Relationship Between Forest Strata Structure and Regeneration in Subtropical Evergreen Broad-Leaved Forest

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Research

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Posted Date: August 25th, 2020

DOI: https://doi.org/10.21203/rs.3.rs-59358/v1

Relationship between forest strata structure and regeneration in subtropical evergreen broad-leaved forest

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Abstract

Background: Regeneration is an extremely important and complex ecological process, which is disturbed by many factors. The current stand structure has an important influence on regeneration. The aim of this study is to provide theoretical reference for improving the regeneration capacity subtropical evergreen broad-leaved forest and formulating management measures of regeneration restoration.

Methods: A permanent plot of 100m × 100m was set up in the evergreen broad-leaved forest of Tianmu Mountain National Nature Reserve, Zhejiang Province, China. The plot was divided into 25 survey units of 20m × 20m by the adjacent grid survey method, and all the trees in the plot were investigated. The tree height, DBH, crown width, density, species richness index, aggregation index, competition index and mingling of each forest stratum were used as the stand structure index. The tree height, DBH, crown width, density and species richness index of regeneration trees were used as regeneration indicators. Redundancy analysis (RDA) was used to explore the relationship between forest strata structure and regeneration of evergreen broad-leaved forest.

Results: In the whole stand, DBH, tree species richness index and crown width were the main structure factors affecting regeneration. In the upper forest stratum, the tree height was the main structure factor affecting regeneration. In the middle forest stratum, the tree species richness index and crown width were the main factors affecting regeneration. In the lower forest stratum, crown width, competition index, tree height and tree species richness index were the main factors affecting regeneration. The effects of tree species richness index and crown width on regeneration in the whole stand were mainly reflected in the middle and lower forest strata in each forest

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stratum.

Conclusions: The influencing order of each forest stratum structure on regeneration was: lower forest stratum > middle forest stratum > upper forest stratum. Different regeneration indicators had different responses to the main stand structure indices, while the young tree height and DBH, and the tree species diversity and density of regeneration trees were most affected by the main stand structure indices. In order to promote the regeneration of evergreen broad-leaved forest in the future, different management measures should be taken for different forest strata, and the threshold value of each index should be controlled.

Key words: subtropical evergreen broad-leaved forest; forest strata; stand structure; regeneration; redundancy analysis (RDA)

1. Introduction

Subtropical evergreen broad-leaved forest is one of the typical forest types in China, which plays an important role in protecting the environment and maintaining the global carbon balance and the sustainable development of human beings (Cao et al., 2010). However, due to the people's unreasonable development and utilization of forest resources in the early stage, the area of evergreen broad-leaved forest had been continuously reduced, resulting in the degradation of ecological functions and other problems (Song et al., 2005; Zhuo and Zheng, 2019). Natural regeneration is the main way of forest resources reproduction, which is particularly important for the restoration and protection of evergreen broad-leaved forest, and has great research and protection significance (Shi et al., 2014; Zhang et al., 2015). Natural regeneration is an extremely important and complex process of forest ecology, which goes through many growth stages (Chen et al., 2018). The success of each stage depends on many factors, so the research on the impact factors of natural regeneration had attracted people's attention.

The current stand structure is one of the main driving factors of regeneration (Boyden et al., 2005; Tinya et.al., 2019), which plays a key role in the succession and recovery of forest (Wan et al., 2019). The stand structure includes non-spatial structure and spatial structure. Non-spatial structure index was used to describe the average characteristics of the stand, which was not affected by the relative position of neighborhood trees (Gong et al., 2009; Tang, 2010). In recent years, there had been much researches on the relationship between non-spatial structure index and regeneration. The smallest beech seedlings regeneration was determined by stand structure indices to a greater extent (Žemaitis et al., 2019). Stand density had no significant effect on the number, base diameter and height of *Pinus tabulaeformis* seedlings (Chen and Cao, 2014). With the increase of canopy density, the density of different regeneration trees showed different trends (Zhang et al., 2010; Huang et al., 2018). Too large tree basal area and tree height of forest were not conducive to regeneration trees growth (Graber, 1976; Ou et al., 2017). Because the forest vertical structure largely determines the differences in the distribution of resources such as water, heat, light and nutrients in the forest (Jiang et al., 2015), it has an important effect on species growth, reproduction, death and resource utilization (Latham et al., 1998; Hao et al., 2007; Zhang et al., 2016; Zhuang et al., 2017; Nasiri et al., 2018). Therefore, the impact of forest vertical structure on regeneration had become one of the focuses of many scholars. In the canopy vertical structure, impact of the middle and lower layers on regeneration diversity was significantly higher than upper layer (Zhou et al., 2017). The higher the forest vertical structure diversity is, the more the favorable regeneration trees are (Donoso and Nyland, 2005). Too large or too small crown index would inhibit regeneration density, while regeneration density had a weaker correlation with small tree proportions, but showed a significant positive correlation with large tree proportions (Zhang et al., 2010). Ou et al. (2017) considered that the crown index, large and small tree proportions had no significant effect on the number of *Excentrodendron hsienmu* seedlings, but the effect on the seedling diameter and tree height was significant. With the gradual improvement of forest management level, stand spatial structure based on the relationship of neighborhood trees is one of the research priorities (Gong et al., 2009; Jiang et al., 2018). A few scholars had carried out the research on the relationship between spatial structure based on the relationship of neighborhood trees and regeneration, but most of their research used the artificially regeneration trees as object trees. For example, Zhang et al. (2004) pointed out that medium mingling and random distribution were suitable for artificial regeneration of *Pinus koraiensis* seedlings in the secondary forest. Luo et al. (2017) found that the average DBH and tree height of *Pinus koraiensis* seedlings in all experiment sites increased with the increase of opening degree in the same aspect. In summary, great achievements have been made on the impact of stand structure on natural regeneration, but the density, basal area, large and small tree proportions, canopy density, tree height and crown index of stand were mainly selected as stand structure indices in these studies, while few studies have reported the relationship between horizontal spatial structure index (aggregation index, competition index, mingling, etc) and natural regeneration. Therefore, it is great theoretical and practical significance to study the relationship between stand structure and natural regeneration by combining spatial structure with non-spatial structure.

In this study, the evergreen broad-leaved forest was divided into three forest strata in the plot. The non-spatial structure index of each forest stratum was determined by survey data, spatial structure index was calculated by using Voronoi diagram based on the relationship of neighborhood trees. Redundancy analysis was used to study the relationship between stand structure indices and regeneration indicators. The main purposes of this study were the following: (1) to understand the effect of dominant factors of whole forest structure and different forest stratum structure on regeneration; (2) to reveal the response of regeneration trees at different growth stages to dominant stand structure indices.

2. Methods

2.1. Study area

The study was conducted in the subtropical evergreen broad-leaved forest of Tianmu Mountain National Nature Reserve, Zhejiang province, China. It is located at latitude 30°18′30″ to 30°24′55″N, longitude 119°24′11″

to 119°28′21″E. Mean annual temperature of study area ranges from 8.8℃ to 14.8℃, mean annual rainfall ranges from 1390mm to 1870mm, mean annual solar radiation ranges from 3270MJ·m^{-2} to 4460MJ·m^{-2}. With the elevation rising, soil type transits from subtropical red soil to wet temperate brown-yellow soil, with red soil below 600m, yellow soil between 600m and 1200m, brown-yellow soil above 1200m. Forest types are diverse, including evergreen broad-leaved forest, deciduous broad-leaved mixed forest, deciduous dwarf forest, coniferous broad-leaved mixed forest, bamboo forest, etc.

We selected a representative section in the evergreen broad-leaved forest of Tianmu Mountain National Nature Reserve, and a permanent plot of 100m × 100m was set up from July to August, 2005. This plot was divided into 25 survey units of 20m × 20m by the adjacent grid survey method (Fig.1). Each grid was used as the investigation unit to measure all the trees in the plot, record each tree species, Coordinates (x, y, z), DBH, tree height and crown width. The main tree species were *Cyclobalanopsis gracilis*, *Cyclobalanopsis glauca*, *Lithocarpus brevicaudatus*, *Litsea coreana*, *Cyclobalanopsis myrsinifolia*. Meanwhile, all regeneration trees were investigated in each grid, record each tree species, DBH, tree height and crown width. The main regeneration tree species were *Camellia fraterna*, *Cyclobalanopsis gracilis*, *Litsea coreana*, *Cyclobalanopsis glauca*, *Lithocarpus brevicaudatus.*

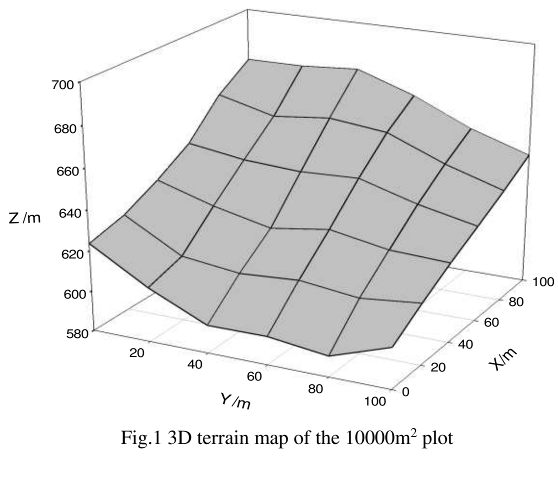

Fig.1 3D terrain map of the 10000m^2 plot

2.2. Vertical stratification

Zhou *et al.* (2019) improved the criterion of forest strata stratification of IUFRO, taking the stand dominance height(h) as the stratification basis. The average of the highest 50 tree heights was taken as the stand dominant height in the plot, and then the difference value (Δh) between the stand dominant height and the minimum tree height (h_{min}) was calculated. According to tree height (H), the trees with DBH ≥ 5cm were divided into upper, middle and lower forest strata. Upper forest strata: H > h_{min}+2/3△h, middle forest strata: h_{min}+1/3△h ≤ H ≤ h_{min}+2/3△h, lower forest strata: H < h_{min}+1/3△h. The survey data calculated that the average stand dominant height was 17.2m, the minimum tree height was 1.5m and the difference value was 15.7m. Therefore, upper forest strata: H > 12m, middle forest strata: 6.7m ≤ H ≤ 12m, lower forest strata: H < 6.7m.

