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Effect of overstory on the seasonal variability of understory herbs in primary broad-leaved Korean pine forest of Changbai Mountain

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In order to study the structure of herbaceous biodiversity and its effect factors in broad-leaved Korean pine forest, a total of 100 1-m^2 sub-plots were established in the 1 ha site which was monthly investigated from May to September in 2009. Data on soil attributes were also investigated (soil organic matter, available nitrogen, available phosphorus, available potassium, soil, water and pH) without light environment (leaf area index (LAI), photosynthetic photon flux density (PPFD) and, canopy presence). In this paper, the relationships between different layers (tree, shrub and herbaceous), soil attributes and light environment were analyzed. The effects of tree and shrub layers, soil attributes and light environment on the structure of herbaceous diversity were also discussed. The results show that there is an obvious seasonal dynamic for the herb in broad-leaved Korean pine forest. It was dominated by *Anemone amurensis* (Korsh.) Kom. and *Corydalis ambigua* Cham. et Schltdl. in May. The highest species richness was in June, when spring ephemeral, early and late-summer plant grew at the same time. July was the growing season and had highest diversity. From August to September, summer plant became withered gradually. There is a significant positive correlation between the diversity in shrub and herb layer Density of shrub layer positively correlated with the cover of herb layer, but negatively correlated with the diversity of herbaceous layer. The effect of the tree layer on the cover and the diversity of herbaceous layer did not arrive at the significant level. The correlation analysis of the cover, diversity and soil attributes, light environment at herbaceous layer, as well as the tree and shrub layer, indicated that available potassium, PPFD, soil water was the key connection between the tree- and shrub layer. The site locates in the broad-leaved Korean pine forest belonged to the old forest which could explain why the tree layer was not related to herbaceous layer in this paper. Therefore, it could be concluded that, the influence of the tree layer on the structure of herbaceous biodiversity carried out through the direct effect on light environment, precipitation and litter.

Key words: Tree layer, shrub layer, herbaceous layer, seasonal dynamic, soil attributes, light environment.

INTRODUCTION

Herbaceous layer in temperate forest places has an important role in energy flow and nutrient cycling in forest ecosystem. Though biomass were few represented at herbaceous layer, number of species reach the maximum level and influences the regeneration of a canopy layer directly. Accordingly, the composition and structure of three-layer influence the herbaceous layer directly or indirectly through change in the distribution of light environment, precipitation, soil fertility as well as the physical characteristics of litter (Gilliam, 2007). The interaction between the herbaceous and tree layer leads to the linkage. This linkage existed in many forest types (Barbier et al., 2008; Antonio and Ricardo, 2009). Gilliam et al. (1995) indicates there is no connection between the herbaceous and tree layers in the infancy phase (20 years after clearing) in West Virginia, but the linkage occurs when forest mature (80~100 years). This linkage may be influenced by environmental gradient, which is confirmed by Gilliam and Roberts (2003). However, at present, the study on the effect of three-layer on the herbaceous layer is insufficient. There is no enough evidence to affirm the mechanism, until now (Stephane et al., 2008). Thus, this paper analyzed the seasonal dynamic of herbaceous diversity and their correlation with soil attributes, light environment, tree and shrub layer in broad-leaved Korean pine forest in Changbai Mountain. It aims at evaluating the structure of herbaceous biodiversity and its effect factors.

MATERIALS AND METHODS

Study site

The site is located in broad-leaved Korean pine forest of Changbai mountain Nature Reserve (N 42°20.211′, E 128°05.705′ and 784 m). The standard type is a gentle slope land belongs to the typical and the temperate continental mountain climate. It has warm and rainy summer, cold and dry winter, with annual average temperature of 3.6°C. Annual precipitation is 700 mm and concentrates between June and September. The soil type is dark brown, forest soil. Forest stand volume is 331.7 $m^3.hm^{-2}$. The density of individual (DBH ≥ 1 cm) is 1,801 $ind.hm^{-2}$. The upper of the tree-layer mainly contains *Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis*, and *Fraxinus mandshurica*. The middle of the tree layer is dominated by *Acer mono*, *Acer barbinerve*, *Corylus mandshurica*, *Syringa reticulata* which dominates the under layer of the forest. During the early spring and ephemeral spring, the main species include *Anemone amurensis*, *Corydalis spp*, and *Adonis amurensis*. During the summer and autumn, the major plant species are *Brachybotrys paridiformis*, *Cardamine leucantha* and *Meehania urticifolia*.

