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不同降雨条件下北京土石山区混生乔灌植物的水分吸收和生态位特征

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摘 要 分析同一林分内上层乔木与下层灌木在不同降雨事件下的水分吸收和生态位变化特征, 探究混生植物的水分利用策略及对水分的竞争/互补关系, 可为北京土石山区植被恢复和管理提供理论依据。在不同降雨类型(干旱期发生的小雨, 简称“干旱小雨”; 相对湿润期发生的中雨, 简称“湿润中雨”; 干旱期发生的暴雨, 简称“干旱暴雨”)雨前和雨后1–4天内分别采集乔木(刺槐(*Robinia pseudoacacia*)、栾树(*Koelreuteria paniculata*)和侧柏(*Platycladus orientalis*))和灌木(荆条(*Vitex negundo*))的木质部、土壤、地下水和雨水样品, 分析其稳定同位素特征及其动态变化, 运用MixSIAR模型计算植物对各种潜在水源的利用比例, 并应用Levins指数和Levins重叠指数计算水分生态位宽度和生态位重叠度。结果表明: 土壤含水量和同位素组成、乔木和灌木吸水深度和水分生态位特征均受降雨类型的影响。(1)干旱小雨后灌木的水分利用对降水更为敏感, 其利用水源由深层土壤向上层土壤转移, 而乔木水分来源依然以地下水为主; 湿润中雨后, 不同林分的乔木和灌木均以0–40 cm土壤水为主要水分来源; 干旱暴雨改变了乔木和灌木的水分利用策略, 雨后灌木的主要水分来源均为0–40 cm浅层土壤水分, 而乔木对不同土层的吸水量趋于均匀。(2)干旱小雨前后, 刺槐和栾树生态位宽度低于对应林下灌木, 而干旱暴雨前后栾树生态位宽度高于林下灌木。侧柏和林下荆条生态位宽度对降雨的响应一致, 即荆条生态位宽度在雨后第1天陡增, 侧柏生态位宽度在雨后第2天陡增。干旱小雨前, 刺槐和林下荆条水分生态位重叠较大, 雨后其随降雨天数增加而递减。除干旱小雨前乔木和灌木具有相同水分来源之外, 乔木和灌木面对降雨具有不同水分利用策略, 从而避免了彼此间水分竞争。

关键词 降雨; 氢氧稳定同位素; 水分利用策略; 水分生态位特征

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Water uptake and niche characteristics of neighboring plants for arbors and shrubs under different rainfall conditions in a rocky mountainous area, Beijing

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Abstract

Aims Our study aims to explore water usage strategies and the competitive or complementary relationships among neighboring arboreal and shrubby plants within the same stand under diverse rainfall conditions. Through an analysis of soil water absorption and water niche characteristics of these neighboring plants, we aim to provide a theoretical basis for vegetation restoration and management in the rocky mountainous areas, Beijing.

Methods Xylem samples were collected from trees including *Robinia pseudoacacia*, *Koelreuteria paniculata*, and *Platycladus orientalis*, as well as from the shrub *Vitex negundo*. Additionally, samples of soil, groundwater, and rainwater were gathered both before and 1–4 days following different types of rainfall events: light rain during a dry period, moderate rain during a wet period, and rainstorms during a dry period. These samples were analyzed to examine the characteristics and dynamic changes of hydrogen and oxygen isotopes composition (δ^2H and δ^{18}O). The MixSIAR model was employed to determine the contribution rates of groundwater and soil water from different soil layers to various plant species. Furthermore, water niche width and niche overlap were assessed using the Levins index and Levins overlap formula, respectively.