2.3. Stand structure indices

2.3.1. Stand non-spatial structure indices

Trees with DBH > 5cm were defined as large trees, and DBH, tree height, crown width, density and diversity index were selected to describe the characteristics of stand non-spatial structure.

The tree species diversity index is used to describe the proportion of species to individuals in a biological community. The tree species richness index was calculated as (Liu et al., 2011):

$$S = \frac{m-1}{\ln(M)} \tag{1}$$

where, S is tree species richness index, m is the number of species in each grid, and M is the total number of individuals of all species in the plot.

2.3.2. Stand spatial structure indices

Mingling, competition index and aggregation index were selected to describe the characteristics of stand spatial structure, and Voronoi diagram based on the relationship of neighborhood trees was used to calculate the stand spatial structure indices, i.e. the trees of which the Thiessen polygons are adjacent to the Thiessen polygon of the object tree are regarded as neighborhood trees (Tang et al., 2007). To eliminate the edge effect, the eight-neighborhood method was used to edge correction of the plot.

Mingling is used to describe the degree of tree species spatial isolation in a forest, and is defined as the proportion of neighborhood trees number that are not the same species as the object tree (Hui and Hu, 2001). The complete mingling (hereinafter referred to as mingling) was calculated as (Tang et al., 2012):

$$M_i = \frac{1}{n_i}\sum_{j=1}^{n_i} v_{ij} \tag{2}$$

$$Mc_i = \frac{1}{2}\left(D_i + \frac{c_i}{n_i}\right)\cdot M_i \tag{3}$$

where, M_i is the mingling of the object tree i; M_{ci} is the complete mingling of the object tree i; N_i is the number of neighborhood trees; V_{ij} is a discrete variable, V_{ij} = 1 when the neighborhood tree j and the object tree i have different tree species, otherwise V_{ij} = 0; c_i is the number of different tree species in pairs of neighborhood trees in the spatial structure unit i; D_i is the Simpson diversity index of the tree species in the spatial structure unit i.

Competition index is used to describe the competitive relationship among trees within a forest. The Hegyi competition index (hereinafter referred to as competition index) based on Voronoi diagram was calculated as (Hegyi, 1974):

$$CI_i = \sum_{j=1}^{n_i} \frac{d_{\mathrm{j}}}{d_i \cdot L_{ij}} \tag{4}$$

$$CI = \frac{1}{Z}\sum_{i=1}^{Z} CI_i \tag{5}$$

where, CI_i is the competition index of object tree i, L_{ij} is the distance between object tree i and neighborhood tree j, D_i is the DBH of object tree i, D_j is the DBH of neighborhood tree j, N_i is the number of neighborhood trees in the spatial structure unit i where object tree i is located, Z is the number of object trees, CI is the stand competition index.

Aggregation index is used to describe the spatial distribution patterns in forest, and is defined as the proportion of the average distance between object trees and their nearest neighborhood trees to the expected average distance under a random tree distribution pattern (Clark and Evans, 1954). It was calculated as:

$$R = \frac{\frac{1}{N}\sum_{i=1}^{N} r_i}{\frac{1}{2}\sqrt{\frac{F}{N}}} \quad (6)$$

Where, R is the aggregation index, N is the number of trees in the plot, F is the plot area, and r_i is the distance from the object tree i to its nearest neighborhood tree.

2.4. Regeneration indicators

The trees with DBH < 5cm were defined as regeneration trees. According to the tree height and DBH, the regeneration trees were divided into three grades: seedlings, saplings and young trees. Seedlings: H ≤ 1.5m, DBH < 1cm; Saplings: H ≤ 1.5m, DBH ≥ 1cm; young trees: H > 1.5m, DBH < 5cm (Tang et al., 2006). The DBH, tree height, crown width, species richness index and number of regeneration trees were selected as regeneration indicators. The species richness index was calculated by using Eq. (1).

2.5. Data analyses

The software IBM SPSS Statistics 20 was used to analyze the differences of different forest strata structure. Redundancy analysis (RDA) is a direct gradient analysis method, which can intuitively analyze the complex relationship between multiple environmental factors and multiple species variables. The correlation between environmental factors and species variables is the product of the line length of species variables and the cosine of the angle between the environmental factors and species variables (Howard et al., 2012; Zhu et al., 2018). The stand structure indices were taken as environmental variables, and regeneration indicators as species variables, the relationship between them was analyzed using the software Canoco 5. Firstly, in order to select a suitable model for redundancy analysis, the data was subjected to the detrended correspondence analysis (DCA). When the maximum gradient of the four axes was less than or equal to 3, the linear model was used; when the maximum gradient was equal to or greater than 4, the unimodal model was used; when the maximum gradient was between 3 and 4, both models could be selected. Secondly, log transformation and centralization were performed on the original data. Variance inflation factor (VIF) was used to test the multicollinearity between variables, and the variance inflation factor was less than 20, which indicated that there was no multicollinearity among the stand structure indices. The most significant stand structure indices affecting regeneration were screened out through interactive forward selection. Finally, the specific relationship between the most significant stand structure indices and regeneration indicators was further analyzed using "Multiple species response curve".

3. Results

3.1. Differences in different forest strata structure

Stand structure characteristics of different forest strata are shown in Table 1. There were significant differences among the different forest stratum structure index except the aggregation index ($p < 0.05$). The mingling has significant differences between upper forest stratum and lower forest stratum, and no significant differences between middle forest stratum and other forest strata. The species richness index has significant differences between upper forest stratum and other forest strata, and no significant differences between middle forest stratum and lower forest stratum. With the rise of forest strata, the mingling increased, and the competition index and species richness index decreased. Therefore, it was reasonable to divide into three forest strata in this subtropical evergreen broad-leaved forest.

Table 1 Stand structure characteristics of different forest strata

Stand	M	CI	R	N (no*ha^{-1})	DBH (cm)	H (m)	W (m)	S
Whole	0.58±0.01ab	8.93±0.26b	0.95±0.02a	1629.00±102.38a	12.70±0.34c	7.17±0.17c	3.58±0.15c	3.72±0.20a
Upper	0.61±0.02a	4.13±0.50d	0.97±0.08a	139.00±19.10d	30.98±1.35a	14.80±0.41a	5.58±0.22a	0.86±0.14c
Middle	0.59±0.01ab	7.45±0.47c	0.92±0.04a	548.00±44.25c	15.83±0.63b	8.50±0.09b	4.18±0.21b	2.41±0.15b
Lower	0.57±0.01b	10.49±0.37a	0.97±0.03a	942.00±75.96b	8.20±0.23d	5.02±0.04d	2.92±0.09d	2.44±0.15b

Note: Different letters in the same column indicate a significant difference at the 0.05 level. M: mingling; CI: competition index; R: aggregation index; N: density; DBH: diameter at breast height; H: tree height; W: crown width; S: species richness index.

3.2. Effect of whole stand structure on regeneration

The results of RDA showed that 49.22% of the regeneration variation was explained by the whole stand structure with 25.23% of that variation being explained from first axis and 19.68% from second axis, indicating that the correlation between whole stand structure index and regeneration was mainly determined by the first axis and second axis. From the interactive forward selection results of whole stand structure indices, DBH, species richness index and crown width had the most significant effect on the regeneration, which the explained variations of regeneration were 18.4%, 9.4%, 7.2%, accounting for about 71.11% of the explained variation of the 8 whole stand structure indices (Table 2).

Table 2 Summary of redundancy analysis results of whole stand structure and regeneration

Name	Mean	Stand. dev.	Inflation factor	Explains %	Contribution %	F	P
Wh_D	12.69	1.68	3.78	18.4	36.1	5.2	0.006***
Wh_S	3.58	0.72	6.34	9.4	18.4	2.9	0.048**
Wh_W	3.72	0.96	3.97	7.2	14.1	2.3	0.07*
Wh_CI	8.63	2.16	2.30	5.7	11.1	1.9	0.126
Wh_R	1.00	0.22	3.21	3.9	7.6	1.3	0.256
Wh_H	7.11	0.82	5.21	2.6	5.1	0.8	0.422
Wh_M	0.57	0.07	2.10	2.4	4.8	0.8	0.484
Wh_N	1629.00	501.58	4.14	1.4	2.8	0.5	0.762
				Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues				0.2523	0.1968	0.0276	0.0156
Explained variation (cumulative)				25.23	44.91	47.66	49.22

Note: Wh_M, Wh_CI, Wh_R, Wh_S, Wh_DBH, Wh_H, Wh_W, Wh_N denotes the mingling, competition index, aggregation index, species richness index, diameter at breast height, tree height, crown width and density of the whole stand.
***: $p < 0.01$; **: $p < 0.05$; *: $p < 0.1$.

