Indeed, edaphic factors including soil nutrient availability and local topography affect seedling growth and survival and therefore plant recruitment (Brown et al., 2013; Holste et al., 2011; Johnson et al., 2017; Machado et al., 2003; Xu et al., 2019).

Our knowledge on how essential elements sustain plant growth,

especially in natural communities, is greater for macronutrients such as nitrogen and phosphorus (Vitousek, 1984; Vitousek et al., 2010), but limited for micronutrients such as manganese and iron (Ågren, 2008). Generally, seedling growth responds positively to increased nitrogen and phosphorus availability (Lawrence, 2003). In natural forests, nutrient availability varies significantly at the landscape level as well as at finer spatial scales (Schreeg et al., 2005; Xia et al., 2016) and the availabilities of several nutrients change with elevation (Ediriweera et al., 2008). A few studies that considered the effect of soil nutrients other than nitrogen and phosphorus on plant performance and species distribution focused mostly on adult trees (Condit et al., 2013; John et al., 2007; Johnson et al., 2017; Norden et al., 2009). Fertilization experiments including micronutrient addition have shown that they are not major drivers of seedling growth (K, Ca, Mg, and S: Wan Juliana

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et al., 2009; micronutrient fertilizer including Cu, Fe, Mn, Zn, Ca, Mg: Santiago et al., 2012). However, Holste et al. (2011) and Record et al. (2016) provided evidence of the importance of soil nutrients, including base cations (sum of potassium, calcium, and magnesium), to seedling growth and survival in a tropical forest, with species-specific effects. Yet, our understanding on how the seedling communities in natural forests respond to individual soil base cations and other soil micronutrients such as manganese is surprisingly limited and mostly based on nutrient addition experiments (Table S1).

In addition to soil properties, light is an important factor contributing to species regeneration success, as it drives the trade-off between growth and survival (Wright, 2002), exerting significant influence on both processes (Beckage and Clark, 2003; Kobe, 1999; Montgomery and Chazdon, 2002). Most plants grow faster with higher light availability (Augspurger, 1984), while survival shows more variability between pioneer and shade-tolerant species (Ashton et al., 2018; Balderrama and Chazdon, 2005). Yet, growth and survival can be negatively affected above a light optimal threshold (Goodale et al., 2014). Commonly, gaps created by falling trees are the major cause of light heterogeneity in forests and substantially contribute to regeneration and species coexistence (Muscolo et al., 2014). However, significant differences in recruitment exist also in forest understory in the absence of gaps, driven by a gradient of low light availability (Montgomery and Chazdon, 2002). Yet, how seedlings are influenced as a community by the natural gradients of canopy openness is less known, as most assessments investigate individual species patterns or pre-selected contrasts in gap versus non-gap conditions or the gap-understory continuum. Furthermore, studies that assess the combined effects of light as well as soil properties are rare. Growth and survival responses to both these abiotic factors are further influenced by water availability at the forest floor (Larson et al., 2016), and species sensitivity to drought has been depicted as a fundamental driver of species distribution in tropical forests (Engelbrecht et al., 2007).

Most studies focus on one or a few soil properties and are often greenhouse experiments (Baraloto et al., 2006; Walters and Reich, 2000), or use transplanted seedlings that are then monitored under field conditions (Andersen et al., 2014). While such studies are important to understand species responses to variation in soil resource availability and to test hypotheses, they can hardly be representative of responses of seedlings growing under natural conditions (Gómez-Aparicio et al., 2008). Further, although plant growth can in some circumstances be considered limited by a single limiting resource - i.e. Liebig's law of the minimum - it is increasingly recognized that interacting co-limitation from two or more abiotic factors are more likely to better represent natural dynamics of plant communities ('multiple limitation hypothesis'; Eskelinen and Harrison, 2015; Gleeson and Tilman, 1992). Indeed, several studies have shown that nutrients can work in combination resulting in synergistic limiting effects (e.g., nitrogen and phosphorous: Harpole et al., 2011) in seedling communities of natural forests. Abiotic factors other than nutrients can also complicate the effects of nutrients, as in the case of nitrogen and light, where light has a stronger effect than nitrogen in affecting seedling growth (Walters and Reich, 2000). Recently, Chou et al. (2018), performed a fertilization experiment on naturally growing saplings in a tropical forest, and found a pervasive nutrient and light co-limitation. However, only a few investigations considered responses of natural seedling communities to local soil conditions (but see Harpole et al., 2011; Norden et al., 2009; Record et al., 2016; Xia et al., 2019).