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Important findings The results indicate that soil water content, δ^2H and δ^{18}O, water absorption depth, and niche characteristics of neighboring arboreal and shrubby plants were significantly influenced by the types of rainfall. Following light rainfall during a dry period, shrubs exhibited heightened sensitivity to precipitation, shifting their water source from deep soil to upper soil layers, while arboreal species predominantly relied on groundwater. After moderate rainfall during a wet period, arboreal and shrubby plants from different forest types primarily absorbed water from soil layers within the 0–40 cm depth range. Rainstorms during a dry period altered the water utilization strategies of arboreal and shrubby plants, with shrubs predominantly sourcing water from the 0–40 cm soil layers, while arboreal species exhibited more uniform water uptake across different soil layers. The niche width of *R. pseudoacacia* and *K. paniculata* was lower compared to corresponding shrubs before and after light rainfall during a dry period, whereas the niche width of *K. paniculata* exceeded that of understory shrubs both before and after rainstorms during dry periods. *Platycladus orientalis* and understory shrubs exhibited similar responses to different types of rainfall, with the niche width of *P. orientalis* experiencing a sharp increase on the first day following rain, while that of shrubs spiked on the second day post-rainfall. For the dry period before light rainfall, there was a substantial overlap in the water niche between *R. pseudoacacia* and understory shrubs, which diminished with an increase in the number of rainfall days thereafter. Except for the dry period before light rainfall, arboreal and shrubby plants demonstrated distinct water utilization strategies across different types of rainfall, thus mitigating water competition between them.

Key words rainfall; hydrogen and oxygen stable isotopes; water use strategy; water niche characteristic

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森林在陆地水文循环中发挥重要作用, 其分布和丰富程度主要受水资源限制(Dodd et al., 1998; Liu et al., 2010)。然而, 全球变暖背景下干旱强度和频率的增加对森林生态系统构成严峻挑战, 特别是在干旱半干旱地区(Yang et al., 2015; Schlaepfer et al., 2017; Bello et al., 2019)。但已有研究发现, 混生植被采用不同水资源利用策略来应对干旱(如资源利用时空划分) (Liu et al., 2010; Moreno-Gutiérrez et al., 2012), 其对维持森林生态系统功能(如水文过程, 养分循环, 初级生产力, 碳固存和生物多样性)至关重要(Schwendenmann et al., 2015; Tang et al., 2019; 裴艳武等, 2022; Sun et al., 2022; Dai et al., 2023)。此外, 水通过调节植物生理特性和空间分布, 在全球范围内广泛影响森林生态系统(Grossiord et al., 2017)。因此, 在水资源有限地区, 评估森林生态系统植物的水分利用特征至关重要。

在群落水分利用策略中, 如何实现物种共存是一个有待解决的科学问题(Peñuelas et al., 2011; Ellner et al., 2019)。具有二态根形态的植物可利用不同深度土壤水分(Liu et al., 2019), 因此, “水分生态位分离”成为解决共存问题的潜在机制。在各种生态系统中, 植物的水分生态位分离现象已被广泛报道, 如黄土高原生态防护林和经济林(Wang et al., 2020; Wu et al., 2022; Dai et al., 2023), 长白山原始林和次生林(Sun et al., 2022), 土石山区针阔混交林(Liu et al., 2019), 温带(Grossiord et al., 2014; Brinkmann et al., 2019)、热带(Antunes et al., 2019)和亚热带森林生态系统(Yang et al., 2015), 稀树草原生态系统(Priyadarshini et al., 2016; Grossiord et al., 2019), 草原生态系统(Yang et al., 2011)和荒漠生态系统(Wu et al., 2016; Tiemuerbieke et al., 2018; Pan et al., 2020; Liu et al., 2023)。迄今为止, 关于混生植被水分利用特征的研究已广泛涉及乔木与乔木间(Grossiord et al., 2014; Yang et al., 2015; Antunes et al., 2019; Liu et al., 2019; Wang et al., 2020)、乔木与草本间(Eggemeyer et al., 2009; Priyadarshini et al., 2016; Grossiord et al., 2019)以及灌木和草本间(Wu et al., 2016; Liu et al., 2023), 但对混生乔木和灌木植物水分来源却鲜有研究。此外, 在人工植被更新阶段, 乔木和灌木混合种植模式是减缓气候变化、恢复退化土地、增强生物多样性和发展可持续人工林的重要手段。因此, 有必要对混生乔木和灌木的水分来源进行深入研究, 分析其竞争/互补关系。