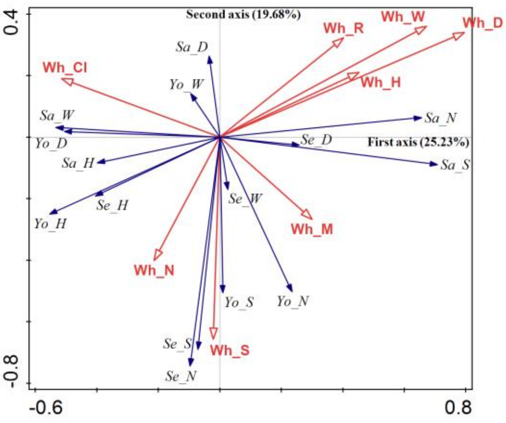

Fig. 2 RDA ordination diagram of whole stand structure indices and regeneration

Note: Hollow arrow represents stand structure indices, solid arrow represents regeneration indicators. Se_N, Se_D, Se_H, Se_W, Se_S denotes seedling density, diameter at breast height, tree height crown width and species richness index; Sa_N, Sa_D, Sa_H, Sa_W, Sa_S denotes sapling density, diameter at breast height, tree height,crown width and species richness index; Yo_N, Yo_D, Yo_H, Yo_W, Yo_S denotes young tree density, diameter at breast height, tree height, crown width and species richness index.

The ordination diagram of RDA showed that the DBH and crown width of whole stand had a strong positive effect on sapling density and species richness index, and a strong negative effect on young tree height and DBH.

The species richness index of whole stand had a strong positive effect on seedling density and species richness index, and young tree density and species richness index (Fig. 2).

The specific effect of the dominant whole stand structure indices on regeneration is shown in Fig. 3. With the increase of the DBH in the whole stand, young tree height and DBH showed a decreasing trend, sapling species richness index showed an increasing trend, and sapling density showed a unimodal distribution. When the DBH of whole stand was between 13cm and 15cm, sapling density maintained a high response value, young tree height and DBH tend to change stably, and the increasing trend of sapling species richness index slowed down (Fig. 3A). With the increase of the species richness index in the whole stand, seedling density and species richness index showed an increasing trend, and young tree density and species richness index showed a unimodal distribution. The young tree density and species richness index kept a high response value when the species richness index of whole stand was between 4 and 5 (Fig. 3B). With the increase of the crown width in the whole stand, young tree DBH and height showed a single valley distribution, while sapling density and species richness index showed a unimodal distribution. Young tree DBH and height maintained a small response value when the crown width was between 4m and 5.5m. The sapling density and species richness index maintained a high response value when the crown width of whole stand was between 4.5m and 6m (Fig. 3C).

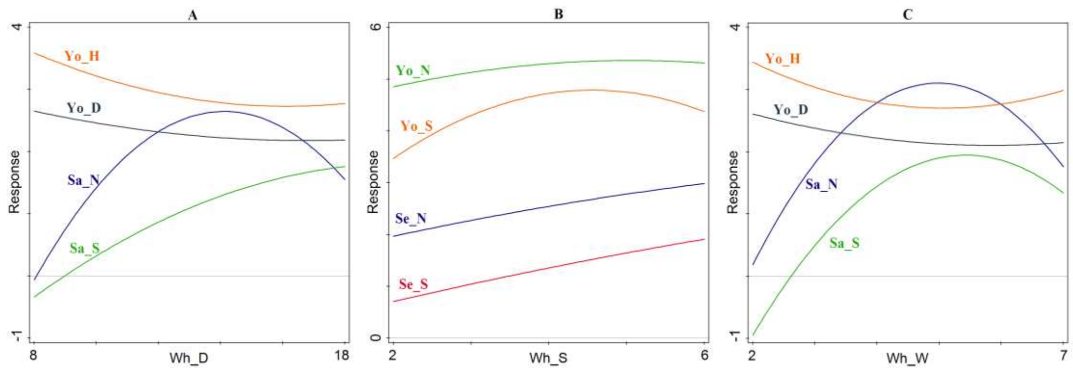

Fig. 3 Regeneration response curves to the dominant whole stand structure indices

3.3. Effect of forest strata structure on regeneration

3.3.1. Effect of upper forest stratum structure on regeneration

The results of RDA showed that 37.76% of the regeneration variation can be explained by the upper forest stratum structure index with 19.83% being explained by the first axis and 10.87% being explained by the second axis. It can be seen that RDA can better explain the relationship between upper forest stratum structure index and regeneration. The interactive forward selection results of upper forest stratum showed that the tree height was the most significant structure factor affecting regeneration, and the interpretation rate of regeneration was 13.9%, which accounts for about 36.81% of the total interpretive ability of the 8 upper forest stratum structure indices (Table 3).

Table 3 Summary of redundancy analysis results of upper forest stratum structure and regeneration

Name	Mean	Stand. dev.	Inflation factor	Explains %	Contribution %	F	P
Up_H	14.8	2.0	2.2	13.9	35.9	3.7	0.02**
Up_N	139.0	93.6	9.7	6.5	16.7	1.8	0.134
Up_M	0.6	0.1	1.8	6.3	16.3	1.8	0.116
Up_CI	3.9	2.7	2.0	4.5	11.5	1.2	0.288
Up_W	5.6	1.1	2.0	2.8	7.2	0.8	0.480
Up_R	0.9	0.5	2.2	2.3	5.8	0.6	0.628
Up_S	0.9	0.7	10.7	1.6	4.2	0.5	0.772
Up_D	30.98	6.6	2.3	0.9	2.3	0.2	0.946
			Axis 1	Axis 2	Axis 3	Axis 4	
Eigenvalues			0.1983	0.1087	0.0578	0.0128	
Explained variation (cumulative)			19.83	30.7	36.48	37.76	

Note: Up_M, Up_CI, Up_R, Up_S, Up_DBH, Up_H, Up_W, Up_N denotes the mingling, competition index, aggregation index, species richness index, diameter at breast height, tree height, crown width and density of the upper forest stratum.

According to the ordination diagram of RDA (Fig. 4), the tree height of the upper forest stratum had a greater positive effect on sapling density and species richness index, and a greater negative effect on seedling height and young tree height and DBH.

The seedling height decreased with the increase of tree height in the upper forest stratum. When the tree height of the upper forest stratum was between 12m and 16.5m, the young tree height and DBH had a single valley distribution, while sapling density and species richness index had a unimodal distribution. When the tree height of the upper forest stratum was between 16.5m and 24m, young tree height and DBH had a unimodal distribution, while sapling density and species richness index had a single valley distribution (Fig. 5).

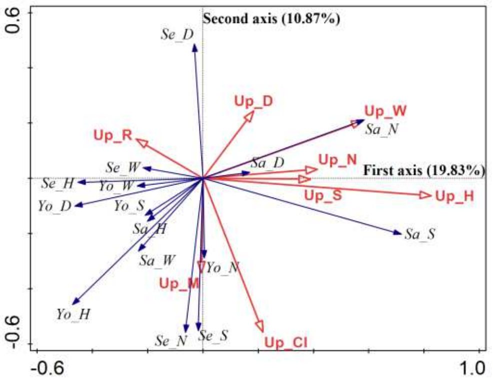

Fig. 4 RDA ordination diagram of upper forest stratum structure indices and regeneration

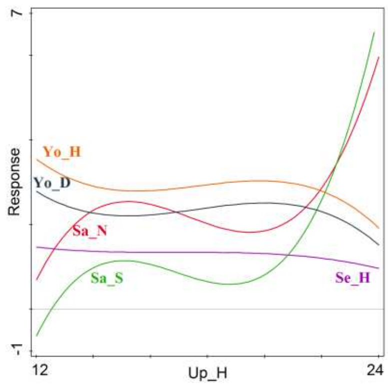

Fig. 5 Regeneration response curves to the dominant upper forest stratum structure index

3.3.2. Effect of middle forest stratum structure on regeneration

The redundancy analysis results of middle forest stratum structure and regeneration is shown in Table 4. 41.45% of the regeneration variation can be explained by the four axes, 38.26% of the regeneration variation can be explained by the first two axes with 23.12% being explained by the first axis and 15.14% being explained by the second axis. This shows that the first two axes can better explain the relationship between middle forest stratum structure and regeneration. The significant structure factors were screened out by interactive forward selection as follow: the tree species richness index and crown width of the middle forest stratum, which explained 16.7% and 14.5% of the regeneration variation, accounting for about 75.27% of the total explained variation of the 8 middle forest stratum structure indices.

Table 4 Summary of redundancy analysis results of middle forest stratum structure and regeneration

Name	Mean	Stand. dev.	Inflation factor	Explains %	Contribution %	F	P
Mid_S	2.4	0.7	3.8	16.7	39.0	4.6	0.006***
Mid_W	4.2	1.0	1.7	14.5	33.8	4.6	0.012**
Mid_D	15.8	3.1	1.8	4.2	9.7	1.4	0.262
Mid_M	0.6	0.1	1.9	2.5	5.7	0.8	0.434
Mid_CI	6.8	2.8	3.1	1.6	3.8	0.5	0.636
Mid_H	8.5	0.4	1.9	1.6	3.7	0.5	0.694
Mid_N	548.0	216.8	3.6	1.0	2.3	0.3	0.886
Mid_R	0.98	0.3	2.9	0.8	2.0	0.2	0.934
			Axis 1	Axis 2	Axis 3	Axis 4	
Eigenvalues			0.2312	0.1514	0.0182	0.0137	
Explained variation (cumulative)			23.12	38.26	40.08	41.45	

Note: Mid_M, Mid_CI, Mid_R, Mid_S, Mid_DBH, Mid_H, Mid_W, Mid_N denotes the mingling, competition index, aggregation index, species richness index, diameter at breast height, tree height, crown width and density of the Middle forest stratum.

The species richness index of the middle forest stratum had a larger positive effect on seedling species richness index and density, and the young tree species richness index and density. The crown width of the middle forest stratum had a larger positive effect on sapling species richness index and density, and had a larger negative effect on young tree height, and sapling crown width and height (Fig. 6).

