



阔叶红松林不同演替阶段灌木叶片碳氮磷化学计量特征及其影响因素

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摘 要 灌木是森林生态系统的重要组成部分, 对于演替进程中灌木叶片化学计量特征的研究, 有助于全面理解和预测森林演替过程。该研究以黑龙江凉水国家自然保护区内处于阔叶红松(*Pinus koraiensis*)林不同演替阶段中的白桦(*Betula platyphylla*)次生林、落叶阔叶混交林、针阔混交林、阔叶红松林的灌木为研究对象, 分析其叶片的碳(C)、氮(N)、磷(P)化学计量特征差异, 并利用层次分割方法检验其与土壤、物种多样性的关系。主要结果为: 1)随着演替的进行, 阔叶红松林的叶片N含量显著高于其他3种林型, P含量与白桦次生林无显著差异, 但显著高于其他两种林型; 2)土壤N、P含量与个体尺度上的叶片N含量均呈显著正相关关系, 土壤P含量与叶片P含量呈显著正相关关系; 3)群落尺度上, 物种多样性和土壤化学性质共解释叶片N含量变异的82%和叶片P含量变异的62%; 4)群落尺度上Shannon多样性指数与灌木叶片的N、P含量呈显著正相关关系, 与灌木叶片的C:N、C:P呈显著负相关关系。总之, 阔叶红松林4个演替阶段灌木均受到氮限制; 相较于土壤的化学性质, 物种多样性更好地解释了灌木化学计量的变异。

关键词 物种多样性; 养分限制; 土壤; 小兴安岭; 阔叶红松林

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Characteristics of shrub leaf carbon, nitrogen and phosphorus stoichiometry and influencing factors in mixed broadleaved-Korean pine forests at different successional stages

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Abstract

Aims Shrubs are an important component of forest ecosystems. This study investigated changes in the stoichiometric characteristics of shrub leaves during forest succession in order to understand and predict the processes of forest succession.

Methods The study was conducted in the Liangshui National Nature Reserve of Heilongjiang Province, with forest stands at different successional stages of mixed broadleaved-Korean pine (*Pinus koraiensis*) forest representing secondary birch (*Betula platyphylla*) forest, mixed deciduous broad-leaved forest, mixed coniferous and broad-leaved forest, and mixed broadleaved-Korean pine forest. Measurements were made on carbon (C), nitrogen (N) and phosphorus (P) contents in leaves of the understory shrubs and soil, and the stoichiometric characteristics of shrub leaves and relationships with soil stoichiometry were examined with hierarchical analysis.

Important findings The N content in shrub leaves was significantly higher in the mixed broadleaved-Korean pine forest than in other three forest types; the P content was significantly higher in the mixed broadleaved-Korean pine forest than in two other forest types except the secondary birch forest. Soil N and P contents were significantly and positively correlated with leaf N content at individual scale, and soil P concentration was significantly and positively correlated with leaf P content. At the community level, 82% of leaf N content variation and 62% of leaf P content variation were explained by species diversity and soil chemical properties; the Shannon diversity index was significantly and positively correlated with the N and P contents in shrub leaves, and negatively with the leaf C:N ratio and C:P ratio. In conclusion, shrubs in mixed broadleaved-Korean pine forests

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at the four successional stages were all N-limited, and species diversity better explains the stoichiometric variations in understory shrubs than soil chemical properties.

Key words species diversity; nutrient limitation; soil; Xiao Hinggan Mountains; mixed broadleaved-Korean pine forest

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作为生物体基本的组成元素, 氮(N)和磷(P)被认为是陆地生态系统中植物体内重要的限制因子(Reich *et al.*, 1997; 贺金生和韩兴国, 2010), 在植物的生长和生理代谢过程中发挥重要作用(Zhang *et al.*, 2020)。揭示植物体内的N、P养分状况对于理解植物的生长状况及对周围环境条件变化的响应至关重要(Su *et al.*, 2021)。

植物体内的化学计量特征既受到一定的限制, 又会展现出一定的灵活性(Sistla *et al.*, 2015), 例如, 植物在不同器官合理分配有限的营养物质, 用以适应不同的环境特征(Zhang *et al.*, 2018b)。植物也具有在外界环境变化时保持其体内元素组成相对稳定的能力, 被称为生态化学计量学的内稳态理论(Sterner & Elser, 2002)。在生态化学计量学的研究中, 常利用植物体内N:P来衡量植物的养分利用和受限制状况(Güsewell, 2004; He *et al.*, 2008)。目前, 对于植物化学计量特征的研究主要集中于不同器官的养分分配策略(Yan *et al.*, 2016), 不同环境条件下受N、P限制的模式(Du *et al.*, 2020), 以及植物器官中N、P含量的增长关系(陈婵等, 2016; Zhang *et al.*, 2018b)等。但是, 目前对于演替过程中植物叶片化学计量特征的变异及其驱动因素的研究还较少(Yan *et al.*, 2006)。