In addition to limitations of our understanding on the effect of soil properties on seedling growth and survival, we acknowledge two geographical gaps: 1) subtropical forests are understudied compared with temperate and tropical ones; 2) studies from species-rich forests in Asia are limited compared with investigations from the Americas. As in the case of temperate and tropical forests, in subtropical forests most research has been conducted on adult trees and the effect of habitat heterogeneity on community composition and spatial distribution

(Chen et al., 2010; Wu et al., 2017; Xu et al., 2019). In an ecosystem functioning experiment in subtropical China, Scholten et al. (2017) described a relationship between soil manganese and tree height, although other nutrients such as calcium and magnesium did not have clear effects. Understanding the relationships between seedling performance and soil properties is even more relevant in a time when soils are undergoing increasing changes in nutrient composition: in subtropical China, forests soils have experienced a significant increase in acidification and a loss of base cations in the last decades, with forest soils becoming more acidic and with several base ions such as magnesium, calcium, and sodium decreasing due to increased nitrogen deposition (Yu et al., 2020). In addition, although in south China the forested area is still remarkable, a great part is constituted by secondary forest and plantations, especially Chinese fir and Eucalyptus spp. (Hu et al., 2014, 2019). Forest conversion to plantations have also led to increased fragmentation, a common issue in China and elsewhere (Liu et al., 2019).

In this study, we investigated the seedling communities of four subtropical forests in south China for two years, and modeled the relationship between abiotic resources (light and soil properties) and seedling growth and survival. Our objective was to assess the effects of individual resource availability and the existing patterns at three levels: 1) landscape level, namely pooling all four forests' data together; 2) forest level, analyzing each forest community independently; 3) species level, selecting the most abundant species. We expected to find statistically clear effects of individual soil characteristics on both growth and survival at the landscape level, as well as increased growth and lower survival with increasing light availability. At the forest level, we expected to find statistically clear but not homogenous effects, indicating separation in soil properties and local adaptation of seedling communities. Similarly, we anticipated differential responses at the species level due to species-specific characteristics and features of the microsites where they are found. Finally, we expected that water availability would have a positive influence on seedling survival and growth during the wetter summer months. Overall, we predicted clear positive effects of light availability on seedling performance, while we expected mixed effects of multiple soil properties on growth and survival, with both being modulated by the seasonality due to differences in water availability and canopy openness.

2. Methods

2.1. Study sites

We conducted our study in four subtropical forests in Guangxi Zhuang Autonomous Region in south China (Fig. S1), using an established plot network for long-term forest dynamics monitoring administered by the College of Forestry, Guangxi University. Our study sites were the forest communities of four National Nature Reserves: (1) Cenwanglaoshan (24°21' N, 106°27' E) where the vegetation is deciduous broad-leaf mixed forests, with mean annual temperature (MAT) of 14 °C and total annual precipitation (TAP) of 1857 mm; (2) Dayaoshan (23°52' N, 110°01' E), which has broadleaf evergreen forest and broadleaf evergreen monsoon forest (MAT is 17 °C and TAP is 1824 mm) but with two of the plots located in an area with rocky terrain; (3) Mulun (25°07' N, 107°54' E), which has a karst landscape with subtropical mixed evergreen deciduous broadleaf forest (MAT of 19 °C and TAP of 1500 mm); and (4) Huaping (25°36' N, 109°50' E), where the vegetation consists of deciduous broad-leaf mixed forest (MAT of 13 °C and TAP of 2100 mm). In the four forest sites, we used a total of 13 one-ha plots, selected along an elevation gradient, from 400 m to 1750 m (1400, 1500, 1550, 1750, and 1850 m asl in Cenwanglaoshan, 500, 650 1200, and 1300 m asl in Dayaoshan, 400 and 650 m asl in Mulun and 820 and 900 m asl in Huaping). The plot areas were selected to represent intact forested areas with minimum disturbance. Surrounding each 1-ha plot, 2 m outside its perimeter,

following the standardized design employed by the Center for Tropical Forest Science seed rain and regeneration monitoring stations, we built eight census stations, one at each corner and in the middle of each side of the plot. Each census station included three seedling quadrats measuring 1-m², placed in three perpendicular directions and 2 m far from a central seed trap, which was not used for this study (Fig. S2). In total, our design included 312 seedling quadrats.