Data collecting

From July to September of 2005, 1 hm^2 area site was established in broad-leaved Korean pine forest used as total station. The site was divided into quadrats (20 m × 20 m) and sub-quadrate (10 × 10 m). In each quadrat, an herbaceous investigation area with 1 × 1 m as dimension, were demarcated by spilings. Totally, 100 herb sites were set up. All the woody plants (Height ≥ 0.3 m) inside the site were numbered and tagged. The species name, height, crown and coordinates were recorded. Species, height, cover (length of the long axis and short axis); numbers of bloom and fruit in the herbaceous site were recorded during the period from May to September. Crown condition was classified by 1 (forest gap) and 0 (under the crown cover). According to the stand presented by Kudo (2008), the herbaceous strata in broad-leaved Korean pine forest can be classified into three types, early spring ephemeral, early summer plant and late summer plant. Tree layer means height of the woody plants were more than 3 m. All woody plants which height is higher than 0.3 m but less than 3 m were belong to shrub layer.

Environmental factors in this research include nitrogen, phosphorus, organic matter, PH value, soil moisture, LAI, PPFD and canopy openness. 500 g soil samples were taken from the surface layer (0 to 20 cm) in the middle of sub-quadrats interval with one. The analysis of soil samples in the lab was done according to the “Soil agricultural chemical analysis method” (Soil Science Society of China, 1999). Soil moisture was measured by HH2 DelLa-TDevices Moisture Meter (UK). PPFD was derived from the fish pictures took above 1 m in each quadrat. WinSCANOPY and XLScanopy were used to get the direct light and scattered light. LAI and canopy openness were calculated according to the method presented by Bonhomme and Chartier (1972); Zhang (2009).

Data analysis

The Shannon-Wiener diversity index and density, both in tree and shrub layer were calculated in each sub-quadrat. The monthly Shannon-Wiener diversity index, evenness and cover degree of herbaceous component were also deduced. According to Mölder’s method (2008), the raw data in May, June, July, August, and September were combined. In that regard, when given specie occurs many times in one quadrat, the biggest cover degree was chosen. The combined data stand for the all herbaceous in the growing season and used to calculate the cover degree and Shannon-Wiener diversity index. This process was carried out through R2.10.0.

Shannon-Wiener diversity index, $H = -\sum p_i \ln p_i$

Where, *H* is Shannon-Wiener diversity index, *pi* the relative frequency.

Evenness, $E = e^H / S$ (Buzas and Gibson, 1969)

Where, *E* is the evenness and *S* the species richness

In order to descript the relationship between species richness and the number of quadrats, rarefaction curve was drawn by the individual number or sample sequence (1, 2, N) as horizontal ordinate and species richness as the y-coordinate. The investigation of sample generally cannot be produced by repeated sampling (Gotelli and Colwell, 2001). The correlation among tree-, shrub- and herb layer; and interaction with the environment were implemented 999 time’s random replacement, inspection through program corPerm2 in R2.10.0 software (Legendre, 2005). The