植物的化学计量特征可以反映植物的许多特性, 同时也受到周围环境状况的影响(Elser & Urabe, 1999)。以往的研究认为, 土壤化学计量特征是植物体内N、P含量的有效驱动因素(McGroddy *et al.*, 2004), 例如, 在土壤中施加氮肥, 可以导致全球陆生植物内N含量平均增加28.5% (Xia & Wan, 2008)。生物多样性被认为是另一个影响植物化学计量特征的重要因素(Olde Venterink *et al.*, 2003), 但是不同研究中多样性与植物体内N、P的化学计量特征关系并不一致。例如, Braakhekke和Hooftman (1999)研究发现, 一定地区内植物的多样性最高时, 该地区的植物体内N、P含量处于中等比例, 不会过高也不会过低, 而Bobbink等(2010)的研究则发现, 植物体内

的单一化学计量与生物多样性呈负相关关系, 因此生物多样性与植物体内N、P含量的关系究竟如何, 还需进一步的研究。

目前对于陆地植物化学计量的研究主要集中于乔木(Cao *et al.*, 2016)和草本(He *et al.*, 2006), 对于灌木的研究较少(Zhang *et al.*, 2018b)。灌木作为森林生态系统的重要组成部分, 在养分利用、土壤肥力改善、调节物种组成(Michalet *et al.*, 2015)、提供栖息地(Boelman *et al.*, 2015)等方面均具有重要作用, 是揭示森林结构的重要指标(Peña-Claros, 2003), 对于群落演替具有至关重要的作用(曹嘉瑜等, 2020)。对于演替进程中灌木化学计量特征的研究, 有助于我们全面地理解森林演替过程中N、P养分的变化。目前对北方温带森林不同演替阶段灌木化学计量特征的研究较少, 尤其是群落尺度上灌木层养分利用特征的研究尚鲜有报道。

阔叶红松(*Pinus koraiensis*)林是我国东北东部山区的地带性顶极森林植被, 是以红松为建群种的典型温带针阔混交林。本研究以黑龙江凉水国家级自然保护区内的阔叶红松林4个演替阶段群落的灌木叶片为研究对象, 分析其化学计量特征, 旨在探索: (1)不同演替阶段灌木叶片化学计量有何差异; (2)土壤N、P含量对个体尺度上灌木叶片化学计量的影响; (3)物种多样性和土壤化学性质与演替过程中灌木叶片化学计量变异的关系, 以期理解阔叶红松林演替变化规律提供基础数据和科学依据。

1 材料和方法

1.1 研究区概况

本研究地位于黑龙江凉水国家级自然保护区(47.18° N, 128.89° E)。该区域属于低山丘陵地带, 具有鲜明的温带大陆性季风气候特征, 降水多集中于夏季, 其中6-8月占全年降水量的60%以上, 年降水量为676 mm, 年蒸发量为805 mm, 年平均气温为-0.3 °C, 地带性土壤为暗棕壤, 占保护区面积的84.91% (徐丽娜和金光泽, 2012)。

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1.2 样地设置与取样方法

本研究样地为阔叶红松林不同演替阶段的4个森林群落, 根据树种组成和林龄划分为白桦(*Betula platyphylla*)次生林、落叶阔叶混交林、针阔混交林以及阔叶红松林(后文分别用演替阶段I、II、III、IV来表示)。在4个森林群落中各设置3个20 m × 20 m的样地, 每个样地间隔不小于20 m, 于2019年夏季对样地内所有胸径>1 cm的木本植物(包括乔木和灌木)进行每木调查、挂牌, 并在各样地内采集植物样品和土壤样品。

植物样品的采集: 根据样地群落调查的结果(表1), 在每个样地中采集样方中出现的所有灌木种。每个灌木种选择3株大小相似、长势良好的标准木, 采集其未受病虫害的叶片, 并将每株标准木的叶片混合作为一份样品。

土壤样品的采集: 在每个样地中采用标准五点取样法进行土壤样品的采集, 在每个点取0–20 cm土层的土壤样品, 并去除其中的根系和凋落物。

1.3 样品测定

将采集到的所有样品在65 °C下烘干至恒质量,

并研磨至通过100目筛。植物和土壤样品的全氮(TN)、全磷(TP)含量在经过浓H₂SO₄-H₂O₂消煮后采用AQ400间断分析仪(SEAL Analytical, Mequon, USA)进行测定, 土壤有机碳(SOC)含量采用multiN/C3000碳氮元素分析仪(Aanalytik Jena AG, Jena, Germany)进行测定。

1.4 数据处理

各样方灌木叶片的化学计量以异速生长方程为基础(李晓娜等, 2010), 利用生物量加权平均法(Zhang *et al.*, 2018a)算出, 公式为:

$$Leaf E_{com} = (\sum E_n \times B_n) / B_{com} \quad (1)$$

式中, $Leaf E_{com}$ 表示各样方叶片的N或P含量(g·kg⁻¹), E_n 表示单个灌木叶片N或P含量(g·kg⁻¹), B_n 表示单个灌木叶生物量(kg), B_{com} 表示样方内灌木叶片总生物量(kg)。