2.2. Data collection methods

In each 1-m² quadrat, we monitored all tree and shrub seedlings for two years: from November 2017 to November 2019. We defined seedlings as individuals ≤ 50 cm in height from the soil surface. At the first census we tagged each individual and measured its height and in subsequent census measurements recorded dead individuals, tagged new recruits, and re-measured height of alive seedlings. We continued to monitor seedlings that attained > 50 cm height during the study period, performing censuses 14 times during the 2-year period. For the first 1.5 year we monitored at one-to-two months intervals, and a final census was conducted after a six months census interval. We took digital photographs of all seedlings, which we used to confirm and adjust our morpho-species classification. Whenever possible, we collected representative specimens outside the monitored seedling quadrats and prepared herbarium specimens that were then used for identification by botanist at the College of Forestry, Guangxi University, and at the Guilin Institute of Botany. Specimens were difficult to prepare for rarer species, for which we mostly relied on recorded photographs. By combining these two methods we classified monitored seedlings to species or morpho-species.

To assess light availability above each seedling quadrat, we obtained the average of four canopy openness measurements taken using a spherical densitometer at the four cardinal directions. We measured canopy openness in January 2018 and August 2018 in order to account for differences in seasonality due to deciduous species losing their leaves during the cold season. All measurements of canopy openness were collected by a single observer (F.M.) to avoid differences between observers.

We used a soil moisture meter (FieldScout TDR100, Spectrum Technologies, USA) to measure soil moisture at the center of each seedling quadrat, making four measurements in November 2017, May 2018, June 2018 and August 2018. We selected 12 cm long rods and measured soil moisture as volumetric water content. For soil properties analysis, we collected four samples per seedling quadrat, after removing the litter layer, just outside the perimeter of each seedling quadrat between September and October 2017, using a soil core with a 5-cmdiameter and 10-cm-depth. Samples were mixed and stored together in a labeled bag. When we could not sample due to high presence of stones and rocky terrain, we collected the samples in the closest available area. However, if we could not find available soil within a radius of ca. 2 m from the seedling quadrat, we did not collect any samples. We air dried the samples in the field station on the collection date until transport to Guangxi University. There, we broke the soil into small pieces, removing roots, stones and other residuals, and let the samples air dry at room temperature for ca. one month. Once dried, we sieved the samples using two mesh sizes: 0.25 mm and 2 mm. For each mesh size, we extracted 100 g of soil, and stored them in a labeled plastic bag. The samples were analyzed at the Xishuangbanna Tropical Botanical Garden Central Laboratory (Yunnan, China) to measure the following soil nutrients: nitrogen (N), carbon (C), phosphorus (P), potassium (K), calcium (Ca), iron (Fe), magnesium (Mg), manganese (Mn), and sulfur (S), as well as soil pH. Soil pH was measured in water (2.5 units of water per unit of soil) with a pH meter (PHS-3C, Shanghai Precision Scientific Instrument Co., Ltd, China). Detailed explanation for how the soil variables were measured can be found in Xia et al. (2015) for total N, total C, available P, and available K, and other nutrients (Ca, Fe, Mg, Mn, and S), were measured following the same method used for available P and K. From the obtained values for C and N concentrations, we calculated the carbon to nitrogen ratio (C:N).

2.3. Statistical analyses

We conducted all the analyses and developed the figures in R (version 3.6.1, R Core, 2019). For soil properties, we had missing values in some quadrats, as it was not possible to find enough soil to sample due to high presence of stones and rocky terrain (13% soil data). We interpolated these missing values using the *knnImputation* function of the R package *DMwR* (Torgo, 2010), and conducted our analysis on the original data as well as the full data, substituting interpolated values for missing data. Using the base *prcomp* function for principal component analysis (PCA) on our 11 soil properties (nine nutrients, C:N ratio, and soil pH) we obtained PCA axis1 (PC1) and PCA axis 2 (PC2) loadings as a comprehensive single variable to represent the combined soil nutrient properties for each seedling quadrat. A second PCA analysis was conducted adding both canopy openness and soil moisture data and results were visualized using *ggfortify* (Tang et al., 2016).

We calculated relative height growth rate (RGR) for each individual as $ln(H_2)-ln(H_1)/(t_2-t_1)$ for each census interval, where H represent seedling height and t_2-t_1 represent the time in days between each census interval. For analysis, we used the mean RGR for each individual, averaged across census intervals. We considered it likely that RGR values > 30% increase for newly germinated seedlings were due to the input from seed reserves more than to canopy light and soil properties, the site conditions we were interested in. Therefore, for seedlings that showed > 30% RGR in the first census interval from initial germination (n = 58 out of 2021 seedlings), we only considered RGR from the second census onwards. Individuals that were only recorded once and did not survive to the next census were not included in our final analyses as their growth rates could not be calculated.