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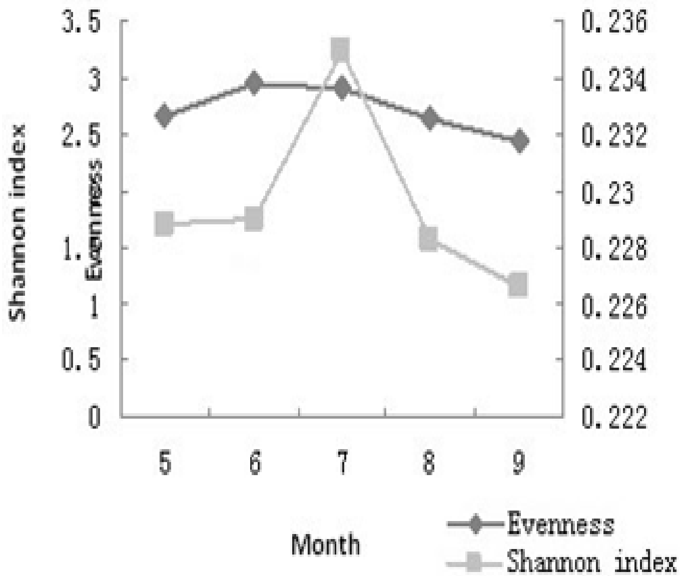

Figure 1. Seasonal dynamics of Shannon-Wiener diversity index of herbaceous plant.

Principal Coordinates of Neighborhood Matrices (PCNM) method was applied. This method is based on a principal coordinate analysis of a truncated pairwise geographic distance matrix between sampling sites. Eigen values associated with positive eigen vectors can be used as spatial predictors in multivariate regression (Dray et al., 2007). Moreover, these Eigen values have the advantage that they are orthogonal to each other and thus represent various structures over the whole range of scales encompassed by the sampling design (Borcard and Legendre, 2002). Firstly, a Euclidean distance matrix with the X and Y coordinates of each 10 × 10 m subplot was created. Then, the calculation of the principal coordinates variables was performed using the "PCNM" library (Legendre, 2007), finally, the principal coordinates variables with positive Moran's *I* value (from now on PCNM variables) was chosen.

Variation partitioning (Borcard et al., 1992) was used to discover the fraction of variation in cover and the herbaceous diversity explained by the environmental and spatial variables. The environmental matrix was created, including together the over storey related factors (tree density, canopy cover and Shannon-Wiener diversity index), shrub layers related factors (shrub density, shrub cover and Shannon-Wiener diversity index), soil attributes (soil organic matter, available nitrogen, available phosphorus, available potassium, soil water and pH) and light regime (LAI, PPFD and canopy presence). The spatial variables were created with PCNM variables. Firstly, we selected a set of environmental and spatial variables explaining a significant portion of variation in each one of the response variables (a + b and b + c, respectively). Then, we determined the fraction of variation explained by the whole set of variables (a + b + c). Partial regression was used to determine the fraction of variation explained by the environmental (fraction a) and the spatial variables (fraction c) when removing their interaction (fraction b). After that, another variation partitioning of the a + b fraction was performed to determine the relative contribution of the over storey, shrub layer, soil and light regime to this environmental fraction. The "pack for" library (Dray et al., 2007) of the R statistical language (R Development Core Team, 2007) was used to select the sets of explanatory variables. The variation partitioning analyses were carried out with the "vegan" library (Oksanen et al., 2011) and the package of the R statistical language (R Development Core Team, 2007). The environmental and response variables were transformed if needed.

RESULTS

Seasonal dynamic of diversity at herb layer

In broad-leaved Korean pine forest, the higher plant included 13 early spring ephemeral species, 37 early summer plants and 21 late summer plants. The type of species varied with the season. In May snow just melting, there are lots of early spring ephemeral species like *A. amurensis*, *Corydalis spp*, *A. amurensis*, early summer plants, *Hylomecon japonica*, *Paris quadrifolia*, *Veratrum nigrum*, and few late summer plants, *Lilium distichum*, *Filipendula palmate*, *Cacalia hastate*. In June, there was still a little early spring ephemeral species, lots of early summer plants and some late summer plants growing. Therefore, the highest species richness happened in this month. From July to September, the early summer plants and late summer plants withered gradually with the decreasing of the species number. Different from the number of species, the Shannon-Wiener diversity index in July was the highest one (Figure 1). From May to September, the evenness index change un-conspicuously. Rarefaction curve showed that with the increasing of number of quadrat, species richness increased gradually. When the number of quadrat was less than 30, the species richness increased sharply. Rarefaction curve and species number were in accordance. The highest species richness occurred in June, and lowest one was in September. There were 26 woody plants (height ≥ 3 m) and 32 woody plants (0.3 m ≤ height < 3 m) in the tree and shrub layer, respectively. There were 21 common species between the tree- and shrub-layer, including small trees, sapling and part of tall shrub. The correlation analysis between the density, cover degree and diversity of tree and shrub layer; and the cover degree and diversity at herb layer show that there was a significant positive correlation between the diversity and the density (Table 1). It was for tree- and shrub layer. The diversity between the herbaceous layer and shrub layer reach the significant positive correlation at the level of 0.01.