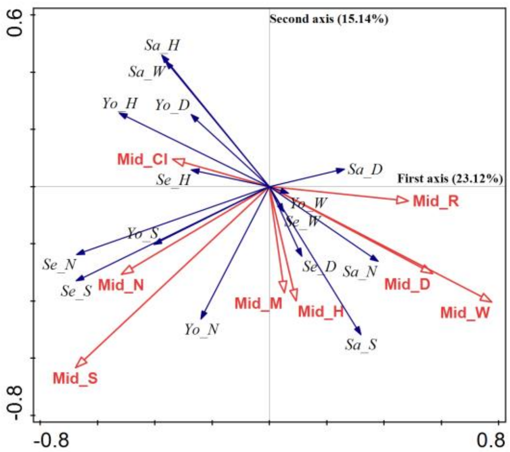

Fig. 6 RDA ordination diagram of middle forest stratum structure indices and regeneration

When the species richness index of the middle forest stratum was between 1 and 1.5, the young tree species richness index first increased after reaching the minimum value, the increasing rate of seedling density slowed down, and the increasing rate of young tree density accelerated. When the species richness index of the middle forest stratum increased to between 3 and 3.5, the young tree species richness index reached the maximum value, and the increasing rate of seedling density began to accelerate, the change of young tree density tended to be stable (Fig. 7A). With the increase of crown width in middle forest stratum, sapling crown width and young tree height showed a single valley distribution, the young tree density and species richness index showed a unimodal distribution. When the crown width of middle forest stratum was between 6m to 7m, the young tree height and sapling crown width reached the minimum value, and the sapling density and species richness diversity reached the maximum value (Fig. 7B).

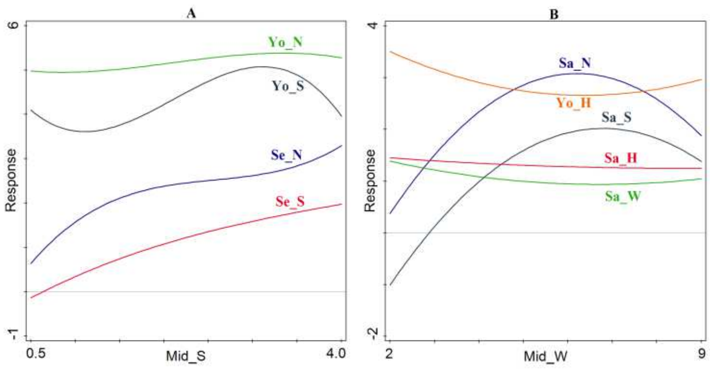

Fig. 7 Regeneration response curves to the dominant middle forest stratum structure indices

3.3.3. Effect of lower forest stratum structure on regeneration

The redundancy analysis results of lower forest stratum structure and regeneration is shown in Table 5. 49.58% of the regeneration variation can be explained by the four axes, 43.78% of the regeneration variation can be explained by the first two axes with 30.09% being explained by the first axis and 13.69% being explained by the second axis. Therefore, the first two axes provided the optimal explanation for the variation in both lower forest stratum structure index and regeneration. From the forward selection results of lower forest stratum, the most significant structure factors affecting regeneration were: crown width, competition index, tree height and species richness index, which the explained variation of regeneration were 11.2%, 10.8%, 9.5%, 7.2%, accounting for 78.06% of the total explained variation of the 8 stand structure indices.

Table 5 Summary of redundancy analysis results of lower forest stratum structure and regeneration

Name	Mean	Stand. dev.	Inflation factor	Explains %	Contribution %	F	P
Low_W	2.9	0.4	1.6	11.2	21.5	2.9	0.040**
Low_CI	10.3	3.3	1.6	10.8	20.9	3.3	0.034**
Low_H	5.0	0.2	1.3	9.5	18.3	2.6	0.044**
Low_S	2.4	0.8	3.6	7.2	13.8	2.3	0.070*
Low_M	0.6	0.1	2.1	3.9	7.4	1.3	0.280
Low_N	942.0	372.1	3.7	3.9	7.6	1.3	0.252
Low_D	8.2	1.1	1.3	3.8	7.3	1.3	0.236
Low_R	1.0	0.3	2.1	1.6	3.1	0.5	0.688
			Axis 1	Axis 2	Axis 3	Axis 4	
Eigenvalues			0.3009	0.1369	0.0423	0.0157	
Explained variation (cumulative)			30.09	43.78	48.01	49.58	

Note: Low_M, Low_CI, Low_R, Low_S, Low_DBH, Low_H, Low_W, Low_N denotes the mingling, competition index, aggregation index, species richness index, diameter at breast height, tree height, crown width and density of the lower forest stratum.

The crown width of the lower forest stratum had a greater positive effect on sapling density and species richness index and a greater negative effect on seeding density and species richness index, and young tree density and height. The competition index of the lower forest stratum had a greater negative effect on regeneration tree density and species richness index. The tree height of the lower forest stratum had a greater negative effect on sapling density and species richness index, and a positive effect on young tree height and DBH. The tree species richness index in the lower forest stratum had a greater positive effect on seeding and young tree density and species richness index (Fig. 8).

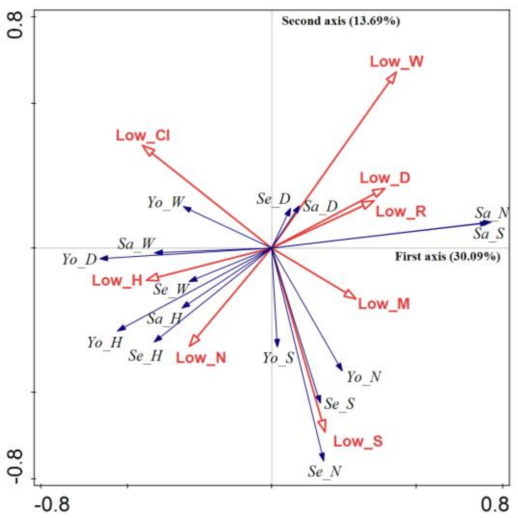

Fig. 8 RDA ordination diagram of lower forest stratum structure indices and regeneration

The specific effect of the main lower forest stratum structure indices on regeneration is shown in Fig. 9. When the crown width of the lower forest stratum was between 2.0m and 3.2m, the seeding density and species richness index, and sapling density and species richness index had a single valley distribution, and sapling density and species richness index reached the minimum value. When the crown width of the lower forest stratum was between 3.2m and 4.5m, the seeding density and species richness index, and sapling density and species richness index had a unimodal distribution, and sapling density and species richness index reached the maximum value (Fig. 9A). With the increase of competition index in the lower forest stratum, the seedling and sapling density and species richness index had a single valley distribution, the young tree density and species richness index showed downtrend. The seedling and sapling density and species richness index reached the minimum value when the competition index in the lower forest stratum was between 13 and 16 (Fig. 9B). With the increase of tree height in the lower forest stratum, the sapling density showed a decreasing trend, young tree DBH and sapling species richness index showed a single valley distribution, and young tree height showed an increasing trend. The sapling species richness index reached the minimum value when the tree height in the lower forest stratum was between 5m and 5.3m. The young tree DBH reached the minimum value when the tree height in the lower forest stratum was between 4.8m and 5m(Fig. 9C). When the tree species richness index in the lower forest stratum was between 1.0 and 2.5, the young tree density showed an increasing trend, the seedling density and species richness index showed a unimodal distribution, and young tree species richness index showed a single valley distribution. When the tree species richness index in the lower forest stratum was between 2.5 and 4.0, the young tree density showed a steady trend, the seedling density and species richness index showed a single valley distribution, young tree species richness index showed a unimodal distribution, which species richness index reached the maximum value (Fig. 9D).

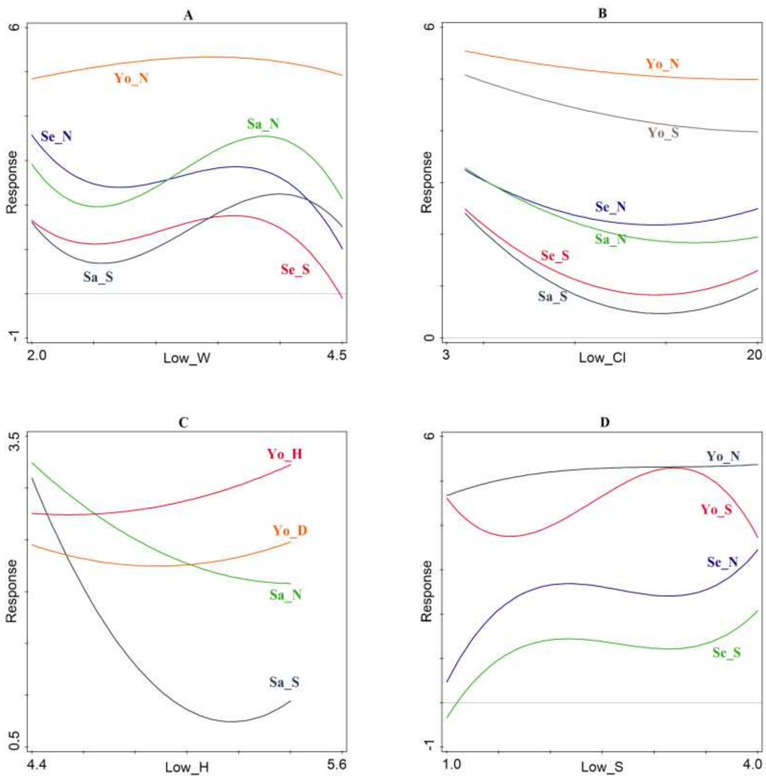

Fig. 9 Regeneration response curves to the dominant lower forest stratum structure indices