As expected, we detected multicollinearity among several soil nutrients (variance inflation factor > 2; correlogram presented in Fig. S3). Therefore, we decided to develop independent models for each variable, namely canopy openness and all measured soil variables. We used scaled and centered values for all predictors and used linear mixed models to model the effect of abiotic predictors on the RGR at the landscape level, forest level and individual species level. For landscape level analyses we used (morpho)-species, recruitment date, initial seedling height, and census station nested into forest site as our random factors. Forest site did not explain any variance in some cases, but removing it did not affect the results, hence we kept it in all models. At the forest level, we followed the same procedure but the random factor was set to census station only. To test the effect of seasonal variation in light availability and soil moisture, for both landscape models and forest models, we conducted analyses on these two variables for winter and summer seasons (considered as November to March and May to October, respectively) separately, pooling relevant data. Furthermore, keeping the same random factors, we ran an additional landscape level model for all data, to test the effect of PC1 and PC2 axes - representing the combined effects of soil nutrient variables - and soil moisture and canopy openness on seedling growth. The use of PC1 and PC2 as variables allowed us to account for multicollinearity among nutrient properties (Johnson et al., 2017). In order to test species-specific responses, we selected the most abundant species (n > 40), and performed separate analyses, using the same models described above, with census station as the only spatial random factor.

To assess the effect of abiotic factors on seedling survival, we used the survival (coded as 0 = dead, 1 = alive) at the last census for each individual seedling as our response variable, excluding all individuals that only survived one census. We performed our analyses with generalized linear mixed models, specifying a binomial distribution, and using the *lme4* package (Bates et al., 2015). The different levels of analyses at the landscape, forest and species level included the same random factors as above (but final seedling height was used instead of



Fig. 1. Principal component analysis (PCA) of the soil properties in our study sites.

initial seedling height). All models for survival were constructed similarly to those conducted for growth above.

In presenting and discussing the results, we followed Dushoff et al. (2019) and use their proposed language of clarity instead of significance to improve statistical communication.

3. Results

3.1. Abiotic characterization of forest sites

The PCA revealed separation of Mulun from the other sites mainly due to approximately 10 times higher levels of the base cations Ca and Mg and for Mn, and was mostly explained by the first axis (Fig. 1, Table 1). The first two axes of the PCA explained 61% of variance, with an additional 9.8% explained by the third axis. The second PCA axis confirmed the site uniqueness of Mulun, but also showed the abiotic environment for Huaping was distinct from Dayaoshan, due to lower P and higher pH, although both of these reserves had values that were a subset of Cenwanglaoshan. While the canopy light environment was similar between seasons across sites, Mulun showed greater soil moisture in summer (Table 1); nevertheless, the contribution from soil moisture to site separation was the lowest of all variables (Fig. 1).

3.2. Growth rate

Our dataset consisted of 2022 individual seedlings, belonging to 166 species or morpho-species, 80 of which were identified to species level. No species or morpho-species was distributed across all sites; seven species were most abundant (> 40 individuals). At the landscape level (i.e. all four forests combined), Ca and Mn had clear positive effects on RGR (i.e. increased growth with increasing Ca and Mn), while Mg had a negative effect (i.e. decreased growth with increasing Mg; Fig. 2). However, at the forest level, the patterns observed at the landscape level were not replicated and were forest-specific, except in our karst forest site Mulun, in which seedling RGR decreased along the Mg continuum (Fig. 2). Some patterns not observed at the landscape level became prominent when forest level analyses were performed. In Cenwanglaoshan, greater availability of soil P increased observed RGR, while the opposite pattern was seen for soil moisture. In Dayaoshan, RGR decreased with increasing soil S. In Mulun, in addition to Mg, RGR decreased along the continuum of soil N and C, and increased under higher soil pH conditions (Fig. 2). The analyses at the landscape and forest level repeated using the interpolated data were qualitatively similar to the results obtained using the original data (Fig. S4).

The seasonal data indicated that soil moisture effects on RGR were site-specific, with different sites showing contrasting patterns. In Cenwanglaoshan, seedling RGR decreased with increasing summer soil moisture; in contrast, in Dayaoshan seedling RGR increased with winter water availability (Table S4). The multivariate model including the PC1 and PC2 axes, soil moisture, and canopy openness as predictors showed general agreement to the results obtained in the individual models: RGR increased along the PC1 axis values, but decreased along the PC2 axis values, although with comparably smaller effect size (Table 2). The PC1 had the bigger effect size and was positively related to soil S, Ca, Mg, and Mn (Fig. 1). Even in this analysis soil moisture and canopy openness did not affect the growth response (Table 2).