不同演替阶段灌木叶片和土壤化学计量特征的差异利用SPSS 22.0中的单因素方差分析进行显著性检验, 若方差齐性, 则使用最小显著差数(LSD)测验法; 若方差非齐性, 则使用Tamhane's T2法进行多重比较, 显著性水平为 $\alpha = 0.05$, 并用Origin 2019

表1 阔叶红松林不同演替阶段乔木和灌木组成

Table 1 Tree and shrub composition at different successional stages in mixed broadleaved-Korean pine forest

演替阶段 Successional stage	乔木组成 Tree composition	灌木组成 Shrub composition
演替阶段I (白桦次生林) Successional stage I (Secondary birch forest)	5白桦; 2红松; 1兴安落叶松; 1水曲柳+春榆+色木槭+山杨+黄檗+枫桦-红皮云杉-裂叶榆-臭冷杉-胡桃楸-紫椴 5 <i>Betula platyphylla</i> ; 2 <i>Pinus koraiensis</i> ; 1 <i>Larix gmelinii</i> ; 1 <i>Fraxinus mandshurica</i> + <i>Ulmus davidiana</i> var. <i>japonica</i> + <i>Acer pictum</i> subsp. <i>mono</i> + <i>Populus davidiana</i> + <i>Phellodendron amurense</i> - <i>Betula costata</i> - <i>Picea koraiensis</i> - <i>Ulmus laciniata</i> - <i>Abies nephrolepis</i> - <i>Juglans mandshurica</i> - <i>Tilia amurensis</i>	7暴马丁香; 1东北山梅花; 1刺五加+珍珠梅+早花忍冬+毛榛子-光萼溲疏 7 <i>Syringa reticulata</i> subsp. <i>amurensis</i> ; 1 <i>Philadelphus schrenkii</i> ; 1 <i>Acanthopanax senticosus</i> + <i>Sorbaria sorbifolia</i> + <i>Lonicera praeflorens</i> + <i>Corylus mandshurica</i> - <i>Deutzia glabrata</i>
演替阶段II (落叶阔叶混交林) Successional stage II (Mixed deciduous broad-leaved forest)	4水曲柳; 2山杨; 1紫椴; 1色木槭; 1白桦+胡桃楸+鱼鳞云杉-春榆-红松-红皮云杉-青楷槭-稠李-裂叶榆-蒙古栎 4 <i>Fraxinus mandshurica</i> ; 2 <i>Populus davidiana</i> ; 1 <i>Tilia amurensis</i> ; 1 <i>Betula platyphylla</i> + <i>Juglans mandshurica</i> + <i>Picea jezoensis</i> var. <i>microsperma</i> - <i>Ulmus laciniata</i> - <i>Pinus koraiensis</i> - <i>Picea koraiensis</i> - <i>Acer tegmentosum</i> - <i>Padus racemosa</i> - <i>Ulmus laciniata</i> - <i>Quercus mongolica</i>	7暴马丁香; 2毛榛; 1瘤枝卫矛+东北山梅花+刺五加+光萼溲疏-早花忍冬 7 <i>Syringa reticulata</i> subsp. <i>amurensis</i> ; 2 <i>Corylus mandshurica</i> ; 1 <i>Euonymus verrucosus</i> + <i>Philadelphus schrenkii</i> + <i>Acanthopanax senticosus</i> + <i>Deutzia glabrata</i> - <i>Lonicera praeflorens</i>
演替阶段III (针阔混交林) Successional stage III (Mixed coniferous and broad-leaved forest)	4臭冷杉; 4红松; 1春榆; 1红皮云杉+鱼鳞云杉+白桦+色木槭-花楷槭-枫桦-紫椴-胡桃楸-稠李 4 <i>Abies nephrolepis</i> ; 4 <i>Pinus koraiensis</i> ; 1 <i>Ulmus davidiana</i> var. <i>japonica</i> ; 1 <i>Picea koraiensis</i> + <i>Picea jezoensis</i> var. <i>microsperma</i> + <i>Betula platyphylla</i> + <i>Acer pictum</i> subsp. <i>mono</i> - <i>Acer ukurunduense</i> - <i>Betula costata</i> - <i>Tilia amurensis</i> - <i>Juglans mandshurica</i> - <i>Padus racemosa</i>	7暴马丁香; 2毛榛+瘤枝卫矛+早花忍冬-刺五加-光萼溲疏-珍珠梅 7 <i>Syringa reticulata</i> subsp. <i>amurensis</i> ; 2 <i>Corylus mandshurica</i> + <i>Euonymus verrucosus</i> + <i>Lonicera praeflorens</i> - <i>Acanthopanax senticosus</i> - <i>Deutzia glabrata</i> - <i>Sorbaria sorbifolia</i>
演替阶段IV (阔叶红松林) Successional stage IV (Mixed broadleaved-Korean pine forest)	4红松; 2枫桦; 1色木槭; 1鱼鳞云杉; 1红皮云杉+青楷槭+紫椴+白桦+黄檗+裂叶榆-水曲柳-山杨-稠李-臭冷杉-花楷槭-春榆-胡桃楸 4 <i>Pinus koraiensis</i> ; 2 <i>Betula costata</i> ; 1 <i>Acer pictum</i> subsp. <i>mono</i> ; 1 <i>Picea jezoensis</i> var. <i>microsperma</i> ; 1 <i>Picea koraiensis</i> + <i>Acer tegmentosum</i> + <i>Tilia amurensis</i> + <i>Betula platyphylla</i> + <i>Phellodendron amurense</i> + <i>Ulmus laciniata</i> - <i>Fraxinus mandshurica</i> - <i>Populus davidiana</i> - <i>Padus racemosa</i> - <i>Abies nephrolepis</i> - <i>Acer ukurunduense</i> - <i>Ulmus davidiana</i> var. <i>japonica</i> - <i>Juglans mandshurica</i>	2东北山梅花; 2瘤枝卫矛; 1暴马丁香; 1光萼溲疏; 1毛榛; 1早花忍冬; 1刺五加; 1龙牙樾木-绣线菊-东北茶藨子 2 <i>Philadelphus schrenkii</i> ; 2 <i>Euonymus verrucosus</i> ; 1 <i>Syringa reticulata</i> subsp. <i>amurensis</i> ; 1 <i>Deutzia glabrata</i> ; 1 <i>Corylus mandshurica</i> ; 1 <i>Lonicera praeflorens</i> ; 1 <i>Acanthopanax senticosus</i> ; 1 <i>Aralia elata</i> - <i>Spiraea salicifolia</i> - <i>Ribes mandshuricum</i>