降水是山地森林生态系统的主要水源, 可决定植被分布、生长和水分利用, 从根本上影响生态系统内所有的水文过程(Zhang et al., 2011; Liu et al., 2015, 2019; Tao et al., 2017)。因此, 研究该地区混生植被水分利用特征对降雨的响应, 不仅为混生植被

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适应性评估和生态建设提供理论依据, 而且可以提高对生物圈-大气反馈生态水文过程的理解(Liu et al., 2023)。已有研究表明, 植物水分利用策略对降雨的敏感性受降雨量大小、降雨类型(持续时间、强度和数量)和植被类型的影响(Liu et al., 2019)。如杨菲等(2022)研究发现, 3.1 mm降雨并未对刺槐(*Robinia pseudoacacia*)和六道木(*Abelia biflora*)水分利用产生明显影响; 106.6 mm降雨后, 刺槐和六道木均增加了0–40 cm土壤水的利用比例, 但六道木对降雨响应更迅速。此外, 降雨前土壤干旱情况也会影响植物水分利用策略。在雨前土壤水分亏缺时, 植被水分利用对降雨更为敏感, 降雨后主要利用水源由深层土壤向上层土壤转移; 而雨前土壤水分充足时, 降雨后不同土层的吸水量趋于均匀(Mei & Ma, 2022)。

北京山区作为华北土石山区组成部分, 是整个华北平原和北京市区的重要生态屏障。但由于人为干扰和降雨异常, 导致该地区水土流失加剧, 植被退化严重, 生态环境脆弱, 因此选择适生树种是该地区植被恢复工程中的难题。刺槐、栾树(*Koelreuteria paniculata*)和侧柏(*Platycladus orientalis*)是北京山区分布面积较广的典型人工林树种, 可在干旱缺水状况下形成相对稳定的人工林, 表现出较强的生态适应性(刘自强等, 2017)。虽然目前对北京山区植被水分来源研究较多(邓文平等, 2014; 刘子赫等, 2022; 张潇等, 2023), 但鲜有研究从竞争角度解释植被对环境的适应机制。本研究以北京山区典型林分乔木(刺槐、栾树和侧柏)和林下灌木(均为荆条(*Vitex negundo*))为研究对象, 分析不同降雨类型(干旱期发生的小雨, 简称“干旱小雨”; 相对湿润期发生的中雨, 简称“湿润中雨”; 干旱期发生的暴雨, 简称“干旱暴雨”)下乔木与林下灌木的水分利用策略和竞争/互补关系, 以期为华北土石山区群落的空间配置和森林高质量管理提供理论依据。

1 材料和方法

1.1 研究区概况

研究区位于北京鹫峰首都圈森林生态系统定位研究站(39.90° N, 116.47° E, 海拔100–1 153 m)内。该区属暖温带半湿润半干旱大陆性季风气候, 年降水量557.3 mm, 降雨主要集中在6–9月, 约占全年降水量的79.80%。年平均气温13.11 ℃, 历史最高气温41.6 ℃, 最低气温–19.6 ℃, 无霜期193天(海淀区气象局1981–2010年)。该区为典型土石山区, 土层瘠薄, 石砾含量较多, 以淋溶性褐土和棕壤土为主要土壤类型。根据北京市水资源公报(2022年度)以及农户对地下水井的估算, 该区地下水位超过35 m。研究区森林覆盖率达96.4%, 现有植被主要是1958年后营造的人工林, 以侧柏、油松(*Pinus tabuliformis*)、栓皮栎(*Quercus variabilis*)和刺槐为主, 也有少量栾树和华北落叶松(*Larix gmelinii* var. *principis-rupprechtii*)等。林下主要灌木为荆条和构树(*Broussonetia papyrifera*)等, 草本植物主要为狗尾草(*Setaria viridis*)等。

1.2 样品采集

选取长势良好、造林树种分布均匀、受人为干扰少的刺槐、栾树和侧柏人工林, 林内分别设置3块坡度和海拔等均相近、面积为20 m × 20 m的样地(表1), 样地间水平距离约100 m。

