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ORIGINAL ARTICLE

Cunninghamia lanceolata sprout population structure, dynamics and biomass allocation changes during *Phyllostachys edulis* expansion in middleō-southern China

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Abstract

Key message **Chinese fir sprouting population lifespan is shortened and survivorship situation and biomass are also changed by bamboo expansion via declines in mother tree density and weakened physiological accommodation.**

Abstract Natural regeneration is a vital means of maintaining forest populations. Although bamboo expansion negatively affects population structures of neighboring communities, its influence on sprouting natural regeneration is still poorly understood. We compared the population structure and biomass allocation of Chinese fir regenerating sprouts in previous (CLS), middle (CPM) and late (PCM) periods of bamboo expansion. Life tables and survivorship curves were used to assess sprouting population structure and survival dynamics, and allometric analysis was conducted on biomass allocation. The results showed that bamboo expansion reduced the number and longevity (maximum age class shorted from X to VI) of the Chinese fir sprouting population and weakened its survival capacity. Survivorship curves indicated that the CLS population conformed more to a recession type (Deevey III) while CPM and PCM tended to be stable types (Deevey II). Highly mortality and survival risk in the early growing stage drove a population decrease. Meanwhile, sprouting component biomasses were decreased first and then increased by expansion effect, leaf and stem biomass had constant relationships with total biomass, and branch biomass had allometric relationships with total biomass. We considered that bamboo expansion changed sprouting population survival and growth mainly through affected Chinese fir mother tree density and growth.

Keywords *Cunninghamia lanceolata* · Sprouting regeneration · Bamboo expansion · Biomass allometry

Abbreviations

Cl	*Cunninghamia lanceolata*
Pe	*Phyllostachys edulis*
PC	Mixed stand of moso bamboo with a few Chinese firs
CPM	Mixed stand of Chinese fir with a few moso bamboo shoots
CLS	Pure stand of Chinese fir
TB	Total biomass
SB	Stem biomass
BB	Branch biomass
LB	Leaf biomass

Introduction

During growth, plants alter investment strategies with heterogeneous environments, which are reflected by changes in population structure and energy or material allocation among organs, achieving a balance between resource availability and population succession (Weiner 2004; Li et al. 2019). Population structure, dynamics and biomass allocation respond to the outside environment varying within different growth periods, successional tendency and reacting mechanisms (Fuchs et al. 2000; Zhang et al. 2008; Liu et al. 2020; Taitelbaum et al. 2020). The latter also reflect individual responses to heterogeneous habitat (Liu et al. 2020), inherent allocation patterns and environmental influences on different plant parts (root, leaf and stem) and the relationship between partial and total biomass allometry (Weiner 2004; Poorter et al. 2012), which could reveal scale-independent inner rules. Therefore, studying population structure and dynamics in heterogeneous habitats could reveal population response mechanisms in a changing environment.

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Sprouting is a frequent mode of vegetation regeneration. Dormant buds are the biological foundation of sprout regeneration and sprout when endogenous hormone is unbalanced, affected by environmental disturbances (e.g., felling, fire, snow load) (Ross et al. 1986; Lilly et al. 2012; Nakano and Sakio 2018), maintaining population succession in the event of scarce seed propagation (Li et al. 2017). Although sprout regeneration is worse than seedling regeneration for obtaining large-diameter wood, the management cost of sprout regeneration is one third of that of seedlings (Ye 2007), and it was easier to adapt the local environment than seedlings, especially in poor site conditions (Li and Ritchie 1999), which had more advantages for medium/small-diameter wood production (Lin et al. 1996); moreover, Higgins et al. (2000) verified sprouting could remediate the path loss of pollen diffusion caused by disturbance. However, the contribution was difficult to evaluate because of changes in the surrounding environment (Dodd et al. 2013). In fact, sprouting responses to heterogeneous habitats remain poorly understood, so it is essential to investigate sprouting ability in various environments, as it is crucial for protection and management of secondary forest (de Lucena et al. 2015; Zhang et al. 2018).

Bamboos are opportunistic-clonal species, which can limit the regenerative processes and maintain lower native species diversity (Lacerda and Kellermann 2019). When bamboo rhizomes expanded into neighboring communities, the survival mode and growth of regenerating species changed (Tang et al. 2007; Wang et al. 2008; Caccia et al. 2009; Liu et al. 2013); however, the changes were mixed. Bai et al. (2013) found decreasing richness and evenness indices of arbor forests and shrubs but increasing herbaceous plants with bamboo expansion. Ouyang et al. (2016) demonstrated the richness and evenness of all species in mixed broadleaf-conifer forests decreased. Moreover, Montti et al. (2014) suggested that a high density of bamboo individuals restricted height growth and canopy gap formation after bamboo shoot death or felling effectively promoted regenerating seedling height growth and density (Holz and Veblen 2006; Wang et al. 2016b), which is most obvious in the first year after gap formation. Studies suggested that the external conditions which seedling regeneration relies on are altered by bamboo expansion, including sunlight, nutrients and biological factors (Caccia et al. 2009; Gopakumar and Motwani 2013). However, our understanding of the reason the decrease remains limited.