物种组成利用胸高断面面积之比进行计算, 物种前的数字代表该物种所占比例的分子, 分母为10。乔/灌木树种前有“+”表示此树种仅占所有乔/灌木的2%–5%, 树种面前有“-”号表示该树种仅占2%以下。

Species composition was calculated using the ratio of stand basal area; the number in front of species represents the numerator of the fraction of the species in the community, and the denominator is 10. A “+” sign in front of a tree/shrub species indicate that the given species accounts for 2%–5% of all trees/shrubs, and a “-” sign before a tree/shrub species indicates that the given species accounts for less than 2% of all trees/shrubs.

制图。叶片与土壤、叶片与生物多样性的相关关系利用SPSS 22.0中的双变量相关分析方法进行分析, 并利用Microsoft Excel 2010制图。采用R 3.6.3的hier.part包(Nally & Walsh, 2004)对群落尺度上灌木叶片化学计量特征及物种多样性和土壤化学性质进行层次分割。

根据群落调查内容, 计算群落内所有胸径>1 cm 的木本植物的物种多样性, 计算公式(方精云等, 2004)包括:

$$\text{物种丰富度: } S = \text{群落中的物种数} \quad (2)$$

$$\text{Shannon多样性指数: } H' = -\sum_{i=1}^S P_i \ln P_i \quad (3)$$

$$\text{Pielou均匀度: } J = H' / \ln S \quad (4)$$

式中, P_i 为物种*i*的个体数在全个体数中的比例。

2 结果

2.1 阔叶红松林不同演替阶段灌木叶片化学计量特征

研究区内的阔叶红松林4个演替阶段的灌木叶片N含量的整体平均值为 $19.1 \text{ g} \cdot \text{kg}^{-1}$, 4个林型的平均值的范围为 $(15.14 \pm 0.28) - (20.61 \pm 1.37) \text{ g} \cdot \text{kg}^{-1}$; 叶片P含量的整体平均值为 $2.28 \text{ g} \cdot \text{kg}^{-1}$, 4个林型的平均值的范围为 $(2.00 \pm 0.11) - (2.92 \pm 0.14) \text{ g} \cdot \text{kg}^{-1}$ 。随着演替的进行, 灌木叶片的N、P含量趋势相近, 即演替阶段I、II、III中灌木叶片的N、P含量均无显著差异($p > 0.05$), 演替阶段IV的N含量显著高于其他3种林型($p < 0.05$), 而P含量与演替阶段I无显著差异($p > 0.05$), 但显著高于其他两种林型($p < 0.05$) (图1)。

演替阶段IV的叶片C:N、C:P均显著低于其他3种林型($p < 0.05$), 不同演替阶段的N:P的范围为 $(7.06 \pm 0.15) - (8.56 \pm 0.34)$, 其中演替阶段III的N:P显著高于其他3种林型($p < 0.05$)。

2.2 土壤氮磷与个体尺度上的叶片化学计量特征的关系

总体上, 相较于土壤N含量, 土壤P含量与个体尺度上的植物叶片的化学含量相关性更强, 土壤P含量与叶片N、P含量均呈显著正相关关系($p < 0.05$), 土壤N含量与叶片N含量呈显著正相关关系($p < 0.05$), 二者均与叶片N:P无显著相关关系($p > 0.05$) (图2)。