Table 1

Mean (\pm SD) canopy openness, soil moisture, and soil properties of the four forests. Soil properties were measured on soil sampled at a depth of 0–10 cm from the soil surface without leaf litter.

	Cenwanglaoshan	Dayaoshan	Mulun	Huaping
Canopy openness (%)	14.85 ± 4.65	14.44 ± 3.52	14 ± 1.98	15.26 ± 4.39
Canopy openness (%), winter	16.83 ± 6.94	13.71 ± 4.47	19.47 ± 8.75	14.32 ± 2.88
Canopy openness (%), summer	12.86 ± 4.13	15.18 ± 3.79	11.05 ± 3.09	13.68 ± 2.5
Soil moisture (VWC %)	28.58 ± 14.18	22.26 ± 6.51	30.06 ± 10.4	26.21 ± 6.06
Soil moisture (VWC %), winter	29.41 ± 30.38	18.65 ± 6.41	24.47 ± 10.33	25.61 ± 5.88
Soil moisture (VWC %), summer	28.37 ± 14.7	23.73 ± 7.56	32.55 ± 11.15	26.42 ± 6.66
Soil pH	4.08 ± 0.57	4.15 ± 0.31	4.18 ± 0.21	7.44 ± 0.3
Soil total N (g kg ⁻¹)	0.92 ± 0.42	0.41 ± 0.32	1.16 ± 0.43	0.52 ± 0.17
Soil total C (g kg ⁻¹)	11.39 ± 7.14	5.2 ± 5.32	11.89 ± 4.42	6.28 ± 2.09
Soil C:N ratio	11.69 ± 2.14	12.3 ± 2.15	10.33 ± 1.57	12.08 ± 1.82
Plant-available soil P (mg kg^{-1})	28.14 ± 30.4	24.03 ± 44.86	4.53 ± 3.15	2.36 ± 2.48
Plant-available soil K (mg kg ⁻¹)	167.16 ± 86.15	109.74 ± 106.77	137.75 ± 47.2	111.78 ± 44.31
Soil Ca (mg kg ⁻¹)	562.61 ± 662.21	81.13 ± 187.39	5576.5 ± 2247.02	28.78 ± 26.96
Soil Fe (mg kg ⁻¹)	481.57 ± 153.28	339.32 ± 138.59	77.1 ± 29.5	273.07 ± 70.02
Soil Mg (mg kg ⁻¹)	108.68 ± 81.49	44.46 ± 63.77	1553.39 ± 430.19	38.41 ± 15.7
Soil Mn (mg kg ⁻¹)	83.96 ± 77.38	18.41 ± 30.84	315.07 ± 84.83	24.22 ± 24.6
Soil S (mg kg ⁻¹)	40.96 ± 28.01	26.6 ± 22.23	68.04 ± 32.67	38.93 ± 11.32



Fig. 2. Effect of measured soil properties, soil moisture, and canopy openness (Canopy op.) on seedling annual growth rate in each forest and in all forests pooled together. Estimated full coefficients and 95% confidence intervals are shown. Significant values are also shown (*0.05; **0.01, ***0.001).

As predicted, the models conducted on the seven most abundant species showed species-specific responses (Table S2). The RGR of three species – *Machilus litseifolia* S.K. Lee, *Eleocarpus glabripetalus* Merr., and *Daphniphyllum pentandrum* Hayata – were not related to changes in any of the abiotic conditions assessed in our study, while the RGR of *Skimmia arborescens* T. Anderson ex Gamble was negatively affected by

all soil nutrients, except Fe, and its RGR increased with increasing soil pH. The RGR of the ubiquitous *Castanopsis hystrix* Hook. f. & Thomson ex A. DC. (found in Cenwanglaoshan, Dayaoshan, and Huaping) and the more site restricted *Acer campbellii* subs. *Sinense* (Pax) P.C. DeJong (found in Cenwanglaoshan) were affected by a few nutrients in a species-specific manner (Table S2).

Table 2

Model estimates of the growth and survival models conducted for all data at the landscape level including the first two PCA axes (PC1 and PC2) representing soil nutrients and soil pH, canopy openness and soil moisture. Data used were the original data, with missing values being discarded. The estimates which did not have their confidence intervals (CI) include zero are in bold.