Chinese fir (*Cunninghamia lanceolata*) and moso bamboo (*Phyllostachys edulis*) are woody species endemic to southern China, and mixed forests comprising these species are widespread (Lin et al. 1996). Mixed forest of moso bamboo and Chinese fir is widely distributed in southern China. The changing biodiversity effect of bamboo expansion to Chinese fir forest has been widely studied; instead of the other broadleaf forests, Xu et al. (2019) showed an increasing trend in the Chinese fir community. In the expanding process, bamboo could realize the efficient utilization of soil via synergy of fine root morphology and nutrient content when expanding into Chinese fir forest (Cai et al. 2019) and occupied the fertile-upper soil layer with their powerful rhizome systems. In addition, stronger stoichiometric homeostasis of juvenile individuals promoted bamboo expansion success (Peng et al. 2021). While the Chinese fir root systems could not obtain sufficient nutrients at the upper layer, our other study found they transferred to the deeper soil layer, which can also be found in other species (Qu et al. 2020). Chinese fir has great sprouting regeneration capacity, although most studies have focused on its sprouting cultivation (Chen et al. 2015, 2018); however, the role of Chinese fir sprouts in population regeneration under the impact of bamboo expansion remains poorly understood.

Therefore, Chinese fir sprouts were the focus of this study. We analyzed population structure and dynamics and biomass allocation of Chinese fir sprouts along with bamboo expansion to clarify: (1) whether and how the population regeneration of Chinese fir was affected with bamboo expansion from a sprout perspective; (2) how the sprouting modular biomass was allocated with the increasing effect of bamboo expansion. We make some suggestions relevant to bamboo-Chinese fir mixed management.

Materials and methods

Study site

This study was carried out in Hongheling Forest Farm (113°28′–113°29′N, 29°26′–29°28′E), a lowland hill area with a subtropical monsoon climate in northeast Hunan Province in the middle of southern China, where mean annual temperature is approximately 16.4 °C, and mean annual precipitation is about 1469.1 mm. Affected by initial farming and long-term rain wash, slope soils have a high proportion of gravel and are shallow (22–90 cm). The investigated stands are comprised of planted, even-aged (21 years) Chinese fir, with uneven-aged moso bamboo. Due to rising labor costs, little management has been conducted in this region, with bamboo rhizomes expanding into the Chinese fir forest to form mixed stands, where undergrowth vegetation consists of *Dryopteris tenuicula*, *Lygodium japonicum*, *Mussaenda shikokiana*, *Clerodendrum cyrtophyllum* and *Callicarpa bodinieri*, etc.

Sampling

Three *Cl* and *Pe* mixed forest interfaces without manual disturbance were randomly chosen in October 2019. To minimize the effect of the neighboring Chinese fir/bamboo forest stand, and improve comparability in expanding stages, in each interface, a belt transect (20 m width × 40 ± *l* m length) was established (*l* was confirmed via the practical situation of bamboo expansion) (Fig. 1). Meanwhile, three quadrats (20 m × 5 m) were established perpendicular to the expansion direction, named CLS, CPM and PCM, representing previous, middle and terminal stages of the affected period, respectively (Peng et al. 2021). Additionally, altitude, longitude, latitude and slope aspect were determined with a G120BD handheld global positioning system (UniStrong LTD, China). Slope gradient was surveyed with a DQY-1 type geologic compass (Harbin Optical Instrument Factory LTD, China); canopy closure was determined according to the proportion of the sky obscured by branches from the plot by cross-shaped walking step by step. In each quadrat, mean soil depth was averaged from three randomly located soil profiles (Table 1).

Sixty-seven sprouting clusters including 844 *Cl* and *Pe* individuals were recorded, their diameter at breast height, height and crown breadth were measured (in each quadrat), and sprouting populations of *Cl* were tallied by quantity, height and basal diameter. Ten sprouts in each cluster were harvested at their base (all individuals were harvested when < 10), divided into branch, leaf and stem, and taken in labeled packages to the laboratory, where they were dried to constant weight at 60 °C.

Diameter classification

Since trees are long-lived, and therefore not yet monitored for complete life cycles, researchers have focused studies of tree population dynamics on diameter as a surrogate for age in a “space for time” approach (Zhang et al. 2008; Wu et al. 2019). To reveal the population structure of sprouts, we adopted this approach, where sprouting samples were