于2023年6月1日至9月30日(植物生长季), 监测每次降雨历时和降雨量。由于雨后采样天数的不同可能会导致植被水分来源的不同(Liu et al., 2019; Mei & Ma, 2022), 根据不同的降雨类型, 采集雨后1–4天的样品。植物和土壤样品分别在雨前、雨后1–4天的晴天9:00–11:00采集(共12次取样), 采样日期和降雨信息见表2。此外, 收集生长季内的雨水和采样日期的井水(代表地下水)。根据中国气象局的

表1 北京土石山区典型林木的样地基本信息(平均值±标准差)
Table 1 Basic information of typical forest trees in a rocky mountainous area in Beijing (mean ± *SD*)

林型 Forest type	海拔 Altitude (m)	坡度 Slope (°)	坡向 Slope aspect	密度 Density (tree·hm^{-2})	胸径 Diameter at breast height (cm)	树高 Tree height (m)	林下灌木 Shrub	灌木高 Shrub height (m)	灌木生物量 Shrub biomass (t·hm^{-2})
RP	146.67	17	东北 Northeast	650	19.36 ± 3.25	9.34 ± 1.36	荆条 *Vitex negundo*	0.91 ± 0.14	1.59 ± 0.18
KP	155.29	15	东北 Northeast	700	8.64 ± 6.36	9.48 ± 1.23	荆条 *Vitex negundo*	0.75 ± 0.18	1.42 ± 0.15
PO	142.45	10	东北 Northeast	850	16.69 ± 4.55	10.25 ± 1.22	荆条 *Vitex negundo*	0.59 ± 0.11	1.33 ± 0.12

KP, 栾树林; PO, 侧柏林; RP, 刺槐林。
KP, *Koelreuteria paniculata* forest; PO, *Platycladus orientalis* forest; RP, *Robinia pseudoacacia* forest.

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表2 采样时间和降雨信息
Table 2 Date of sampling and rainfall information

降雨日期 Rain event date	降雨量 Rainfall amount (mm)	降雨强度 Rainfall intensity ($mm \cdot min^{-1}$)	降雨类型 Rainfall type	雨前 BR	雨后第1天 1st AR	雨后第2天 2nd AR	雨后第3天 3rd AR	雨后第4天 4th AR
2023-06-19	8.60	0.07	干旱小雨 Light rainfall during a dry period	2023-06-18	2023-06-20	2023-06-21	2023-06-22	ns
2023-08-21	13.44	0.04	湿润中雨 Moderate rainfall during a wet period	2023-08-15	2023-08-21	2023-08-22	ns	ns
2023-09-08–2023-09-10	85.20	0.04	干旱暴雨 Rainstorm during a dry period	2023-09-06	2023-09-10	2023-09-11	2023-09-12	2023-09-13

2023-08-21和2023-09-10降雨在凌晨, 因此将2023-08-21和2023-09-10作为雨后第1天。ns代表没有取样。
Because on 2023-08-21 and 2023-09-10 rainfall occurred in the early morning, so we took 2023-08-21 and 2023-09-10 as the first day after the rain. AR, after rain; BR, before rain. The 'ns' indicate no sample was taken.

降雨等级划分标准, 对3次典型降雨事件进行了监测, 分别为小雨、中雨和暴雨。根据土壤相对湿度和干旱指数(R)确定土壤干旱与湿润状态, 其中R < 60%为干旱阶段, R > 60%为湿润阶段(张语馨等, 2023)。小雨事件发生在土壤干旱阶段, 前半个月未降雨, 雨前7天的土壤体积含水量平均值为0.05 $m^3 \cdot m^{-3}$左右, R约为20%。中雨发生在土壤湿润阶段, 在此之前有一场历史罕见的"7 • 31"特大暴雨事件, 雨前7天的土壤体积含水量平均值约为0.19 $m^3 \cdot m^{-3}$, R约为70%。暴雨则发生在土壤干旱阶段, 雨前7天的土壤体积含水量平均值约为0.10 $m^3 \cdot m^{-3}$, R为40%左右。根据天气预报, 将降雨前1天的典型晴天定义为雨前; 若雨前1天不是典型晴天, 则选择距离降雨日最近的典型晴天采集日期作为雨前。