The analysis among the environmental variables (Table 2) indicates that there were significant positive correlations among content of organic matter, available phosphorus, and available potassium at the level of 0.001. Soil moisture negatively related with organic matter. Soil acidity and alkalinity is positively related with available phosphorus and available potassium. LAI index significantly is positively correlated with PPFD at the level of 0.01, but significantly, negatively correlated with soil

Table 1. Correlation coefficients between density (D), coverage (C) and diversity (H) of the tree and shrub layers, and coverage (C) and diversity (H) of herbaceous layers.

Parameter	Tree D	Tree C	Tree H	Shrub D	Shrub C	Shrub H	herbaceous H	Herb C
Tree D	1	-0.068	0.322**	0.094	0.105	0.159	0.069	0.074
Tree C		1	0.089	0.068	0.031	0.112	0.128	-0.11
Tree H			1	-0.102	0.156	0.141	0.046	-0.074
Shrub D				1	0.081	0.248*	-0.01	0.098
Shrub C					1	0.013	-0.102	-0.14
Shrub H						1	0.242**	-0.009
herbaceous H							1	0.127
herbaceous C								1

*P < 0.05, **P < 0.01, ***P < 0.001.

Table 2. Correlation coefficients between the nine quantitative environmental variables.

Parameter	O.M	N	P	K	Soil water	pH	PPFD	LAI	Gap
O.M	1	-0.183	0.521***	0.357***	-0.308**	0.016	0.120	0.060	-0.054
N		1	0.140	0.231*	0.007	-0.175	0.086	-0.077	-0.071
P			1	0.668***	0.017	0.341**	0.182	0.158	0.098
K				1	0.020	0.421***	0.143	-0.091	0.025
Soil water					1	0.076	-0.214*	-0.231*	0.390***
pH						1	0.023	-0.230*	0.073
PPFD							1	0.286**	-0.006
LAI								1	-0.022
Gap									1

*P < 0.05, **P < 0.01, ***P < 0.001.

Table 3. Relationship between species richness (SR), Shannon-Wiener diversity index (H), and coverage (C) of three layers (tree, shrub, and herbaceous layer) and environmental parameters, respectively.

Parameter	O.M	N	P	K	Soil water	pH	PPFD	LAI	Gap
Tree number	-0.270**	0.017	-0.282**	-0.290**	0.009	-0.184	-0.108	0.005	0.161
Tree C	0.092	-0.236*	-0.215*	-0.148	-0.205*	-0.094	0.082	-0.058	-0.083
Tree eH	-0.181	0.096	-0.277*	-0.120	-0.113	-0.091	-0.130	-0.063	-0.140
Shrub number	-0.074	-0.188	-0.112	-0.137	0.107	-0.034	-0.158	-0.088	0.279**
Shrub C	-0.162	0.064	-0.163	0.032	-0.049	-0.033	0.068	0.220*	-0.001
Shrub H	-0.110	-0.094	-0.216*	-0.269**	-0.031	-0.214*	-0.198*	0.004	-0.152
herbaceous H	-0.161	-0.050	-0.131	-0.081	0.149	-0.069	-0.261*	-0.183	-0.270**
herbaceous C	-0.035	0.095	0.279**	0.398***	0.436***	0.227*	-0.065	-0.311**	0.294**

* P < 0.05, **P < 0.01, ***P < 0.001.

moisture and PH value. Soil moisture significantly is positively correlated with forest gaps at the level of 0.001.