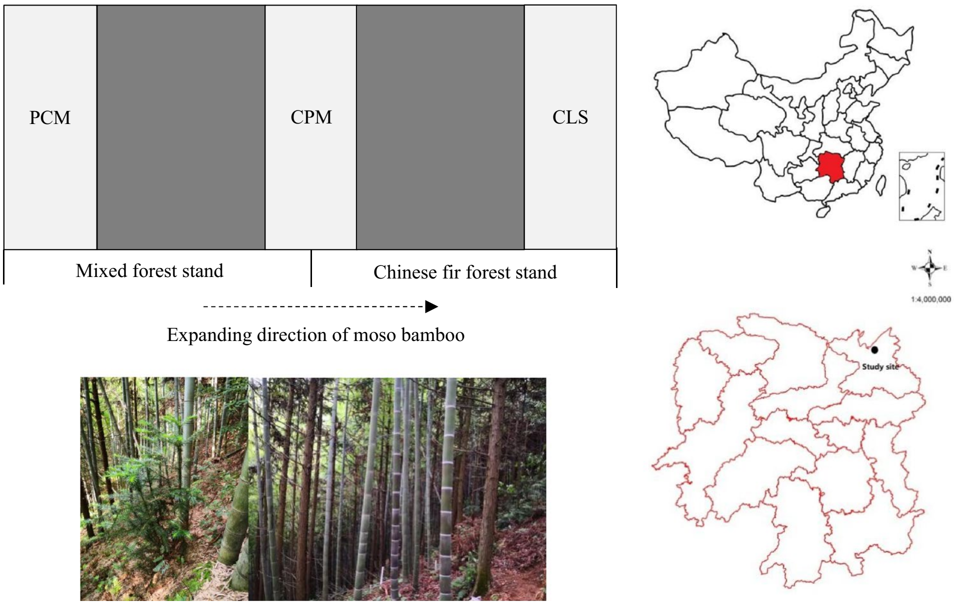

Fig. 1 Schematic diagram of sampled stands (20 m width × 40 ± *l* m length with three quadrats of 20 m × 5 m) in Hongheling Forest Farm in Hunan Province, south-central China. *CLS* Chinese fir forest, *CPM* Chinese fir forest mixed with a few moso bamboos, *PCM* moso bamboo forest mixed with a few Chinese firs

Table 1 Site characteristics and dominant species densities of three sampling plots at Hongheling Forest Farm located in northeast Hunan Province in south-central China

Category	Plot 1	Plot 2	Plot 3
Longitude and latitude	113°29′28.5"N, 29°26′43.8"E	113° 29′33.6"N, 29°27′2.8"E	113°28′9.6"N, 29°2846.7"E
Altitude (m)	33	158	45
Slope (°)	32–42	15–27	38–40
Slope aspect	NW	SE	W
Canopy closure	0.88	0.92	0.90
Soil depth (cm)	35–86	22–90	30–75
Volume weight of soil ($g \cdot cm^{-3}$)	1.22 ± 0.36	1.28 ± 0.25	1.35 ± 0.28
Cl-mother plant density ($plant \cdot ha^{-1}$)	1912	1913	2375
Cl-sprouting density ($plant \cdot cluster^{-1}$)	12.0 ± 1.7	15.4 ± 0.9	12.3 ± 3.1
Pe-density ($plant \cdot ha^{-1}$)	1500	3037	2788

divided into ten classes with 2-mm basal diameter intervals. Basal diameter $d<4$ mm was defined as class I (the individuals of $d<2$ mm were rarely counted; here, we incorporated them into class I), 4 mm $\leq d<6$ mm was defined as class II, and so on until $d\geq 20$ mm was defined as class X.

Statistical analysis

Population structure and dynamics

Static life tables, which are an important measure to reveal population dynamics, were created using the number of individuals. However, they include multi-generation overlap in specific age dynamics and do not track a particular population over its whole life history. Therefore, a negative mortality rate in the table may reflect systematic sampling errors, and so previous studies have modified the statistics with a smoothing treatment (Zhang et al. 2015; Peng et al. 2018). Here, we followed the approach of Qin et al. (2020), therein $l_x=a_x/a_0\times 1000$; $d_x=l_x-l_{x\text{-}1}$; $q_x=d_x/l_x$; $L_x=(l_x-l_{x+1})/2$; $T_x=\sum L_x$; $e_x=T_x/L_x$. Here, x is age class; a is the number of individuals in the population (mean number per cluster); l is standard survival of population; d is mortality number; q is mortality ratio; L is interval longevity; T is total life; e is life expectancy.

Survivorship curves are depicted with age class as the x-axis and log values of l_x as the y-axis and fitted by power function (Deevey III) and exponential function (Deevey II) to elaborate survival status (Hett and Loucks 1976). The imitative effect was assessed with coefficients of determination and F values.

Allometric analysis

Trait differences were analyzed using one-way repeated measures ANOVA with SPSS 19.0 (IBM, Armonk, NY, USA). Trait allometry was described by $\log_{10}$ function as follows:

Here x is modular biomass, Y is total biomass, function slope b is allometric exponent, and a is a constant. Standard major axis (SMA) analysis was conducted to calculate b and its difference from 1.0; if the slope had no significant difference, the common slope was listed. We used the Wald test to determine significant differences in slope offsets along common slopes, using the smart package in R 4.0.1 software.

Results

Comparison of mother plant and sprout traits of Chinese fir in expanding stages

All sprouting traits were significantly different among stages except for stem biomass (Table 2, $P=0.203$). Height and base diameter in CLS were significantly higher than in CPM ($P=0.000$) and PCM ($P=0.000$), and sprouts had the highest cluster density in PCM, while leaf, branch and total biomass were lowest in CPM. Sprouting traits tended to initially decline and then increase, which suggests a stress reaction during early expansion. For the mother tree, there were no significant differences in growing traits except density, which in CLS was highly significantly greater than for CPM and PCM ($P=0.000$).