	Estimate	Standard error	Lower CI	Higher CI
Growth				
PC1	0.1224	0.044	0.036	0.208
PC2	-0.0759	0.042	-0.159	0.007
Canopy openness	-0.0183	0.035	-0.085	0.048
Soil moisture	-0.0421	0.035	-0.111	0.027
Survival				
PC1	-1.3067	0.301	-1.90	-0.717
PC2	-0.2597	0.266	-0.262	0.782
Canopy openness	-0.3816	0.185	-0.743	-0.02
Soil moisture	0.0751	0.177	-0.271	0.422

3.3. Survival

At the landscape level, eight out of 13 abiotic environmental variables studied here affected the survival of seedlings, indicating these variables exerted greater influence on survival compared to RGR. Higher availability of soil Fe and soil C:N ratio favored survival, while soil Ca, Mg, Mn, N, and S reduced survival (Fig. 3), and increased canopy light also decreased seedling survival. Patterns were forest-specific and dependent on the abiotic factor. In Dayaoshan, survival increased with increasing soil pH and C:N ratio, but decreased with increasing soil N, P and K. In Mulun, we saw a positive influence on survival from soil Fe and soil moisture. However, survival of Cenwanglaoshan and Huaping seedlings were not influenced by any of our variables. Analyses performed with interpolated soil data generally confirmed these findings (Fig. S5). The only seasonal effect on survival was observed in Mulun where increased summer soil moisture favored survival (Table S5). Here again, our multivariate model showed that soil nutrients affected seedling survival: PC1 axes showed strong negative effect on seedling survival, which was mainly driven by soil S, and to a less extent by soil Mg, Mn, and Ca (Table 2). In contrast to what was observed for the growth model, here canopy openness had a deleterious effect on seedling survival.

The species level analysis showed that *C. hystrix* and *S. arborescens* seedling survival was affected by soil nutrients. Survival of *C. hystrix* decreased with increasing soil N and S, and survival of *S. arborescens* decreased along the soil Ca and Mn continuum (Table S3).

4. Discussion

We found that soil base cations and micronutrients had the strongest effect on both seedling growth and survival across the subtropical landscape studied here. Although we expected increased growth and survival with increasing light availability, and lower growth and survival under drier soil conditions, the seedling growth rates were not strongly affected by light conditions or soil moisture. Canopy openness



Fig. 3. Effect of measured soil properties, soil moisture, and canopy openness (Canopy op.) on seedling survival in each forest and in all forests pooled together. Estimated full coefficients and 95% confidence intervals are shown. Significant values are also shown (*0.05; **0.01, ***0.001).

did show a marginal negative effect on seedling survival, but this pattern was no longer detectable for seasonal light conditions, and wetter soils in the summer diminished plant growth. The landscape level patterns were not generalizable at the forest level and we observed forest-specific responses, especially for the soil properties. Similarly, individual species showed different responses to our predictors, as expected given species-specific adaptations to abiotic conditions. Such species-specific patterns could also be responsible for what observed at the forest and landscape level. For example, the relative abundance of shade-tolerant or light-demanding species could be a reason for the effects of canopy openness we observed.

4.1. Responses to soil N and P

Soil N and P are known to be important to plant growth in nutrientlimited forests (Martinelli et al., 1999; Vadeboncoeur, 2010; Vitousek et al., 2010), and they have been studied intensively. We did not find clear support for their relationship with seedling RGR at the landscape level, and only soil N had a stronger effect on survival. Contrary to commonly reported patterns of increased seedling RGR at higher N levels (Holste et al., 2011), we mostly found lower RGR at higher concentrations of soil N on growth. In Mulun, the only site where we found a clear effect of soil N, RGR decreased along the soil N continuum. The species level results were also mixed, with two species showing clear effects but in opposite directions, namely higher and lower RGR with increasing soil N, and the other species showing no clear responses. In contrast to what was observed by Walters and Reich (2000) and Record et al. (2016), increased soil N displayed predominantly negative effects on seedling survival. However, most studies on soil N and its relationship with seedling dynamics focused on growth rather than survival, which has been less studied, and when survival has been investigated, N often does not have an effect (Gómez-Aparicio et al., 2008). Soil P has been reported as the most dominant limiting nutrient in subtropical forests (Huang et al., 2016; Li et al., 2018), but our forest-level assessment did not find consistent patterns: while one of our sites, Dayaoshan, showed increased RGR along the soil P gradient, the other sites showed a weaker negative relationship. Studies often reported that P addition increases RGR (Vadeboncoeur, 2010; Wan Juliana et al., 2009). In contrast to the results by Record et al. (2016), but similar to the findings by Baraloto et al. (2006) on Neotropical tree seedlings, none of the most abundant species that we analyzed responded to the soil P gradient in their survival, and only two of them had increased (A. campbellii subs. sinense) or decreased (S. arborescens) RGR with increase in available soil P. Our results suggest that these subtropical forests do not experience limitation from either soil N or P at the community level, and that seedling RGR, in particular, is not clearly affected by different availability of these nutrients among microsites. However, results are also species-specific and this should be considered when studying the response of a single species to P availability.