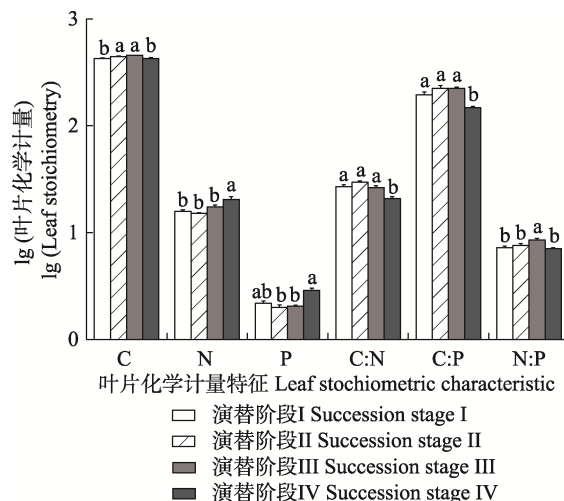


图1 阔叶红松林不同演替阶段群落尺度上叶片的化学计量特征(平均值±标准误)。不同小写字母表示叶片同一化学计量特征间差异显著($p < 0.05$)。全碳(C)、全氮(N)、全磷(P)含量的单位为 $\text{g} \cdot \text{kg}^{-1}$ 。

Fig. 1 Leaf stoichiometric characteristics at community level in mixed broadleaved-Korean pine forests at different successional stages (mean \pm SE). Different lowercase letters of the same organ indicate significant differences ($p < 0.05$). The unit of total carbon (C), total nitrogen (N) and total phosphorus (P) content is $\text{g} \cdot \text{kg}^{-1}$.

2.3 物种多样性与土壤化学性质对群落尺度上叶片化学计量特征的影响

层次分割结果显示, 在群落水平上物种多样性和土壤化学性质共解释叶片N含量变异的82%和P含量变异的62%, 其中Shannon多样性指数分别解释叶片N含量变异的26.66%和叶片P含量变异的35.96%; 对于叶片C:N和叶片C:P的变异, 物种多样性和土壤化学性质共解释74%和59% (表2), 说明物种多样性和土壤化学性质对灌木叶片化学计量变异具有较高的解释率。

Shannon多样性指数和丰富度均与叶片N、P含量具有显著的正相关关系($p < 0.05$)、与叶片C:N和叶片C:P具有显著的负相关关系($p < 0.05$) (图3), 与叶片C含量无显著相关关系($p > 0.05$)。

3 讨论

3.1 不同演替阶段灌木叶片化学计量特征的差异

本研究中, 阔叶红松林4个演替阶段的灌木叶片平均N含量为 $17.22 \text{ g} \cdot \text{kg}^{-1}$, 略低于我国灌木叶N平均含量 $19.1 \text{ g} \cdot \text{kg}^{-1}$; 而平均叶P含量为 $2.28 \text{ g} \cdot \text{kg}^{-1}$ 高于我国的灌木的平均值($1.11 \text{ g} \cdot \text{kg}^{-1}$) (Han *et al.*, 2005), 这可能是因为本研究地所处的北方地区气候较为寒冷, 导致落叶灌木叶片寿命缩短、生长速