Table 2 Description of Chinese fir mother tree and moso bamboo traits within three forest stands affected by bamboo expansion

Plant types	Traits	CLS	CPM	PCM	*F* values	*P* values
Cl-sprout	Height (cm)	40.82 ± 1.81A	31.93 ± 1.43B	34.34 ± 1.05B	8.20	0.000^{***}
	Base diameter (mm)	5.41 ± 0.24A	3.2 ± 0.13B	3.77 ± 0.12B	33.767	0.000^{***}
	Cluster density (plant·cluster^{-1})	10.1 ± 1.27B	12.5 ± 1.30AB	16.0 ± 1.27A	5.772	0.006^{**}
	Stem biomass (g)	0.29 ± 0.04a	0.24 ± 0.01a	0.31 ± 0.03a	1.605	0.203
	Leaf biomass (g)	0.94 ± 0.09A	0.68 ± 0.04B	1.01 ± 0.07A	6.31	0.002^{**}
	Branch biomass (g)	0.24 ± 0.04A	0.13 ± 0.01B	0.21 ± 0.02A	4.941	0.008^{***}
	Total biomass (g)	1.33 ± 0.14A	0.99 ± 0.06B	1.43 ± 0.11A	5.332	0.005^{***}
Cl-mother tree	DBH (cm)	44.93 ± 4.16a	49.87 ± 4.16a	43.07 ± 4.31a	0.696	0.504
	Height (m)	10.33 ± 0.43a	10.43 ± 0.51a	8.7 ± 0.69a	3.065	0.057
	Canopy width (m)	2.89 ± 0.21a	2.94 ± 0.23a	3.05 ± 0.22a	0.151	0.861
	Density (plant·ha^{-1})	2563.6 ± 62.22A	2013 ± 96.08B	1329.4 ± 72.01C	62.715	0.000^{***}
Pe	DBH (cm)	–	11.19 ± 1.5A	10.02 ± 1.68B	20.832	0.000^{***}
	Height (m)	–	11.02 ± 2.09a	10.77 ± 1.5a	0.691	0.407
	Density (plant·ha^{-1})	–	2813 ± 212.1A	1725 ± 156.5B	40.231	0.000^{***}

Letters in each column denote significant ($P<0.05$) or highly significant difference ($P<0.01$) with 95% confidence interval

$^{***}P<0.001$, $^{**}P<0.01$

Static life table and survivorship curves

As indicated by Table 3, the sprouting *Cl* population was mainly at age class I (63.53% of total classes). Age class II had 19.96%. All of the other classes were < 10% and decreased with age class. In the regenerating CLS population all age classes I–X were represented, CPM contained had age class range I–VIII. PCM had age class I to VI, and the longevity of *Cl* sprouting was shortened with increasing expansion. Meanwhile, CPM and PCM clusters had higher densities than CLS at ages I–II and lower densities in age classes III–X. Mortality ratio with age (q_x) fluctuated to a varying degree (Table 3). The population mortality ratio peaked in age classes I, IV and IX in CLS, in classes I, IV and VI in CPM and in age class II in PCM; an adapting heterogeneity was showed in various expanding stages. Meanwhile, with increasing expansion, life expectancy (e_x) also fluctuated, for example, peaks appeared in age classes II and VI in CLS, where the individuals had strong vitality via a biotic filter.

As Fig. 2 and Table 4 shows, survivorship curves initially decreased sharply and then slowly, more closely fitting a Deevey III model ($R^2 = 0.948$, $P < 0.01$ for CLS), indicating

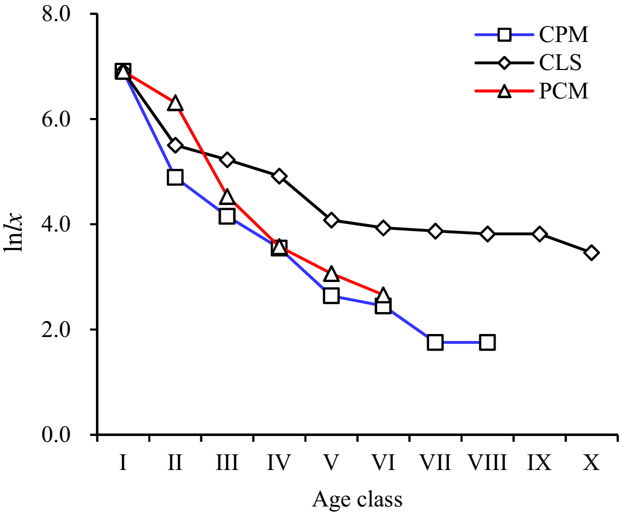

Fig. 2 Survivorship curves of Chinese fir sprouting population illustrated with age class and log function of *lx* in three expanding stages. CLS = Chinese fir forest; CPM = Chinese fir forest mixed with a few moso bamboos; PCM = moso bamboo forest mixed with a few Chinese fir