在每个样地内, 避开边缘区, 分别选取长势良好, 冠幅、胸径和树高较为一致的3株乔木(刺槐、栾树和侧柏), 距离每株采样乔木基部1 m附近分别选取1株具有代表性的灌木(荆条)。所选取的样木均能代表样地乔木和灌木生长的平均水平。采集直径约4 mm, 长为4–5 cm的已栓化枝条, 同株样木取3个样品作为重复。迅速剥去枝条的表皮和韧皮部, 将木质部样品装入50 mL离心管中, 用Parafilm膜密封, 放入装有冰袋的保温箱中, 带回实验室抽提植物水分。

在乔木和灌木中间位置, 使用土钻采集土壤样品。根据该地区植物根系分布深度和土壤水分变化幅度, 将土壤分成0–20、20–40、40–60和60–80 cm共4层。采集1份土样迅速装入50 mL离心管中, 用Parafilm封口膜密封, 放入保温箱, 迅速带回实验室冷冻(–20 ℃)保存, 用于同位素测定; 另一份装入铝盒中, 放烘箱中105 ℃烘24 h至恒质量, 用以测量土壤质量含水量。

在无林旷地随机布设3个自制的简易降雨采集装置(直径为10 cm样品瓶与广口为15 cm长颈漏斗连接, 漏斗内放置乒乓球防止雨水蒸发分馏)。待降雨结束后, 立即将瓶内雨水样品混合后装入50 mL离心管中, 并用Parafilm封口膜密封, 置于–20 ℃冰箱保存。

1.3 同位素样品测定

采用全自动真空冷凝抽提系统(LI-2100, 理加联合, 北京)提取植物和土壤样品中的水, 抽提时长均为3 h。木质部、土壤和降雨的水样经13 mm × 0.22 μm有机过滤器过滤后, 用液态水同位素分析仪(DLT-100, LGR, Lawrenceville, USA)测定其氢氧稳定同位素组成(δ^2H和δ^{18}O), 其中δ^2H精度为±0.1‰, δ^{18}O精度为±0.3‰。测定所有数据通过光谱污染校正曲线进行修正, 以去除水样中有机污染物干扰。

分析得出的δ^2H和δ^{18}O用相对维也纳标准平均海洋水(VSMOW)千分率(‰)表示:

$$\delta X = \frac{R_{\text{sample}} - R_{\text{vsmow}}}{R_{\text{vsmow}}} \times 1000 \quad (1)$$

式中, δX为δ^2H和δ^{18}O (‰), R_{sample}为样品的δ^2H和δ^{18}O, R_{vsmow}为VSMOW的δ^2H和δ^{18}O。

1.4 植物水分来源分析

采用贝叶斯混合模型(MixSIAR)量化植物对各潜在水源的利用率。该区地下水位超过35 m, 但由于土层较薄, 地下水主要存储于基岩的孔隙、裂隙或溶隙之中。此外, 结合该区水分来源的研究成果(Liu et al., 2019; 张潇等, 2023), 本研究假设植物水源主要为土壤水和地下水。模型中源数据包括0–20、20–40、40–60、60–80 cm土壤水和地下水的δ^2H和δ^{18}O平均值和标准差, 混合物数据为刺槐、栾树、侧柏和荆条植物茎干水的δ^2H和δ^{18}O。分馏数据设为

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“0”, 默认不发生同位素分馏。马尔可夫链蒙特卡罗运行步长设置为“very long”, 误差结构设定为“Residual Only”, 模型结果使用Gelman-Rubin和Geweke诊断确定模型是否收敛, 若不收敛则增加运行时长, 直至结果收敛, 输出结果用平均值表示。

1.5 水分竞争性分析

水分生态位宽度采用Levins指数(Levins, 1968)计算:

$$B_i = \frac{1}{\sum_{j=1}^{r} P_{ij}^2} \quad (2)$$

式中, B_i为物种i的水分生态位宽度, P_{ij}为物种i对第j层土壤水的利用比例, r为总土层数。

水分生态位重叠度用Levins重叠指数(Levins, 1968)计算:

$$Q_{ik} = \frac{\sum_{j=1}^{r} P_{ij} P_{kj}}{\sum_{j=1}^{r} P_{ij}^2} \quad (3)$$