The analysis between three layers (tree, shrub and herbaceous layer) and environmental factors (Table 3) showed that soil organic matter and tree density were significantly and negatively correlated. Available nitrogen significantly related to tree cover degree. Available phosphorus is significantly and negatively correlated with the density, cover degree and diversity in tree layer and diversity at shrub layer, while positively related to the cover degree at herbaceous layer. Available potassium is significantly and negatively correlated with the density, cover degree and diversity at tree-layer and diversity at shrub layer, but positively related with the cover degree at herbaceous layer. The cover degree was significantly and positively related with soil moisture at the level of 0.001, but negatively with LAI index. In addition, the cover degree at herbaceous layer and density at shrub layer were both positively related with forest gaps at the level of 0.01. Above all, soil nitrogen and potassium were significantly correlated on the environmental factors coexisting at tree, shrub and herbaceous layer. The density of shrub layer and cover degree of herb-layer was positively related to forest gaps; that is, the distribution of tree crown. At three different layers, the effect of environmental factors on the density of tree layer, the diversity of shrub layer and cover of herbaceous layer was the most obvious.

Result of variation partitioning taking monthly herbaceous coverage and diversity as the dependent variable respectively, and environment variables and space variables (explanatory variables) showed that available potassium and soil moisture which were screened from the environmental factors could explain 12.0% of variation. Spatial variable simply could explain 1.9% of the variation. The environmental factors and spatial variable could totally explain 19.4% of variation (Figure 2a). Available potassium and forest gaps screened from the environmental factors explained 7.5% of diversity variation at herbaceous layer during the whole growing season. The environmental factors and spatial variable could totally explain 28.5% of variation (Figure 2b). The analysis of monthly cover degree and diversity showed that in May the significant influencing factors on cover degree was the density of shrub. However, variable potassium also had a certain effect without reaching the significant level. The environmental factors could simply explain 3.0% of variation. The environmental factors and spatial variable could totally explain 29.6% of variation (Figure 2c).

The extremely significant factors influencing on diversity at herbaceous layer were available in potassium, LAI and forest gaps. The environmental factor composed by them could explain 16.5% of diversity variation. The environmental factors and spatial variable could totally explain 39.8% of variation (Figure 2d). In June, the extremely significant factors influencing on diversity at herbaceous layer where available potassium and shrub density, which could explain 8.3% of the variation. The environmental factors and spatial variable could totally explain 17.9% of variation (Figure 2e). The main effects of herb diversity where available potassium and shrub density, which could explain 7.5% of the variation. The environmental factors and spatial variable could totally explain 19.1% of variation (Figure 2f). In July, shrub density, available potassium and LAI had an extreme and significant impact on herb cover degree. Tree density has also significantly effect on herbaceous cover degree.

Environmental factors could explain 22.9% of the variation. The combination of environmental and spatial variable could explain 32.1% variation (Figure 2g). The herbaceous diversity significantly related to forest gaps, available potassium and PPFD in this month. The composition of them could explain 13.3% of diversity variation. The environmental and spatial factors totally explain 24.2% of variation (Figure 2h). Variation partitioning was not implemented in August, because there was no significant correlation between the cover degree and diversity at herbaceous layer and each environmental factor. In September, LAI and forest gaps had a significant impact on the herb cover degree. The influence of PPFD decreased. The environmental variation composited by them could explain 14.0% of the variation. The environmental and spatial factors totally explain 20.8% of variation (Figure 2i). In contrast, the shrub density and diversity had an impact on the herb diversity and did not reach to the significant level. Thus, the density and diversity at shrub-layer could only explain 5.1% of diversity variation. The environmental and spatial factors totally explained 14.8% of variation (Figure 2j). All the above results suggested that the environmental factors influencing the herbaceous cover degree were different accordingly to the period. Extremely and significantly potassium available is correlated with the herb cover degree, but negatively correlated with herbaceous diversity in the early and middle of the growing season.