Table 3 Static life table of the Chinese fir sprouting population in three expanding stages

Expanding stage	Age class	a_x	l_x	lnl_x	d_x	q_x	L_x	T_x	e_x
CLS	I	6.47	1000	6.9	755	0.75	623	1315	1.31
	II	1.59	245	5.5	59	0.24	216	692	2.82
	III	1.21	186	5.2	50	0.27	161	476	2.55
	IV	0.88	136	4.9	77	0.57	98	315	2.31
	V	0.38	59	4.1	14	0.24	52	217	3.67
	VI	0.29	45	3.8	8	0.17	41	165	3.68
	VII	0.24	37	3.6	0	0.00	37	124	3.32
	VIII	0.24	37	3.6	2	0.05	36	87	2.32
	IX	0.23	36	3.6	3	0.09	34	50	1.41
	X	0.21	32	3.5	0	0.00	16	16	0.50
CPM	I	9.61	1000	6.9	867	0.87	566	768	0.77
	II	1.28	133	4.9	69	0.52	98	202	1.52
	III	0.61	64	4.2	29	0.45	49	104	1.63
	IV	0.33	35	3.5	21	0.60	24	55	1.57
	V	0.17	14	2.6	2	0.17	13	30	2.16
	VI	0.11	12	2.4	6	0.50	9	17	1.51
	VII	0.06	6	1.8	0	0.00	6	9	1.52
	VIII	0.06	6	1.8	0	0.00	3	3	0.52
PCM	I	9.33	1000	6.9	450	0.45	775	1214	1.21
	II	5.13	550	6.3	457	0.83	321	439	0.80
	III	0.87	93	4.5	57	0.62	64	118	1.27
	IV	0.33	36	3.6	14	0.40	29	54	1.50
	V	0.20	21	3.1	7	0.33	18	25	1.17
	VI	0.13	14	2.7	0	0.00	7	7	0.50

Ten age classes were divided with 2-mm basal diameter intervals: CLS = Chinese fir forest; CPM = Chinese fir forest mixed with a few moso bamboos; PCM = moso bamboo forest mixed with a few Chinese firs

Table 4 Survivorship curve model fits with power function (Deevey III) and exponential function (Deevey II) for Chinese fir sprouting populations at different expansion stages

Expanding stage	Curve model	Equation	R^2	F value	P value
CLS	Deevey III	$y=6.990x^{-0.305}$	0.948	72.834	0.001^{***}
	Deevey II	$y=7.300e^{-0.108x}$	0.947	71.644	0.001^{***}
CPM	Deevey III	$y=7.242x^{-0.578}$	0.967	118.654	0.000^{***}
	Deevey II	$y=7.887e^{-0.205x}$	0.974	150.425	0.000^{***}
PCM	Deevey III	$y=7.799x^{-0.554}$	0.927	50.626	0.002^{***}
	Deevey II	$y=8.595e^{-0.201x}$	0.976	72.434	0.000^{***}

$^{***}P < 0.001$

Table 5 Chinese fir sprout parameters affected by bamboo expansion in different forest plots analyzed by SMA regression

Expanding stage	SB-TB		LB-TB		BB-TB	
	b	R^2	b	R^2	b	R^2
CLS	0.95 (0.85,1.07)	0.64	1.02 (0.98,1.06)	0.96	1.62 (1.26,2.08)	0.34
CPM	1.00 (0.9,1.11)	0.67	1.03 (0.99,1.06)	0.96	2.00 (1.58,2.52)	0.24
PCM	0.96 (0.88,1.04)	0.76	1.01 (0.98,1.03)	0.98	1.49 (1.26,1.76)	0.53
P values$^{\#}$	0.657		0.417		$0.000<0.001$	

TB total biomass, *SB* stem biomass, *LB* leaf biomass, *BB* branch biomass. R^2 is determined coefficient, P values$^{\#}$ indicate the difference between each common slope and 1.0

Table 6 Test for common slope and shifts in Chinese fir modular biomass relationships in forest stands

Parameter		*SB-TB*	*LB-TB*	*BB-TB*
Common slope		0.97 (0.91,1.03)	1.01 (1.00,1.03)	–
Heterogeneity of slope		$P=0.77$	$P=0.71$	$P=0.13$
Shift along common axis	CLS	-0.026^{a}	0.006^{a}	0.000^{b}
	CPM	0.033^{a}	-0.007^{a}	0.057^{a}
	PCM	-0.021^{a}	0.004^{a}	-0.042^{a}

Slope 95% CI denoted in brackets; superscript letters denote the significant difference of shift in expanding stages with multiplied comparison; the same letter denotes no significant difference

that the CLS population belonged to a recession type which had high mortality in the early stages (age classes I–II). In contrast, CPM and PCM more closely fitted a Deevey II model ($R^2_{\text{CPM}} = 0.974, R^2_{\text{PCM}} = 0.976$, $P<0.01$), indicating more stable populations with similar mortality in each age class.