式中, Q_{ik}为物种i和物种k的水分生态位重叠度, P_{kj}为物种k对第j层土壤水的利用比例。

1.6 数据处理

采用SPSS 22.0软件对数据进行处理和分析, 用单因素方差分析法对不同采样时间的土壤含水量和土壤水的δ^2H和δ^{18}O、木质部水的δ^2H和δ^{18}O进行差异分析, 差异显著性($p < 0.05$)用邓肯法(Duncan)检验。用Origin 2022软件作图。

2 结果和分析

2.1 降雨和雨水稳定同位素的变化特征

研究期间(2023年6–9月)该区总降雨量839.01 mm (图1), 其中“7 • 31”北京暴雨(7月29–31日)降雨量428.60 mm, 占采样期间降雨量的51.08%。6月共降雨2次, 总雨量13.20 mm, 单次最大雨量8.60 mm (采集), 属干旱月份(3个林分土壤体积含水量平均值约为0.05 $m^3 \cdot m^{-3}$)。8月共降雨8次, 总雨量70.01 mm, 单次最大雨量41.01 mm, 属湿润月份(土壤体积含水量约为0.18 $m^3 \cdot m^{-3}$)。9月共降雨2次, 总雨量92.40 mm, 单次最大雨量85.20 mm (采集), 属干旱月份(土壤体积含水量约为0.14 $m^3 \cdot m^{-3}$)。

根据研究区采集降雨同位素值, 得到当地大气降水线(LMWL)方程: $\delta^2H = 8.111\delta^{18}O + 10.846$ ($R^2 = 0.89$), 与全球大气降水线(GMWL, $\delta^2H = 8\delta^{18}O + 10$)相比, 斜率和截距均略大(图2), 表明当地降水的蒸发富集现象并不明显, 可能与研究期间降雨较为丰盈有关。3种降雨类型下的土壤水线的斜率和截距均小于当地大气降水线(图2), 且大于地下水线(GWL), 表明研究区内土壤水受降水和地下水共同补给, 且在补给过程中经历了与蒸发相关的同位素重组分富集过程。其中降雨8.60 mm (干旱小雨)前后的斜率最小且土壤水的δ^2H和δ^{18}O最大, 乔木和灌木木质部水同位素组成在降雨13.44 mm (湿润中雨)前后最小。

2.2 降雨前后土壤含水量和水同位素的变化特征

不同类型降雨事件对土壤含水量的影响存在差异(图3)。降雨8.60 mm对3个林分深层土壤(40–80 cm)含水量无显著影响, 而显著提高了刺槐0–40 cm、栾树和侧柏0–20 cm土壤含水量(图3A–3C)。与雨前相比, 降雨13.44 mm后第1天显著提高了刺槐和侧柏土壤0–40 cm含水量, 显著提高了栾树0–20 cm和40–80 cm土壤含水量(图3D–3F)。降雨85.20 mm后3个林分均可明显观测到降雨补给作用, 补给程度随土层加深而减小(图3G–3I)。

土壤水的δ^2H和δ^{18}O受降雨事件的影响(图4)。雨前土壤水的δ^2H和δ^{18}O随着土层的加深呈递减的趋势。8.60 mm降雨显著降低刺槐20–40 cm、栾树0–40 cm、侧柏0–20和60–80 cm土壤水的δ^2H和δ^{18}O, 但对刺槐和栾树样地深层土壤(60–80 cm)水

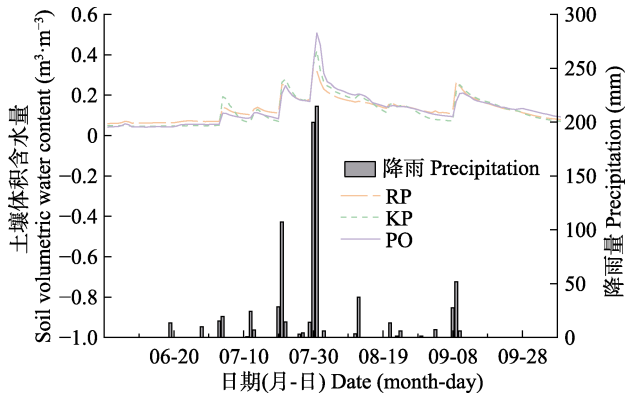


图1 北京土石山区采样期间土壤体积含水量和降雨的变化。KP, 栾树林; PO, 侧柏林; RP, 刺槐林。土壤体积含水量($m^3 \cdot m^{-3}$)是每个样地在10、30和50 cm深度测量的平均值。