DISCUSSION

The results show that the diversity at shrub layer was extremely and significantly positive with the herbaceous layer. The density at shrub layer was positive with the cover degree at herbaceous layer, but negative with the herb diversity. The effect of the tree layer on cover degree and diversity at herbaceous layer did not arrive at the significant level. As the species below in the canopy, the negative relation between the number of shrub and diversity at herbaceous layer were accepted (Kwiatkowska, 1994; Godefroid et al., 2005; Baker and Van Lear, 1998; Hicks, 1980). In accordance with the previous results (Ewald, 2000; Neumanna and Starlinger 2001; Aubert et al., 2004), the cover degree was not significantly related to the diversity at herbaceous layer. In addition, the fact that diversity at tree layer was positively related with the one at an herbaceous layer and this was also found (Hicks, 1980; McCune and Antos, 1981; Bradfield and Scagel, 1984; Ingerpuu et al., 2003; Mölder et al., 2008). However, previous research showed that the effect of the tree layer on the herbaceous layer was significant and positive in the “general stand” (exclude of old forest and planted forest), but did not reach the significant level in the old forest and planted

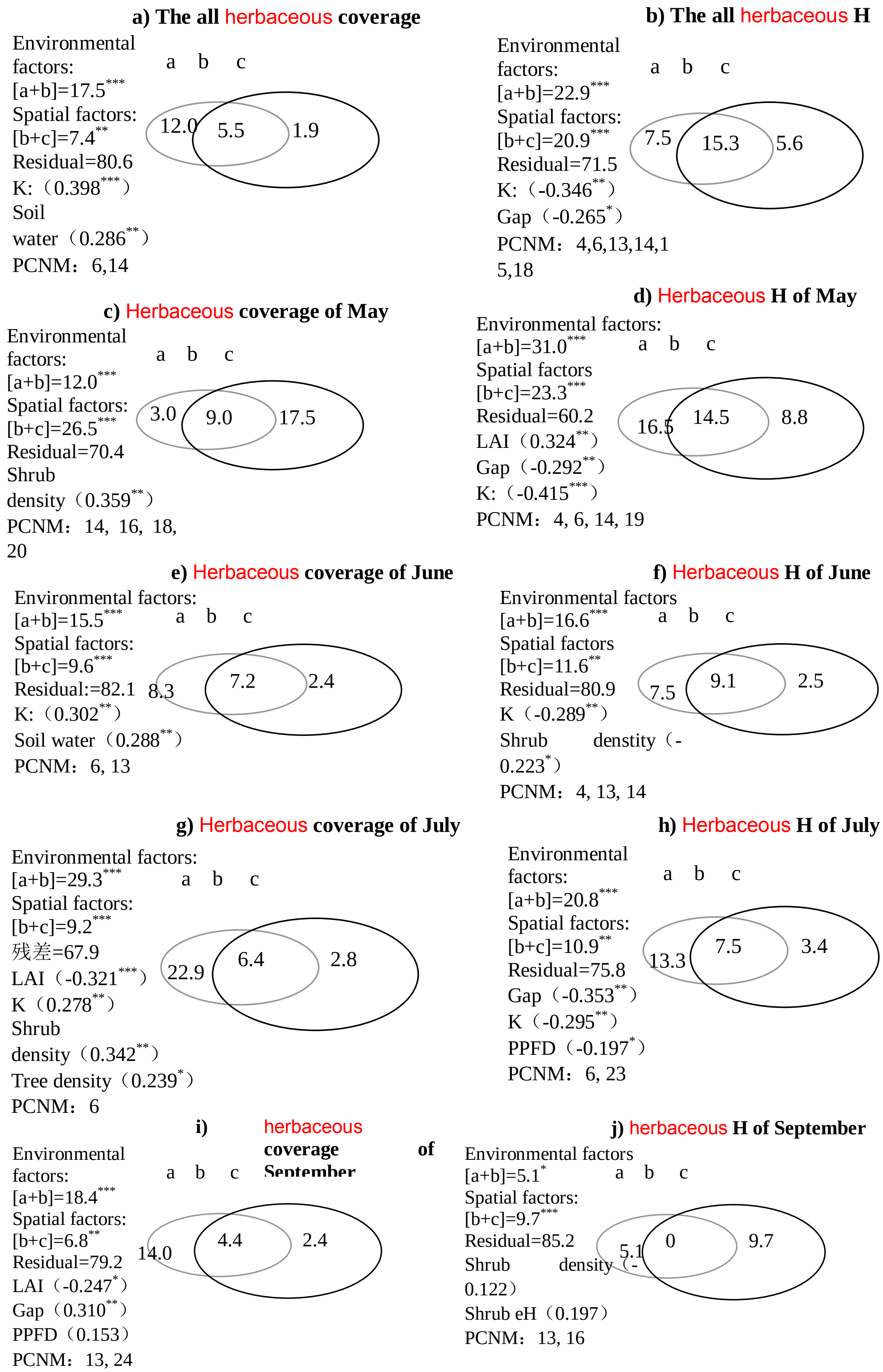

Figure 2. Result of variation partitioning (H: Shannon-Wiener diversity index).

forest. The site locates in the broad-leaved Korean pine forest belonged to the old forest which could explain why the tree layer was not related to herbaceous layer in this paper.

Results of variation partitioning indicated that available potassium were extremely and significantly positive with the herbaceous cover degree in the early and middle of the growing season but negatively with the diversity. Self-correlation analysis of soil and light available showed that available potassium, soil organic matters, available phosphorus and pH were extremely and significantly positive at the level of 0.001, but they extremely and significantly negative with tree density at the level of 0.01. Available potassium was extremely and significantly negative with shrub density. This suggested that available potassium was the key factor to connect the three layers. The possible reasons were the tree layer influenced the distribution of organic matters, potassium and phosphorus in the soil, which in turn effect the distribution of herb. The advantage herbaceous grew well in the area rich in nutrition. Numbers and cover degree of individual increased, leading the greatest cover degree at herbaceous layer. Oppositely, the advantage's growth was restricted in the area lacking nutrition. It provided chances for other species' invading and made herb diversity to be higher.