Biomass allocation of sprouts

Sprout modular biomass pairwise comparisons were all significantly correlated (Table 5). While *SB-TB* and *LB-TB* were not significantly different in expanding stages, the *SB-TB* common slope was 0.97 (95% CI 0.91–1.03) (Table 6, Fig. 3), and *LB-TB* was 1.01 (95% CI 1.00–1.03), which was not significantly different from 1.0. Therefore, *LB* and *SB* had constant relationships with *TB*, while the *BB-TB* common slope was significantly different from 1.0 ($P=0.000<0.001$), indicating an allometric relationship. Although the *SB-TB* and *LB-TB* slopes showed no obvious shift along a common axis (Table 6, Fig. 3), CPM slope shifts were higher than those of PCM and CLS.

Correlations among sprout, mother tree and bamboo

Both the mother tree and bamboo could affect sprout growth to some extent (Table 7), as indicated by significantly positive correlations between mother tree DBH and cluster density ($r=0.663$) and between mother tree canopy width and sprout basal diameter ($r=0.600$). However, mother tree density was significantly negatively correlated with sprouting height ($r=-0.803$) and cluster density ($r=-0.667$), which showed that the dominant factor affecting each sprout trait was different. In terms of bamboo density, there was a significantly negative relationship between mother tree density and bamboo density ($r=-0.915$), while there were no significant correlations between mother tree growing traits

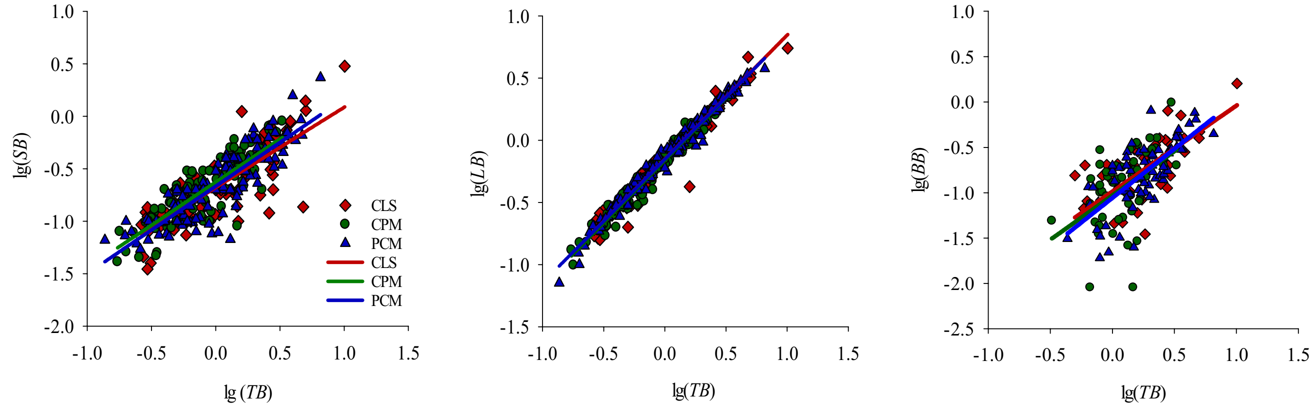

Fig. 3 Relationships between component biomass and total biomass of Chinese fir sprouts in different bamboo expansion stages. *TB* total biomass, *SB* stem biomass, *LB* leaf biomass, *BB* branch biomass

Table 7 Spearman correlations among mother tree, bamboo and sprouting traits. Numbers in bold denote a significant or highly significant correlation

Trait factors		Sprout				Mother plant			
		Height	Basal diameter	Total biomass	Cluster density	DBH	Height	Canopy breadth	Density
Mother tree	DBH	– 0.017	– 0.117	0.111	0.633*	–	–	–	–
	Height	– 0.467	– 0.433	– 0.076	0.204	0.717*	–	–	–
	Canopy width	0.212	0.600*	0.053	0.452	0.367	0.051	–	–
	Density	– 0.803**	– 0.334	0.190	– 0.667*	0.121	0.467	– 0.233	–
Moso bamboo	Density	– 0.695*	– 0.119	– 0.252	0.712*	0.051	– 0.254	0.068	– 0.915**
	DBH	0.402	0.243	0.333	0.079	– 0.307	0.033	– 0.485	0.402
	Height	0.521	0.184	0.083	0.371	0.214	0.085	0.136	0.521

Equation: $\lg Y = a + b\lg x$

$^{**}P < 0.01$, $^{*}P < 0.05$

(DBH, height and canopy breadth), and bamboo DBH and height indexes did not significantly affected mother tree and sprouts. However, bamboo density was significant negatively correlated with sprouting height ($r = -$ 0.695), while significantly positively affected the sprouting cluster density ($r = 0.712$).