Fig. 1 Variations of soil volumetric water content and precipitation during the sampling period in a rocky mountainous area in Beijing. KP, *Koelreuteria paniculata* forest; PO, *Platycladus orientalis* forest; RP, *Robinia pseudoacacia* forest. The soil volumetric water content ($m^3 \cdot m^{-3}$) were the mean of measurements at the depths of 10, 30 and 50 cm for each plot.

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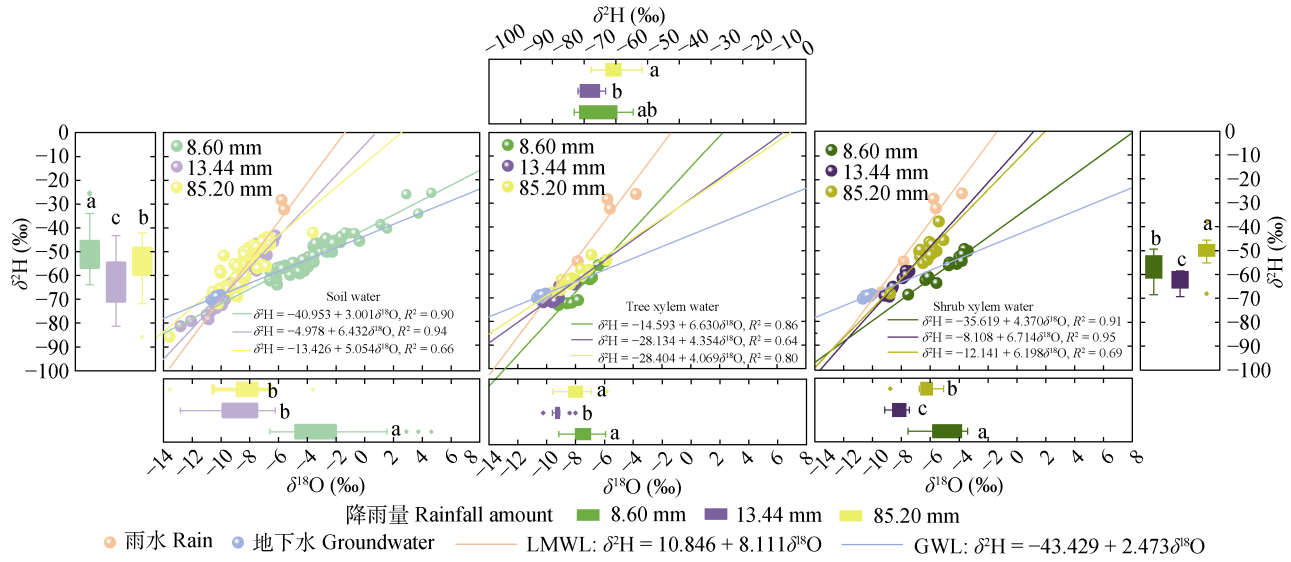


图2 不同降雨类型下土壤水、乔木木质部水、灌木木质部水、雨水、地下水的氢氧同位素组成(δ^2H和δ^{18}O)分布特征(平均值±标准差)。Soil water, 土壤水; Tree xylem water, 乔木木质部水; Shrub xylem water, 灌木木质部水; 降雨量, 8.60、13.44和85.20 mm; LMWL, 大气降水线; GWL, 地下水线。不同小写字母表示降雨类型间存在显著差异($p < 0.05$)。

Fig. 2 Distribution characteristics of hydrogen and oxygen isotopes composition (δ^2H and δ^{18}O) of soil water, tree xylem water, shrub xylem water, rain and groundwater under different rainfall types (mean ± *SD*). Rainfall amounts, 8.60 mm, 13.44 mm and 85.20 mm; LMWL, local meteoric water line; GWL, groundwater line. Different lowercase letters indicate significant differences at different rainfall types ($p < 0.05$).