4. Discussion

4.1. Effect of whole stand structure on regeneration

In the subtropical evergreen broad-leaved forest community, DBH, tree species richness index and crown width were the main whole stand structure indices affecting regeneration. The DBH and crown width of the whole stand could inhibit the individual size growth of regeneration trees, but to a certain extent could promote the regeneration of young tree density and species richness index, which is similar to the results of many scholars (Ou et al., 2017; Wu et al., 2019). It is generally believed that the larger DBH and crown width of the forest, the older stand age and the more mature seed trees in the forest, which can provide enough provenance for regeneration. Some researches showed crown width plays a role of shading and shelter for regeneration, and affects the growth of regeneration trees by changing habitat conditions such as light and humidity in the forest (Zhu et al., 2003; Yu et al., 2015; Huang et al., 2020). Our results clearly showed that the larger or smaller crown width of the whole stand could inhibit the regeneration of seedling density, sapling density and sapling species richness index, but could promote the growth of young tree height and DBH. Too small crown width causes abundant sunlight reaching the forest floor directly, some regeneration trees lose moisture easily and intolerant tree species may compete strongly with regeneration trees for the available resources, thereby reducing regeneration trees survival or growth (Lombaerde et al., 2019). If the crown width is too large, the photosynthesis of the regeneration trees is blocked and cannot grow well. Tree species richness was one of the main drivers affecting regeneration (Adam et al., 2013; Tinya et al., 2019). In this study, the species richness index of whole stand was positively correlated with the density and species richness of the regeneration trees. The reason may be that different tree species have different ways of regeneration (Shi et al., 2013), and the seed size and quality also have certain differences (Cheng et al., 2018), making them adaptable to different habitats. Therefore, in the regeneration management of subtropical evergreen broad-leaved forest in the future, the DBH, crown width and tree species richness index of the whole stand can be reasonably regulated according to the needs of the management objectives, so as to promote the regeneration.

4.2. Effect of forest strata structure on regeneration

The vertical stratification of tree crowns is a forest attribute that influences both tree growth and understory community structure (Latham et al., 1998). In the upper forest stratum, the tree height was the main stand structure factor affecting regeneration. In the middle forest stratum, the tree species richness index and crown width were the main stand structure indices affecting regeneration. In the lower forest stratum, the crown width, competition index, tree height and species richness index were the main stand structure indices affecting regeneration. The crown width and tree species richness index in the middle and lower forest strata had significant effects on the regeneration, which is similar to that found by Zhou et al. (2017). Compared to the effects of each forest strata and the whole stand on the regeneration, it is observed that the tree species richness index and crown width of the whole stand play a shelter role for regeneration trees and provide the seed source of dominant tree species which mainly comes from the middle and lower forest strata. Because the main dominant tree species in the middle forest stratum and the lower forest stratum were *Cyclobalanopsis gracilis*, *Cyclobalanopsis glauca*, *Lithocarpus brevicaudatus*, *Camellia fraterna*, etc., which had a large number and strong natural regeneration ability. While the number of trees in the upper forest stratum was relatively small, in addition to *Cyclobalanopsis gracilis*, *Cyclobalanopsis glauca*, *Lithocarpus brevicaudatus*, there were also deciduous species and coniferous species, such as *Quercus fabri*, *Liquidambar formosana*, *Cunninghamia lanceolata*, *Torreya grandis*, etc. The opening degree of object tree represents the light intensity in the forest where the object tree is located, and is defined as the sum of the proportion of the distance between object tree and its neighborhood trees to the neighborhood tree height (Luo et al., 1984; Luo et al., 2017). This indicates that the light intensity of a certain site in the forest is largely determined by the neighborhood trees height and the distance between the neighborhood trees and object trees. The tree height of the upper and lower forest strata had a significant impact on regeneration, because the tree height of the upper forest stratum is too high, which makes the light intensity and temperature increase in the forest, leading to the individual size growth of regeneration trees being inhibited. The increase of tree height of the lower forest stratum can provide the growth space for regeneration trees and reduce the competition for depletable resources, thus promote the individual size growth of regeneration trees. This research finding showed that the competition index of the lower forest stratum mainly affected the species richness index of regeneration trees. The smaller the competition index, the better the tree species diversity and density of regeneration. The smaller size and larger number of individuals in the lower forest stratum lead to the fierce competition for nutrients, living space and other resources by regeneration trees, which made the competition index of the lower forest stratum have significant effect on regeneration. The order of each forest stratum structure effect on regeneration was: lower forest stratum > middle forest stratum > upper forest stratum, which mainly affected the regeneration tree species richness index, as well as young tree height and DBH. Therefore, different management measures can be formulated for different forest strata to improve the regeneration ability or restoration of subtropical evergreen broad-leaved forest.

5. Conclusions

In this paper, redundancy analysis was used to study the relationship between different forest strata structure and regeneration, it can not only independently determine the contribution and explanation of each stand structure variable (Liu et al., 2011), but also reduce the number of stand structure variables that can effectively explain the regeneration variation. It can be seen from the ordination diagram of RDA that although the competition index of the whole stand and the crown width of the upper forest stratum had no significant effect on the regeneration, they had strongly correlated with sapling density and richness index. Hence the effect of non-significant stand structure indices on a certain regeneration indicator should not be neglected in the process of forest management.

The influencing order of each forest stratum structure on regeneration was: lower forest stratum > middle forest stratum > upper forest stratum. Different regeneration indicators had different responses to the main stand structure indices, while the young tree height and DBH, and the tree species diversity and density of regeneration trees were most affected by the main stand structure indices. In the whole stand, 49.58% of the regeneration variation was explained by stand structure indices, which indicated that the influence factors of regeneration were not only stand structure. Some studies had found that soil conditions had a significant effect on regeneration (Madson and Laisen, 1997; Liu et al., 2011), and different terrain factors also play an important role in the growth of regeneration trees (Tyagi et al., 2011; Kang et al., 2012; Redmond and Kelsey, 2018). Therefore, comprehensively understand the regeneration impact mechanism of subtropical evergreen broad-leaved forest is urgently needed in further study.

Acknowledgments

The authors thank the Tianmu Mountain National Nature Reserve Administration for their support during our research.

Author Contributions

Conceptualization, Junsong Long; Data curation, Mengping Tang; Formal analysis, Junsong Long; Funding acquisition, Mengping Tang; Investigation, Mengping Tang; Methodology, Junsong Long; Writing-original draft, Junsong Long; Writing-review & editing, Mengping Tang. All authors have read and agreed to the published version of the manuscript.

Funding

This work was financially supported by the National Natural Science Foundation of China (31870617).

Availability of data and material

The data are available upon a reasonable request to the Authors.

Competing interests

The authors declare that they have no competing interests.