Discussion

Population characteristics of sprout regeneration affected by bamboo expansion

Plants maintain their population structure through natural regeneration, which reflects long adaptation to local habitat conditions (Villlellas et al. 2013). Although bamboo expansion effects on native species abundance have been widely reported, its effects on tree population dynamics are still poorly understood. We observed that sprouting by Chinese fir was influenced by bamboo expansion, and it was manifested in a gradually decreasing population as a whole and a shortening in population longevity from age class X to VI (Fig. 2), which suggested that bamboo expansion had a negative effect on a sprouting population. This observation also supported the conclusion that bamboo expansion lowered native community diversity and abundance (Yang et al. 2010). Mortality ratios (q_x) of three stages fluctuating with age classes (Table 3) indicated that they resulted from a combination of many factors. Ye (2007) suggested that increasing numbers and growth of sprouts were associated with increasing nutrient requirements. In our study, there were no significant differences in growing traits except density, which in CLS was highly significantly greater than in CPM and PCM, indicating bamboo expanding process caused the weak individual mortality, lowering nutrient uptake of mother trees by expansion (Peng et al. 2021), and density-dependent effects associated with individual interspace further hampered nutrient supply for sprouts.

Survivorship curves showed (Fig. 2; Table 4) that CLS had high sprout mortality, while CPM and PCM maintained similar mortality at each age period, suggesting that bamboo expansion changed sprout survival. Comparing the populations at various expansion stages, population density increased and then decreased from CLS to PCM, which is likely a stress response to bamboo expansion. Bamboo has strong rhizome systems, and its expansion can change soil nutrient mineralization (Song et al. 2013, 2016) and microbial community structure (Lin et al. 2014b; Xu et al. 2015), worsening external conditions for plants. Altman et al. (2016) considered that severe disturbance combined with a biotic understory filter of bamboo forest could disrupt ecosystem dynamics by reducing native tree recruitment, as supported by this study.

Population dynamics

In this study, mortality ratio at age class VIII in CLS was close to 1.0, while the ratio was > 9.0 after age class II in CPM and PCM (Table 3). Overall environment was likely to influence sprouts' survival in early stages, reflecting the heterogeneous survival strategies of populations in relation to bamboo expansion. This observation is supported by previous research maintaining that survival capacity of a population is via a reduction in its individual numbers in early stage (Zhang et al. 2008; Peng et al. 2018). The survival function analysis indicated that similar functions for CLS and CPM differed from PCM with higher sprout mortality and that nutrient availability in CPM affected by the expansion might be more obvious than in the others. With an increasing sprout population, the mother tree consumes more nutrients and competes with sprouts, which might accelerate mother tree decline and even death.

Here, we only considered the effects of expanding bamboo shoots and stock plants on the sprout population. However, there are many factors that restrict natural regeneration (e.g., moisture availability, light, understory vegetation and soil factors) (Denslow et al. 1991; Tian et al. 2006; Chen et al. 2015). Therefore, a further investigation on how bamboo expansion affects tree survival and subsequent effects on natural regeneration should be conducted.

Biomass allocation effect of bamboo expansion

Optimal partitioning theory (OPT) and allometric partitioning theory (APT) are two concepts. OPT considers that plants allocate more biomass relative to the organ that has the lowest gaining capacity for limited resources. Conversely, allometric partitioning theory (APT) states that biomass allocation among organs is a power function of plant size and independent of environmental variation (Liu et al. 2020), that is, the biomass allocation is determined by hereditary. We found that the component biomass significantly differed during bamboo expansion, initially declining and then increasing (Table 2), which caused a stress response when bamboo expanded into the Chinese fir forest, similar to the results of recent studies (Cai et al. 2019; Liao et al. 2021). It might be correlated with the changing population structure by endogenous hormone adjustment affected by bamboo expansion. Sprouting population longevity declined and numbers increased with bamboo expansion. The increasing ratio of early ages showed a decreased biomass in CPM, when weak mother plants died in PCM, promoting sprout growth and density increase (Ye 2007). The mean biomass rose, which demonstrated the sprouts' response strategy to the expansion. Furthermore, we found that *LB* and *SB* both had constant relationships with *TB*, while *BB*-*TB* showed an allometric relationship reflected by obvious shifts along a common axis. The CPM offset was higher than for PCM and CLS, suggesting that the relative growing ratio of CPM branch biomass was higher than for CLS and PCM. It is well known that Chinese fir sprouts branch with age; consequently, our results support the allometric partitioning theory (APT) rather than OPT, consistent with the conclusion of Liu et al. (2020).

Spearman correlation analysis demonstrated that total biomass was not correlated with the mother tree (Table 7), and therefore we speculated that sprouting biomass allometry was inherently determined, not by the external environment. In conclusion, bamboo expansion affected sprout biomass mainly by changing its population structure. However, quantitative analysis of habitat relationships with allometric growth traits in bamboo expansion were not conducted, and further study of this is recommended.