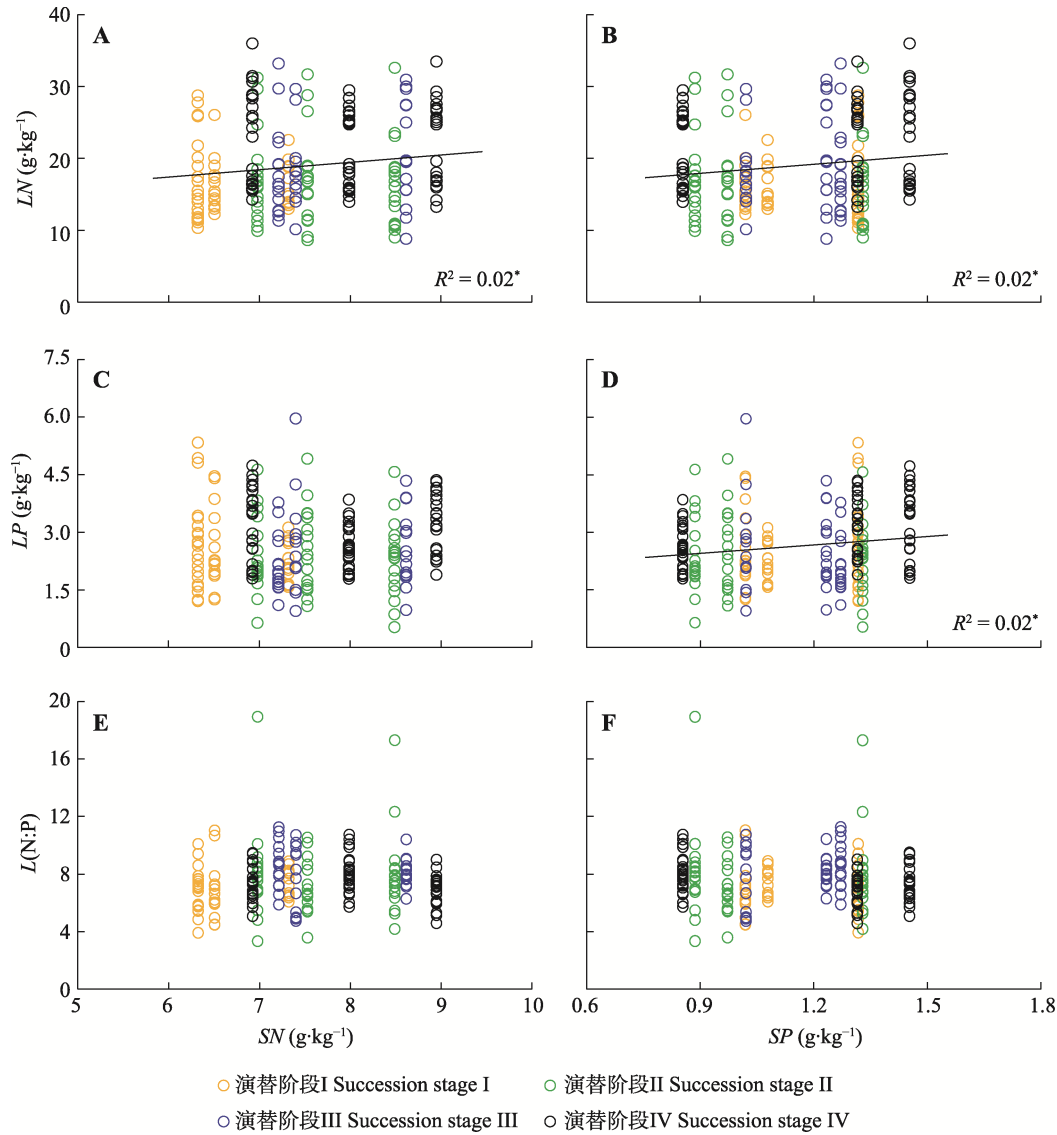


图2 阔叶红松林不同演替阶段土壤氮(N)、磷(P)含量与个体尺度上的叶片化学计量特征的关系。*, $p < 0.05$ 。LN, 叶片N含量; LP, 叶片P含量; L(N:P), 叶片N:P; SN, 土壤N含量; SP, 土壤P含量。

Fig. 2 Relationships of soil nitrogen (N) and phosphorus (P) contents with leaf stoichiometric characteristics at individual scale in mixed broadleaved-Korean pine forests at different successional stages. *, $p < 0.05$. LN, leaf N content; LP, leaf P content; L(N:P), leaf N:P ratio; SN, soil N content; SP, soil P content.

表2 物种多样性和土壤化学性质对群落尺度上阔叶红松林叶片碳(C)、氮(N)、磷(P)化学计量的层次分割结果
Table 2 Results of hierarchical partitioning for the effects of species diversity and soil chemical properties on leaf carbon (C), nitrogen (N) and phosphorus (P) stoichiometry at community scale in mixed broadleaved-Korean pine forests

叶片化学计量 Leaf stoichiometry	R^2	物种多样性解释度 Interpretation of species diversity (%)			土壤化学性质解释度 Interpretation of soil chemical properties (%)		
		H'	S	J	SC	SN	SP
LC	0.69	8.80	4.44	15.05	45.31*	8.01	18.38
LN	0.82	26.66*	36.11**	4.94	5.73	5.14	21.42
LP	0.62	35.96*	40.18*	6.82	9.16	3.24	4.64
L(C:N)	0.74	28.88*	33.41**	4.51	13.25	6.52	13.43
L(C:P)	0.59	34.79*	33.99*	8.25	16.55	4.31	2.11
L(N:P)	0.46	22.12	16.76	23.11	9.23	3.60	25.17

*, $p < 0.05$; **, $p < 0.01$. LC, 叶片C含量; LN, 叶片N含量; LP, 叶片P含量; L(C:N), 叶片C:N; L(C:P), 叶片C:P; L(N:P), 叶片N:P。H', Shannon多样性指数; J, Pielou均匀度指数; S, 物种丰富度。SC, 土壤C含量; SN, 土壤N含量; SP, 土壤P含量。
*, $p < 0.05$; **, $p < 0.01$. LC, leaf C content; LN, leaf N content; LP, leaf P content; L(C:N), leaf C:N ratio; L(C:P), leaf C:P ratio; L(N:P), leaf N:P ratio; H', Shannon diversity index; S, Species richness; J, Pielou evenness index. SC, soil C concentration; SN, soil N concentration; SP, soil P concentration.