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Figures

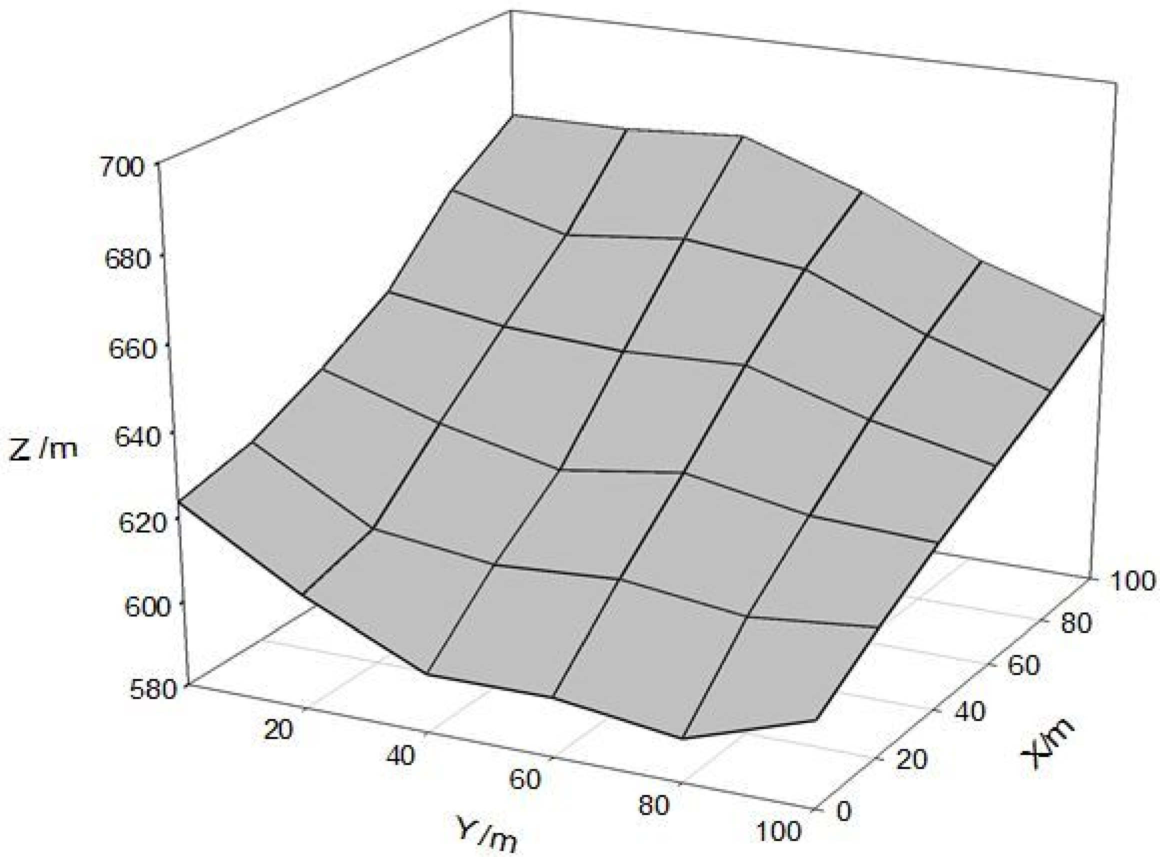

Figure 1

3D terrain map of the 10000m2 plot

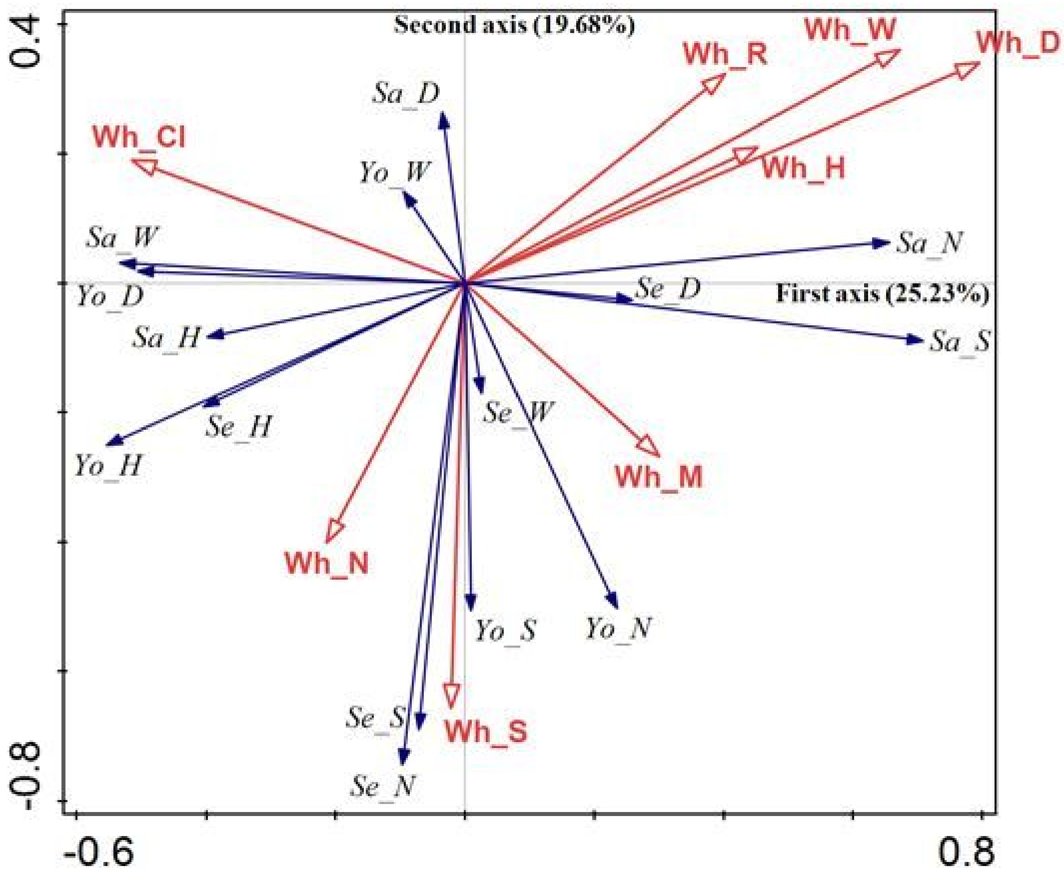

Figure 2

RDA ordination diagram of whole stand structure indices and regeneration Note: Hollow arrow represents stand structure indices, solid arrow represents regeneration indicators. Se_N, Se_D, Se_H, Se_W, Se_S denotes seedling density, diameter at breast height, tree height crown width and species richness index; Sa_N, Sa_D, Sa_H, Sa_W, Sa_S denotes sapling density, diameter at breast height, tree height,crown width and species richness index; Yo_N, Yo_D, Yo_H, Yo_W, Yo_S denotes young tree density, diameter at breast height, tree height, crown width and species richness index.

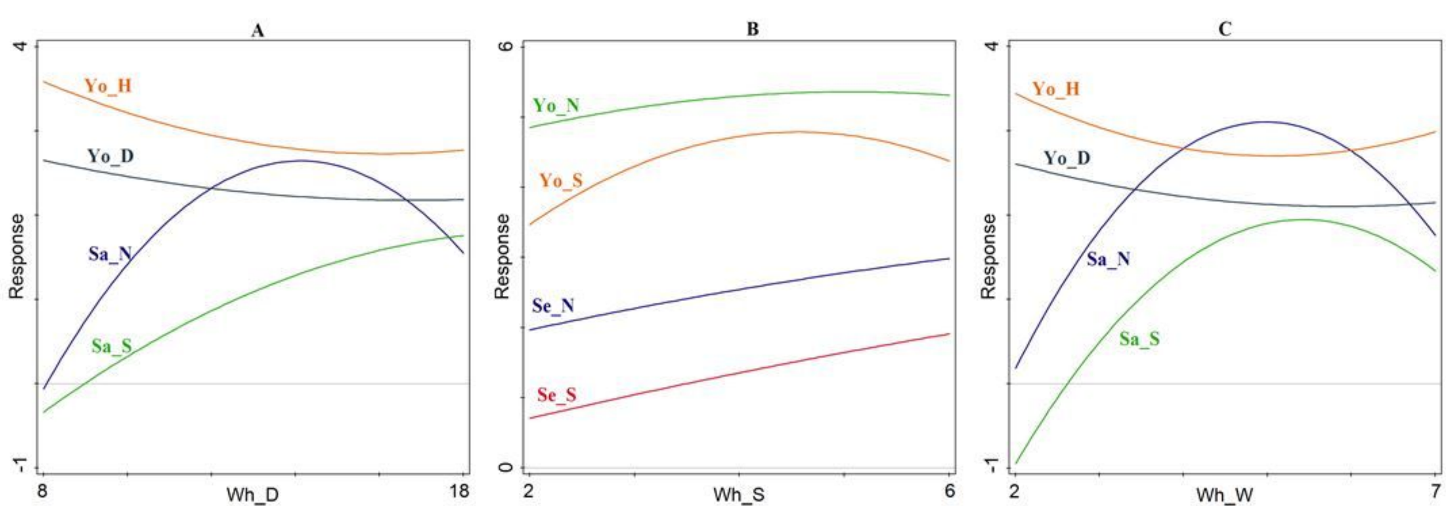

Figure 3

Regeneration response curves to the dominant whole stand structure indices

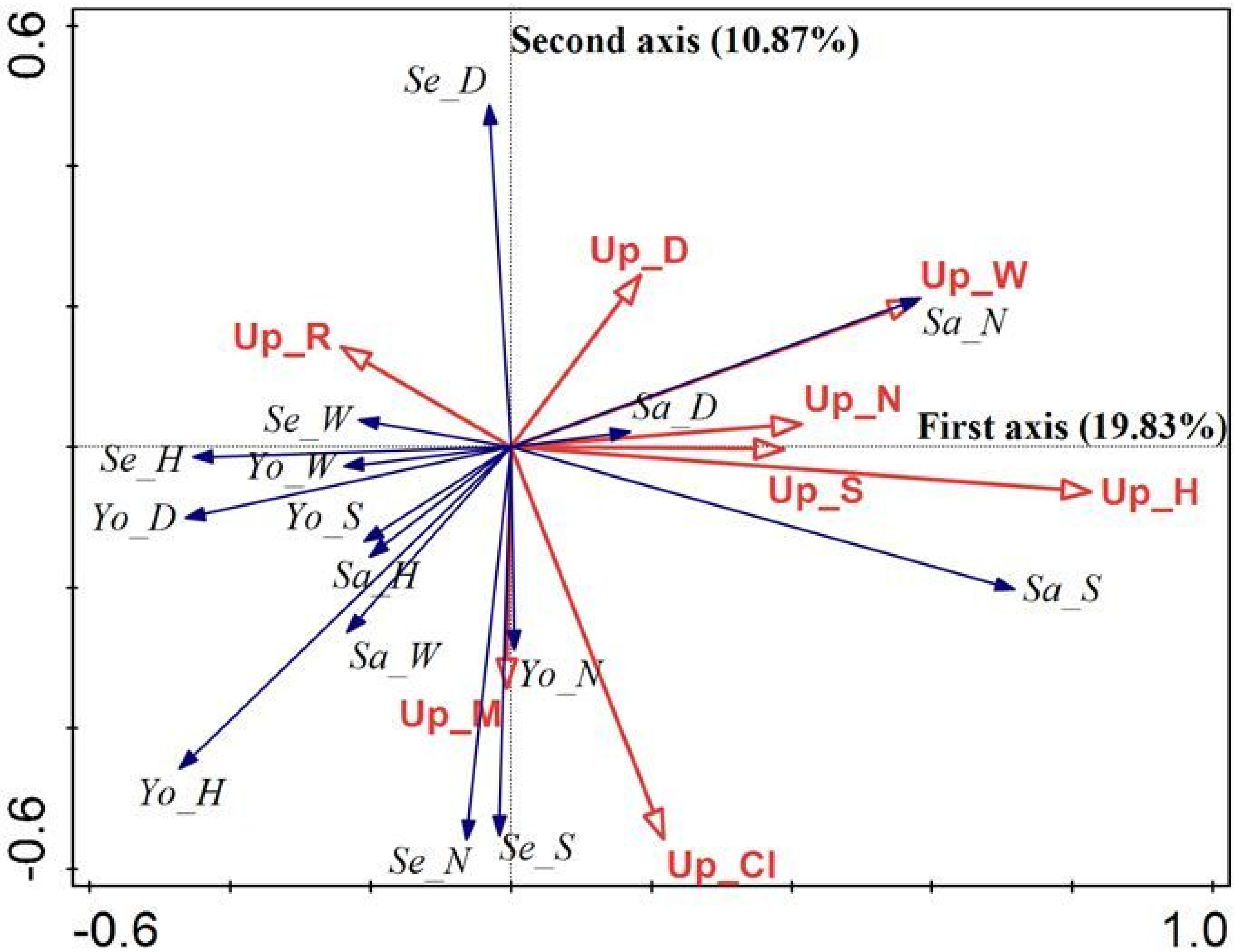

Figure 4

RDA ordination diagram of upper forest stratum structure indices and regeneration