Mechanism of bamboo expansion affecting sprout regeneration

Expanding bamboo had strong rhizome systems and could decrease the neighboring plant reproduction via restrained seed germination by allelopathy (Bai et al. 2013) and competition for upper soil resource (Yang et al. 2017). However, different from the seedling regeneration, few studies have focused on sprouting regeneration affected by invasion. Our study demonstrated that the effect could decrease the sprout population's life span while promoting bud sprouts, which might be related to the changing growth situation of mother plants. Bamboo expansion could decrease the native soil carbon storage, restraining mineralization and nitrate capacity (Fukushima et al. 2015; Wang et al. 2016a). Nutrient acquisition of bamboo rhizomes' fragmented distribution formed heterogeneous soil biochemistry (Changa and Chiub 2015). Native microbial community structure, distribution and enzyme activity changed accordingly (Lin et al. 2014b; Xu et al. 2015). For native species, our further study found the upper layer of soil occupied by bamboo rhizomes. Chinese fir root system had to grow toward the deeper layer to avoid the direct competition with bamboo for spatial resources. Meanwhile, the difference in stoichiometric structure in functional root systems was also narrowed with bamboo expansion to optimize resource acquisition (Peng et al. 2021). Therefore, Chinese fir trees adjust their morphology and physiology to adapt to the changing environment.

Combining the results (Table 2 and Table 7), we found sprouts were more sensitive than mother trees to the effect. It is well known that the nutrients for sprouts come from the mother trees, which considering changing physiology and growth would be bound to the former. Gao et al. (1994) stated that the Chinese fir mother trees' endogenous hormone adjustment caused the buds to sprout. For example, cytokinin rose to a higher concentration and heteroauxin (IAA) and inhibitory substance levels were low when sprouting started (Lin et al. 1996), which involves a complicated adjustment to balance growing demand between themselves and their sprouts (Lin et al. 1996; Peng et al. 2004; Ye 2007). The adjustment might be closely associated with nutrient and water acquisition of mother trees. On the one hand, parts of the root system are concentrated in deeper and infertile soil layers because of increasing bamboo influence (Qu et al. 2020) and inhibited plant growth (Lin et al. 2014a). There is a lower stoichiometric homeostasis of the Chinese fir root system compared to juvenile bamboo (Peng et al. 2021). Thus, because of a disadvantage in nutrient competition, the mother tree needs to adjust resource allocation strategies to improve self-resistance, which limits nutrient and water availability for sprouts, ultimately leading to sprout mortality. On the other hand, having greater basal space helps avoid competition among sprouts. Weaker mother plants are eliminated and stronger individuals retained by bamboo expansion, thus promoting dormant buds to sprout and grow taller. Previous studies suggested that the height of stumps could significantly promote sprouting number, basal diameter and height (Chen et al. 2015) because the mother tree loses apical dominance, accelerating the dormant buds' sprouting and growth. The result was consistent with a previous study (Pang et al. 2016). However, these effects are not based on altering the remaining mother tree growth traits; therefore, we speculated that bamboo promoted sprout density while restraining their growth relatively mainly via adjustments to the Chinese fir population structure and lowered nutrient acquisition from mother trees by means of eliminating weaker individuals.

Besides mother tree influences, the external environment also regulates Chinese fir sprouting, and healthy, vigorous mother trees generally have wider crowns and limited undergrowth of dormant bud sprouts (Gao and Ye 1994; Milios and Papalexandris 2019); however, light was not the key external factor promoting sprouts. It indirectly controlled sprouting by increasing soil temperature. Lin et al. (1996) found that when mother trees fell, sunlight increased the soil temperature, and buds began to sprout when soil temperature rose to 20 °C. In our study, although Chinese fir sprouts differed in some ways during bamboo expansion stages, the Chinese fir canopy was narrowed by mortality and occupied by bamboo shoots immediately, meaning that understory light and soil temperature were not obviously changed. Therefore, we considered that bamboo expansion effects on the Chinese fir sprouting population were not caused by via changing sunlight and soil temperature. In addition, understory vegetation abundance and diversity decreasing with bamboo expansion has been widely reported (Yang et al. 2010, 2017), which was also found in our study plots. However, whether the decreasing understory is the driver for the sprouting population is poorly understood. We recommend further study on the mechanisms driving sprouting regeneration and physiological regulation in response to bamboo expansion.

Conclusions

Our research demonstrates that bamboo expansion decreases sprout cluster longevity and introduces instability into the Chinese fir sprout population, which results in modular biomass change and branch allometry. We consider that sprouts are mainly compromised by bamboo expansion through changes in Chinese fir mother trees. Therefore, removing bamboo shoots adjacent to fir sprouts and thinning sprout clusters should create favorable conditions for strong sprout cultivation and optimize the sprouting forest's potential productivity in Chinese fir cutover lands.

Author contributions All authors contributed to the study conception and design. Guidance for the scientific opinion on the issue was given by LQ and WA. The idea and method for the experiment were conceived by CP, JT and ML. Material preparation, data collection and analysis were performed by CP, YM and MY. The first draft of the manuscript was written by CP, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript. Meanwhile, the authors express their gratitude to EditSprings (https://www.editsprings.cn/) for the expert linguistic services provided and are sincerely grateful to the anonymous reviewers for valuable suggestions to improve the article.

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Data and material availability All data are fully available without restriction.

Code availability Not applicable.

Declarations

Conflict of interest All authors declare that they have no conflict of interest.

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