4.2. Responses to soil base cations, Mn, and S

The effects of soil nutrients other than soil N and P have been seldom investigated in natural forests and even in fertilization experiments (Record et al., 2016; Scholten et al., 2017). The response of two tropical species to K in a shade house experiment was tested by Neba et al. (2016), who found increased growth to K addition in one species. Positive effects of K addition on seedling growth have also been reported by Santiago et al. (2012). In our study, we found no clear effects of soil K at the landscape level on the RGR of our seedling communities. In addition, only one of our seven more abundant species responded to differences in soil K. These results might be explained by a relatively equal concentration of soil K in our four sites, which limits the variation in the responses of seedling to K concentration (Table 1).

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was higher at the high end of the gradient, but RGR decreased with increasing Mg. At the forest level, we found seedling RGR to strongly decrease with increasing soil Mg in Mulun, which has the highest concentration of Mg. High Ca and Mg concentrations are expected in karst landscapes such as the Mulun forest (Ford and Williams, 2007). For soil Ca, this result is similar to what was reported by Vadeboncoeur (2010), and in part by Kobe et al. (2002), who found that seedling growth is generally enhanced by Ca addition treatments. On the contrary, seedling survival decreased with increasing soil Ca at the landscape level and also within each forest, although the effects were weaker. Survival was also lower at higher Mg availability. Therefore, there was an apparent trade-off between growth and survival with respect to soil Ca, but not for soil Mg. Other studies also present contrasting results for Ca on survival and growth (e.g. Kobe et al., 2002, no effect of Ca fertilization on seedling survival; Juice et al., 2006, positive effect on both seedling growth and survival in a young sugar maple cohort in the United States).

Calcium is an indispensible nutrient for plants, but excessive concentrations can be toxic and reduce plant growth (White and Broadley, 2003). Our results might suggest that plants adapted to soils with higher Ca availability experience a growth-survival trade-off, with an overall higher RGR, but also higher mortality possibly due to some negative effects on other physiological process related to Ca uptake and mobilization pathways (White and Broadley, 2003). However, there was no apparent trade-off between growth and survival with respect to soil Mg. Magnesium is an important nutrient mainly involved in plant growth and development. Magnesium is a component of plant chlorophyll and several enzymes involved in carbon metabolism (Gransee and Führs, 2012). However, at higher concentrations Mg can be toxic and have negative effects, which may be reflected as reduced growth. Concentration of soil Mg was higher in the karst forest of Mulun, where soil can be subjected to higher weathering compared to the other forests and the RGR was negatively responded to the soil Mg gradient.

The only species whose survival was clearly influenced by soil Ca, *S. arborescens*. It showed a negative slope, similarly to the two species that responded to soil Mg, which experienced higher RGR at lower levels of soil Mg. For all patterns described here, it is important to remember that the effects are species-specific and conclusions on species for interests should be addressed through focused studies.

We found patterns of seedling responses to soil Mn comparable to those of soil Ca. Manganese is another micro-nutrient essential for plant growth and photosynthetic activity, but which can be toxic at higher concentrations (Millaleo et al., 2010). We are not aware of any study reporting the response of seedling performance to soil Mn gradient in forests, as most research on the subject focuses on crop species or on the toxic effect of Mn at high concentration (Mcquattie and Schier, 2000). Given that there is a strong correlation between Mn and Ca (Fig. S3), it is not surprising that the response to our seedlings communities to Mn closely resembled that of the Ca response, suggesting a similar trade-off. Sulfur is another key nutrient to plant growth, which has received little attention outside of agriculture research (Scherer, 2001), or in studies of S effects on soil acidification (Bethers et al., 2009). Here, in our subtropical landscape, we show that seedling survival is negatively affected by soil S gradients and this result was fairly consistent at the forest level, while seedling RGR negatively responded to soil S in one forest (Dayaoshan). While S is an essential element for plant defensive compounds, soil acidity due to S deposition can cause deleterious effects on forest ecosystems (Hawkesford and De Kok, 2007). South China has experienced increasing acidification in the past decades (Liu et al., 2010), which might have impacted the responses identified in this study. The mechanisms governing these responses need to be further studied to clarify whether it is due to altered concentrations of elements such as base cations resulting from acidification of the topsoil.