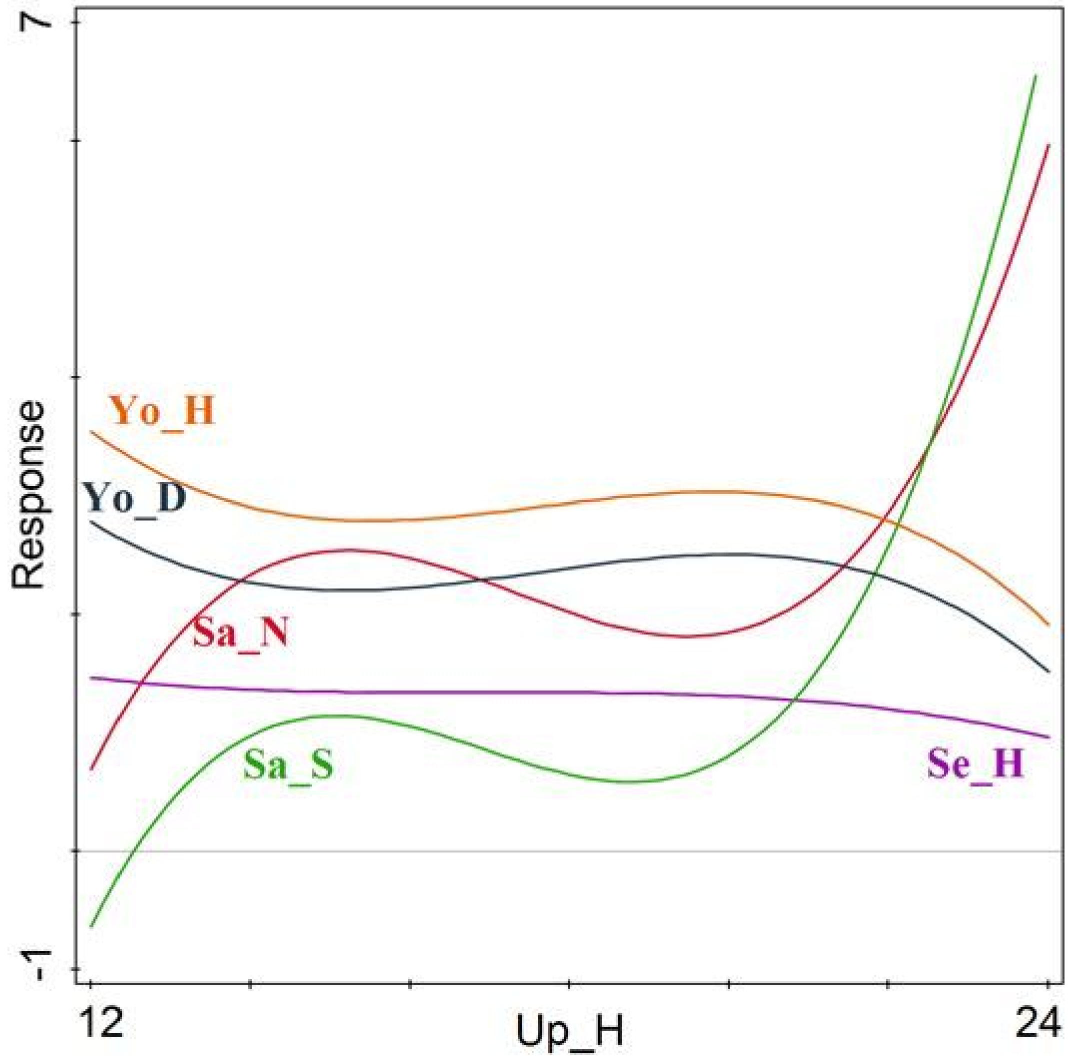

Figure 5

Regeneration response curves to the dominant upper forest stratum structure index

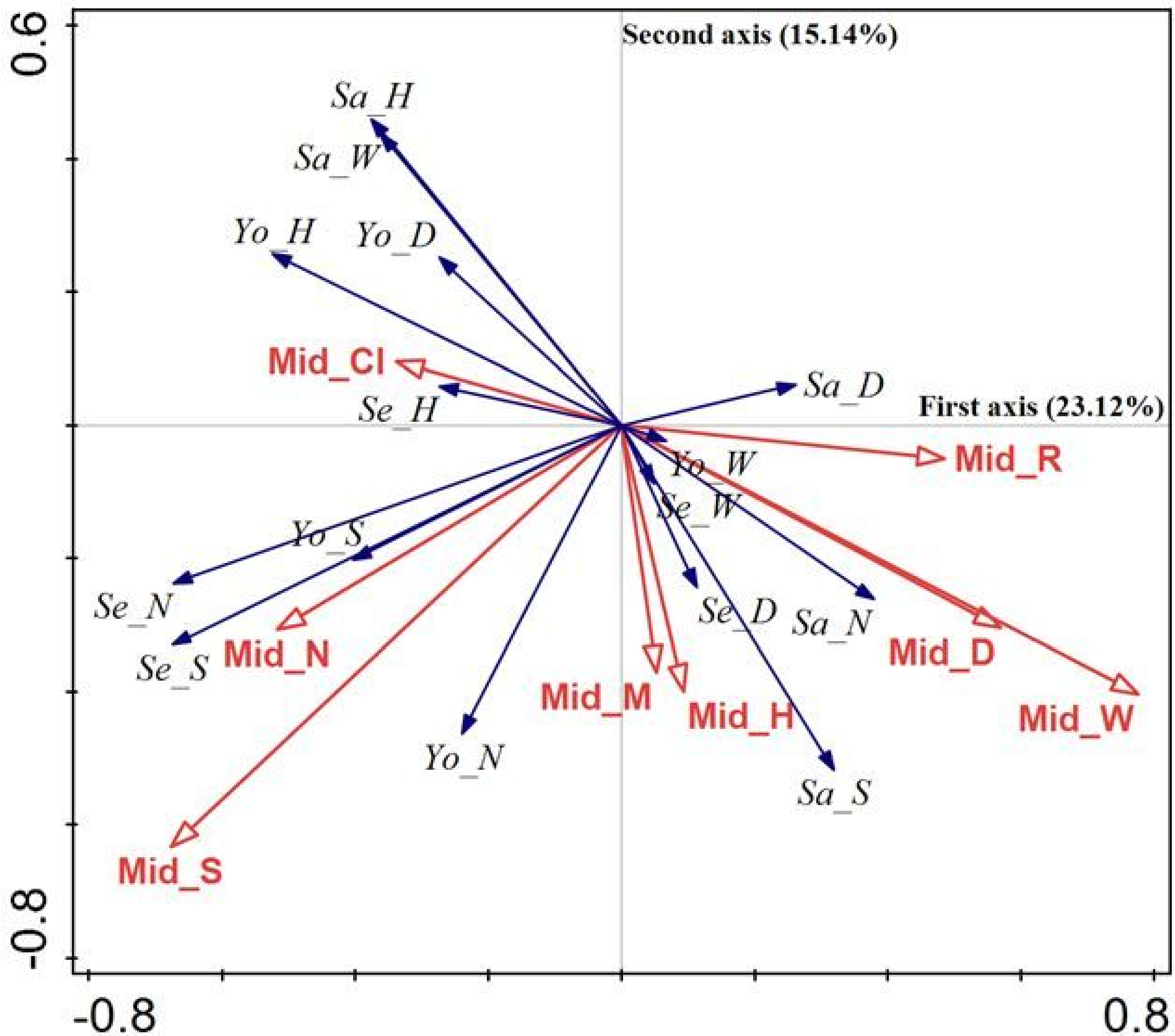

Figure 6

RDA ordination diagram of middle forest stratum structure indices and regeneration