Light condition was considered as the limited factor for the coverage and richness of vegetation (Hill, 1979; Kirby, 1988; Bazzaz, 1990; Jennings et al., 1999). The light environment under the canopy was determined by canopy structure, which also controlled the temperature and moisture under the forest, especially for the density of the forest crown (Sharpe et al., 1996). Environmental factor under different species was different (Porte et al., 2004) which influenced the vegetation under the forest. It may be due to the temperature and moisture related to the light condition (Nihlgard, 1969). The light under the storey could be a comprehensive factor which stands for the difference of this microenvironment. Most research explained the effect of tree-layer on herbaceous layer through the light environment. In this paper, PPFD, LAI and forest gap were used as the light indicator. Results showed that the herbaceous cover degree and existence of forest gap were positive with the PPFD, but negative with the LAI in September. However, the diversity of herb was negative with the existing forest gap in May and July. Under the forest gap, there was enough light to improve the growth of advantage herbaceous and enlarge the herbaceous cover. On the other hand, Shannon-Wiener diversity index decrease because of the difficult invading of disadvantage species. Therefore, the relationship between the herb coverage and forest gaps was the opposite of the herb diversity. It could be concluded that light environment was also an important factor which influences the herbaceous coverage and diversity.

Soil moisture has an extremity and positive response

both to herbaceous coverage and forest gaps, but negatively related to the tree coverage and content of organic matters. It suggested that soil moisture is another important factor connecting with tree and herbaceous layer. Soil moisture was relevant with coverage at tree layer and forest gaps, which indicated that the distribution of forest crown had an impact on the distribution of light environment and precipitation, thereby on the growth of herbaceous plants.

Hill (1979) considered that the mechanism of tree layer impact on herbaceous layer was through light, precipitation and litter content. In this paper, it was found that organic matters, nitrogen, phosphorus, potassium, soil, water and light factor were strongly relevant with tree and herb layer. It indicated that though the density, coverage, and diversity at the tree layer did not have a direct impact on the coverage and diversity at herbaceous layer, it effects the distribution at herbaceous layer through changing the distribution of soil nutrient, water and light.

Conflict of Interests

The author(s) have not declared any conflict of interests.

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