Seedling RGR along the soil Ca continuum at the landscape level

4.3. Responses to soil moisture and canopy openness

Soil water availability is as important as soil nutrients for plant growth and survival, and is also subject to seasonal variation in many ecosystems, with consequences on species distributions (Comita et al., 2009). In our study, seedling RGR decreased with increase in soil moisture in summer in Cenwanglaoshan, and in contrast increased with increasing moisture in Dayaoshan in winter, indicating seasonal responses to water availability at the forest level. Further long-term and experimental studies can discern these patters to establish causal relationships between water availability for the seedlings and their relative growth rate. In our results, greater soil moisture resulted in greater seedling survival in Mulun, a karst forest where water runoff could be higher and therefore species living in microsites with higher water availability are favored, particularly in the wetter summer months. While species in this karst landscape have diversified their water use strategies (Geekiyanage et al., 2019), it is likely that seedlings do not hold a root system to reach underground water or run though the rock pores, and therefore rely more on soil water.

Canopy openness did not show any effect on RGR at the landscape, forest, or species level. This is surprising, because in the light limited forest understory, a positive relationship between light availability and seedling growth can be expected (e.g. Augspurger, 1984; Beckage and Clark, 2003). In our forests, canopy openness was quite homogeneous (Table 1). However, seedling growth has been shown to be sensitive to very small changes in canopy openness in the shady understory (Montgomery and Chazdon, 2002). Our results do not agree with such patterns, and provide instead evidence of a greater effect of soil properties rather than light. Several studies also reported clear effects of increasing light on seedling survival (Balderrama and Chazdon, 2005). In our study, we found that seedling survival decreased with increasing light availability at the landscape level (Fig. 3; Gómez-Aparicio et al., 2008). It is important to note that, at the community level, responses might be confounded by opposite responses of pioneer and shade-tolerant species (Balderrama and Chazdon, 2005). However, the clear negative relationship found at the landscape level was not found at the forest level (Fig. 3) or at the individual species level (Table S3). Our results suggest that for the subtropical seedlings studied here, RGR and survival are not strongly affected by light availability.

5. Conclusions

Our study is the first to report clear effects of nutrients such as Ca, Mg, and Mn on growth and survival of naturally regenerating seedling communities. Forests in subtropical China have experienced important changes in their soil composition during the last decades, mostly due to soil acidification and associated processes (Liu et al., 2010). Soil acidification has resulted in a decrease in base cations concentration in forest soil which could have severe effects on forest functioning and processes (Yu et al., 2020). We cannot conclude if such changes are also affecting seedling performance responses to nutrient availability, as our study was conducted over a short time period compared with soil change dynamics, but we suggest that long-term studies should focus on examining responses to such nutrients which could profoundly affect forest regeneration and structure. The results of this study can be relevant not only from an ecological perspective, but can be also of use to forest practitioners in this region, which hosts extensive forested area yet mostly constituted by secondary forest and plantations, especially Chinese fir and Eucalyptus spp. (Hu et al., 2014, 2019). Specifically, we highlight the site specific responses in the communities of the four forests we analyzed due to different soil conditions. We recommend that the soil properties of reforestation sites should be taken into account with respect to a wide range of soil nutrients when planning for restoration activities. More focused studies on the effects of soil properties on the most commonly planted tree species can provide additional support to decision makers as well as optimize afforestation practices. For example, when planning new fertilization experiments on species of interests for reforestation programs, practitioners should also evaluate the response to nutrients such as calcium, magnesium, and manganese along with the commonly used nitrogen and phosphorus. This could be useful for improving the production capacity of seedlings that will be planted, as well to favor the establishment success in the reforestation sites.

CRediT authorship contribution statement

Francesco Martini: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft. **Shang-Wen Xia:** Methodology, Formal analysis, Writing - review & editing. **Chaobo Zou:** Investigation, Writing - review & editing. **Uromi Manage Goodale:** Conceptualization, Methodology, Supervision, Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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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.2020.118382.

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