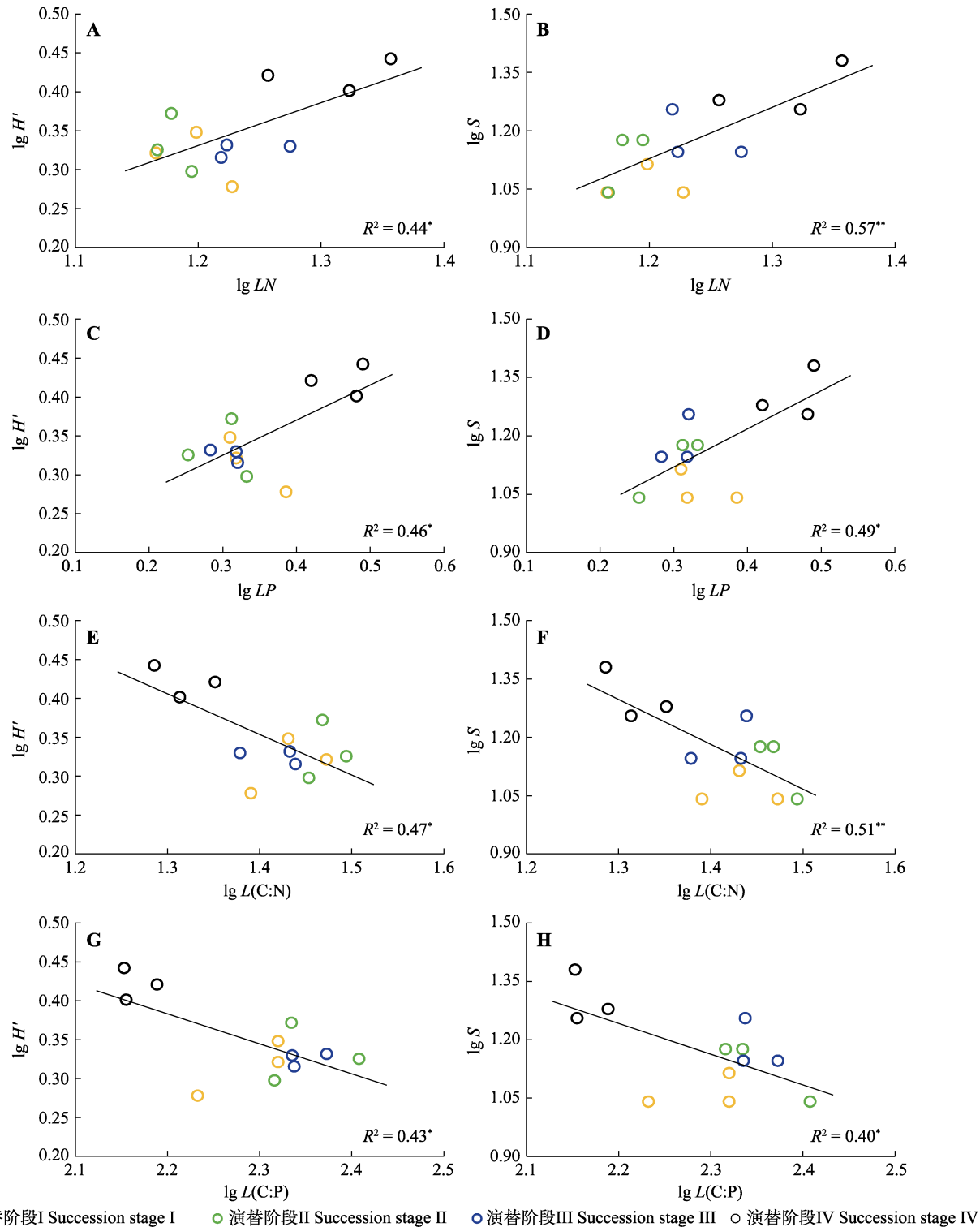


图3 阔叶红松林不同演替阶段叶片氮(N)、磷(P)含量、碳(C):N和N:P与Shannon多样性指数、物种丰富度的线性关系。*, $p < 0.05$; **, $p < 0.01$ 。H', Shannon多样性指数; S, 物种丰富度。LN, 叶片N含量; LP, 叶片P含量; L(C:N), 叶片C:N; L(C:P), 叶片C:P。

Fig. 3 Linear relationships of leaf nitrogen (N) and phosphorus (P) contents, carbon (C):N ratio and C:P ratio with Shannon diversity index and Species richness in mixed broadleaved-Korean pine forest at different successional stages. *, $p < 0.05$; **, $p < 0.01$. H', Shannon diversity index; S, Species richness. LN, leaf N content; LP, leaf P content; L(C:N), leaf C:N ratio; L(C:P), leaf C:P ratio.