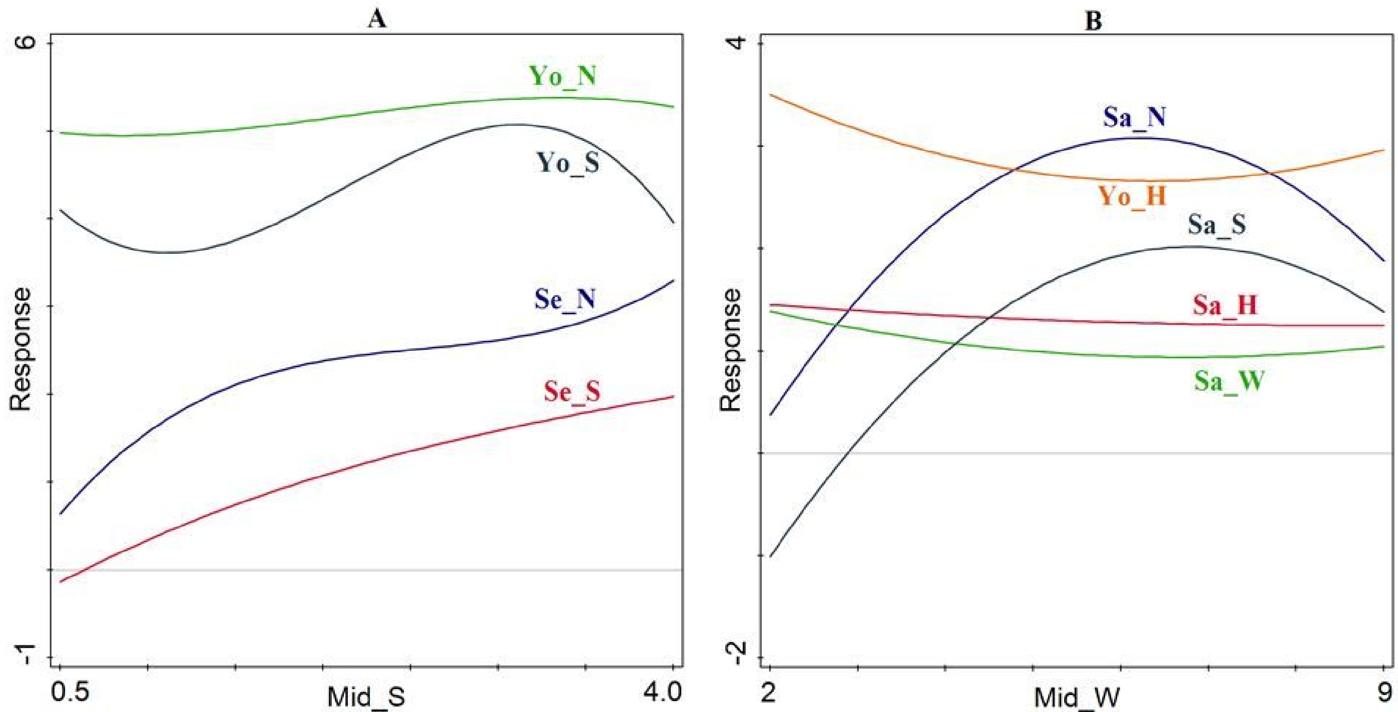

Figure 7

Regeneration response curves to the dominant middle forest stratum structure indices

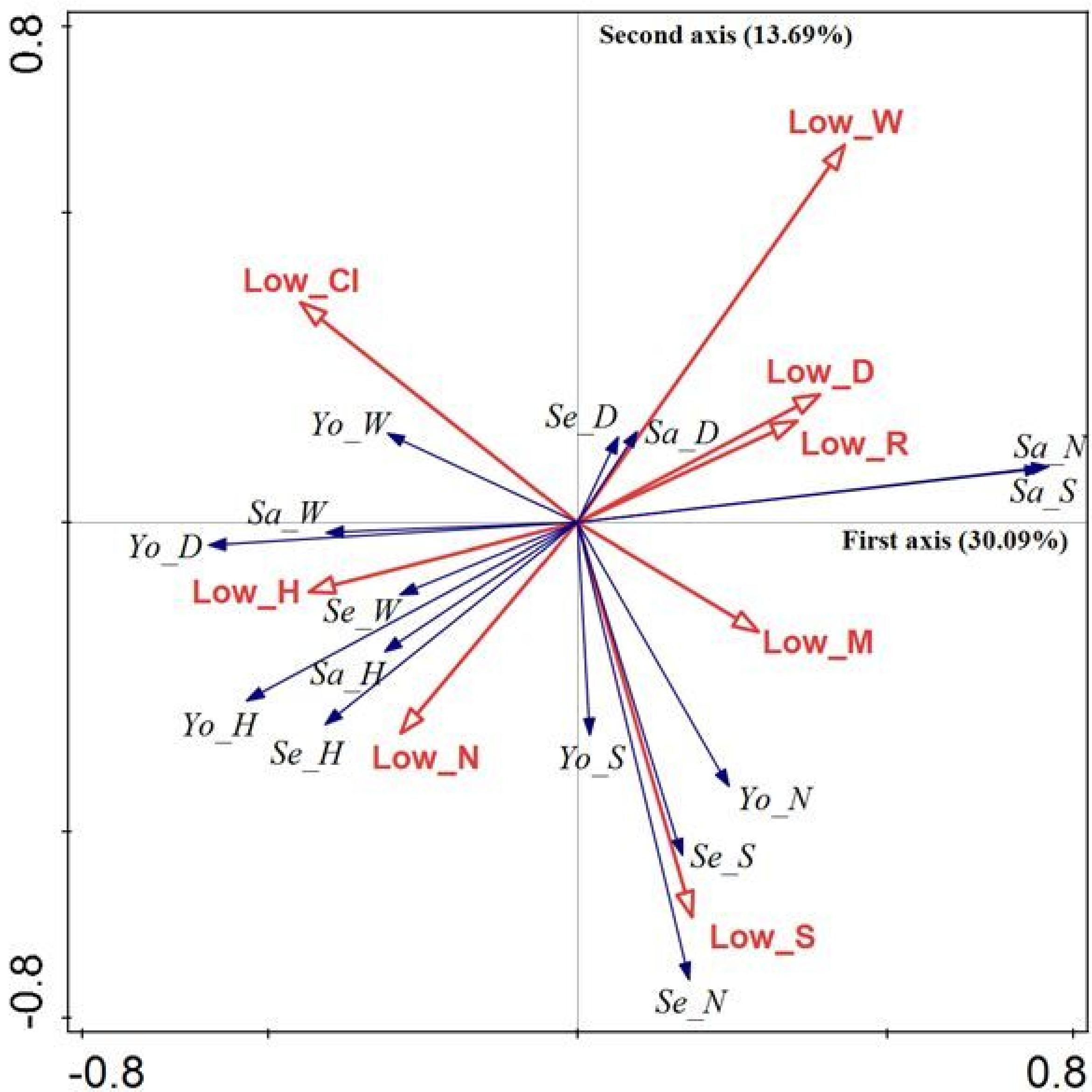

Figure 8

RDA ordination diagram of lower forest stratum structure indices and regeneration

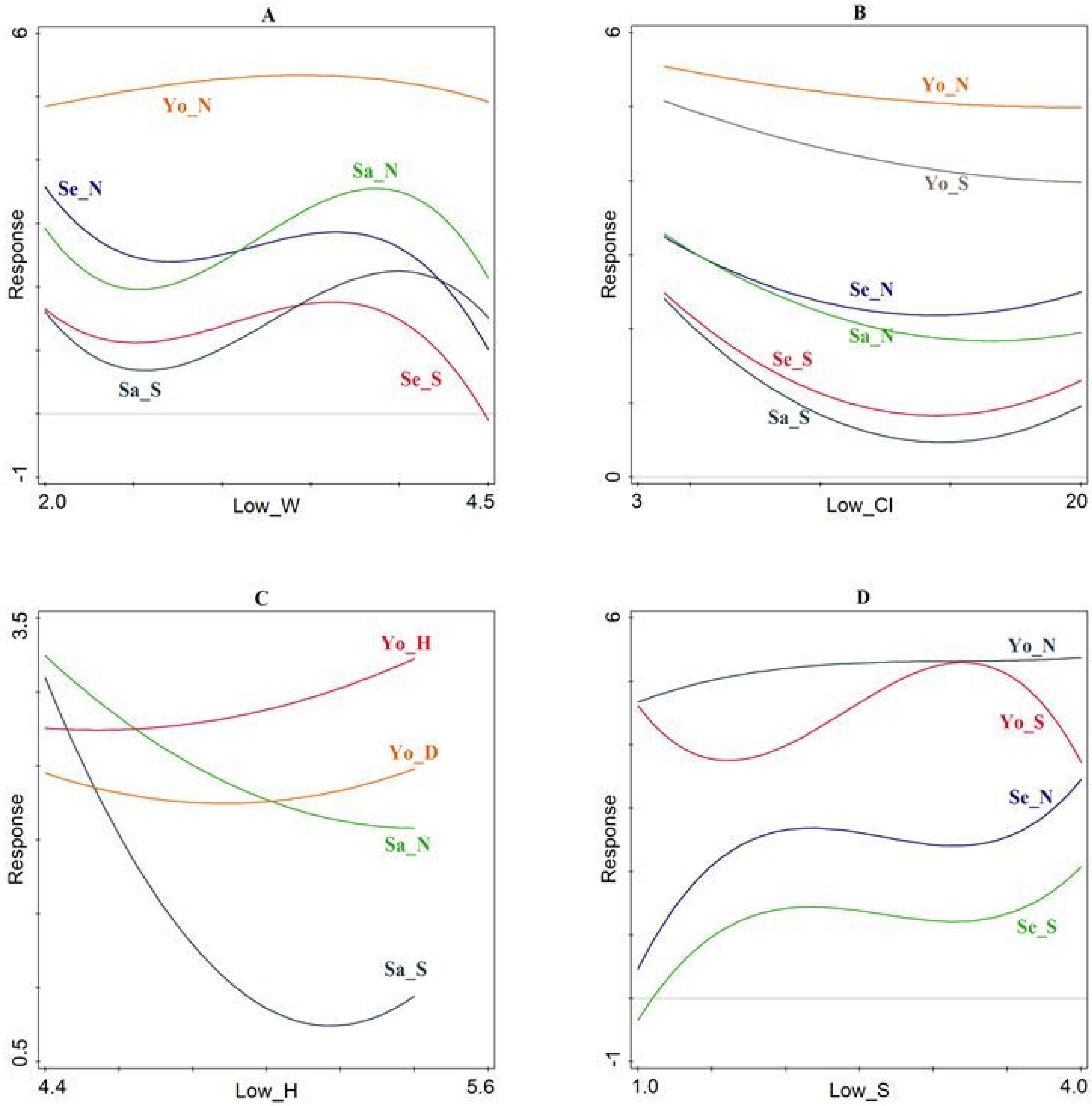

Figure 9

Regeneration response curves to the dominant lower forest stratum structure indices