率增高(van Ommen Kloeke *et al.*, 2012), 根据生长速率假说, 生长速率更高的植物需要更多的P来维

持植物体内RNA的高速合成, 对P的需求量更大(Güsewell & Koerselman, 2002; Sterner & Elser,

2002)。同时,植物在这种环境中需要储存更多的脂质P在叶片中,用以抵抗寒冷,导致植物体内P含量高(Chapin III *et al.*, 1986; Han *et al.*, 2011)。

植物器官的N:P通常可以作为判断植物受何种养分限制的指标(Aerts & Chapin III, 1999)。因为研究区域、研究植物群落有所不同,不同研究提出作为区分N、P限制位点的N:P指标常常有所差异,目前常用的指标认为N:P在14和16之间时,植物不受N、P限制或者受N、P两种营养元素的共同制约; $N:P < 14$, 植物主要受N限制; $N:P > 16$, 植物主要受P限制(Koerselman & Meuleman, 1996)。

在本研究的4个演替阶段中灌木叶片的N:P均小于14。这表明本研究中4个演替阶段的灌木均受到N限制。以往的研究认为,在缺乏灾难性干扰的条件下,随着森林生态系统的自然演替,森林生态系统将趋向于受到P限制(Wardle *et al.*, 2004; 刘兴诏等, 2010),这与本文的研究结果并不相符,这有两个可能的原因:(1)本研究地区属于温带森林,年平均气温低,土壤发育晚(Reich & Oleksyn, 2004),土壤P的可利用性更高(McGroddy *et al.*, 2004),所以导致植物P含量较高,由于植物体内N:P的变化主要是由P浓度的变化所驱动(Tian *et al.*, 2018),因此灌木叶片表现出低N:P的特征;(2)相对于乔木,灌木体型小,生长速率高(Koerselman & Meuleman, 1996),通常表现出较低的N:P(Makino *et al.*, 2003)。

3.2 土壤氮磷对个体尺度上的灌木叶片化学计量特征的影响

本研究中的4个森林类型土壤的平均N:P为6.73,低于我国土壤平均N:P (9.3)(Tian *et al.*, 2010),表明本研究地区土壤N含量相对于P含量而言处于较低的状态。土壤P含量与个体尺度上叶片N、P含量均表现出显著的相关性($p < 0.05$),而土壤N含量则只与叶片N含量具有显著相关性($p < 0.05$)。这可能与土壤N的有效性不足时,植物通过增加吸收土壤中的P来促进体内P的有效性,进而刺激N吸收有关(Sistla *et al.*, 2015),因此土壤P含量对个体尺度上的叶片N、P含量均表现出一定的影响。

同时,土壤N含量与个体水平上的叶片N含量显著相关表明,即使土壤中N含量相对较低,从土壤中吸收N仍是植物获取N的主要方式。这是因为比起从空气中和衰老叶片中获取N,植物从土壤中获

取N的成本更低、更便捷(Chen *et al.*, 2015; Zheng *et al.*, 2020)。

3.3 物种多样性和土壤碳氮磷对群落尺度上的叶片化学计量特征的影响

土壤化学性质与群落尺度上的叶片化学计量无显著相关关系(表2),这可能与白桦次生林、落叶阔叶混交林和针阔混交林中具有单一优势灌木——暴马丁香(*Syringa reticulata* var. *amurensis*)有关,即群落中存在单一优势物种时,此物种的N、P含量对群落尺度的N、P含量具有重要影响,而在本研究中,暴马丁香N、P含量虽然随着土壤N、P含量的增加而具有增加的趋势,但二者之间无显著相关关系($p > 0.05$, 未发表数据),导致土壤化学性质在群落尺度上与叶片化学计量无显著相关关系。群落尺度上的植物和土壤N、P含量的关系也很好体现了生态化学计量的内稳态理论,即生物为保持整个有机体的稳定,在长期的进化过程中形成了在外界环境变化时保持其化学含量相对稳定的能力(Sterner & Elser, 2002)。

物种多样性与群落尺度上灌木叶片的N、P含量呈显著正相关关系($p < 0.05$, 图3)。这可以用以下两个原因解释:(1)随着物种多样性的增加,灌木所面临的光资源的竞争增大,需要获取更多的营养物质供给叶片用于合成光合作用所需的酶、核糖体等物质,来维持个体的生存和繁殖(Evans & Poorter, 2001);(2)物种多样性的增加使得灌木可以更彻底地利用有限的资源,以此增加自身的N、P含量(Roscher *et al.*, 2008)。同时,随着物种多样性的增加,相邻树种养分获取策略互补的可能性增加,这种互补性可以促进植物对养分的吸收(Teste *et al.*, 2014)。由于C在植物内的含量较高且变异较小(Reich & Oleksyn, 2004),灌木叶片内的C含量与植物多样性无显著相关关系($p > 0.05$),因此随着植物多样性的增加,植物叶片内C:N和C:P均降低($p < 0.05$)。

本研究探讨了阔叶红松林4种演替阶段灌木的化学计量特征。结果显示在群落尺度上4种演替阶段的灌木均受到N限制;相较于土壤的化学性质,物种多样性更好地解释了灌木化学计量的变异。为了更好地理解不同演替阶段中物种化学计量的变异规律,在今后的研究中需要进一步开展对于不同演替阶段中的种间、种内变异的研究。

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