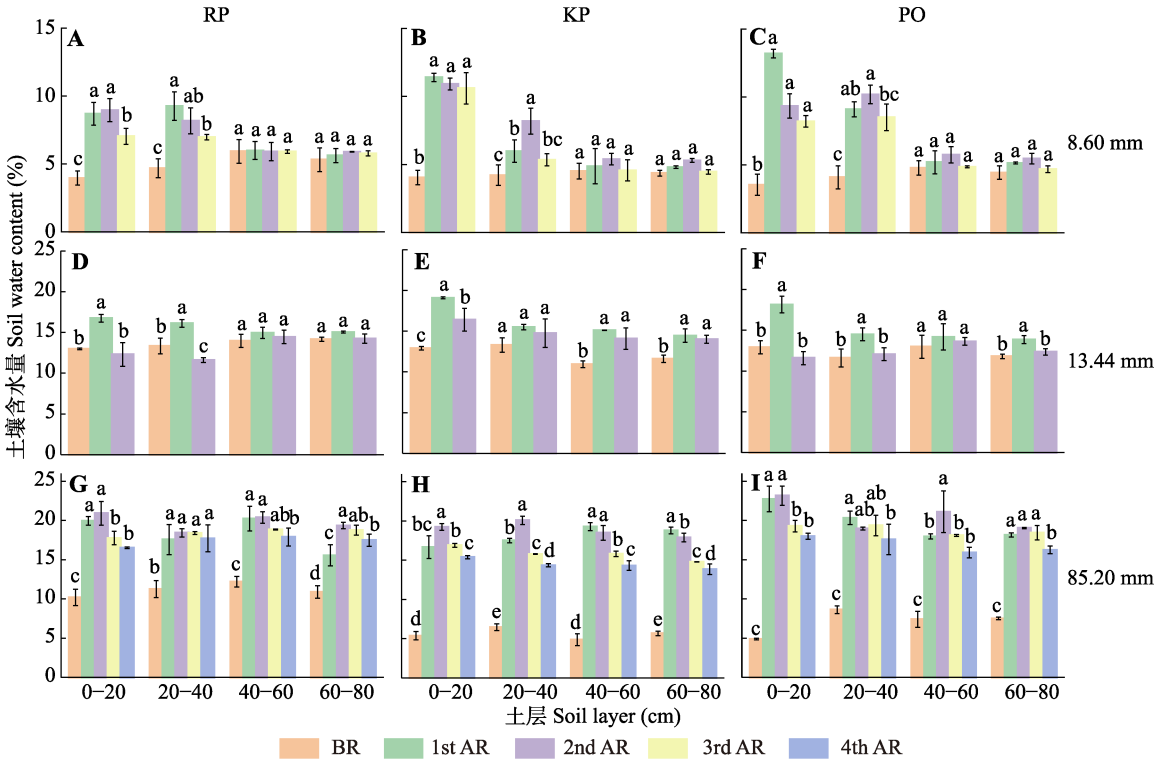


图3 不同降雨量降雨前后不同林分土壤含水量变化(平均值±标准差)。KP, 栾树林; PO, 侧柏林; RP, 刺槐林。降雨量, 8.60、13.44和85.20 mm; BR, 雨前; 1st AR, 雨后第1天; 2nd AR, 雨后第2天; 3rd AR, 雨后第3天; 4th AR, 雨后第4天。不同小写字母表示同一土层不同采样时间土壤含水量存在显著差异($p < 0.05$)。

Fig. 3 Variations of soil water content in different stands and rainfall amounts before and after rainfall (mean ± *SD*). KP, *Koelreuteria paniculata* forest; PO, *Platycladus orientalis* forest; RP, *Robinia pseudoacacia* forest. AR, after rain; BR, before rain. Rainfall amounts, 8.60, 13.44 and 85.20 mm. Different lowercase letters indicate significant differences in soil water content under the same soil layer at different sampling times ($p < 0.05$).

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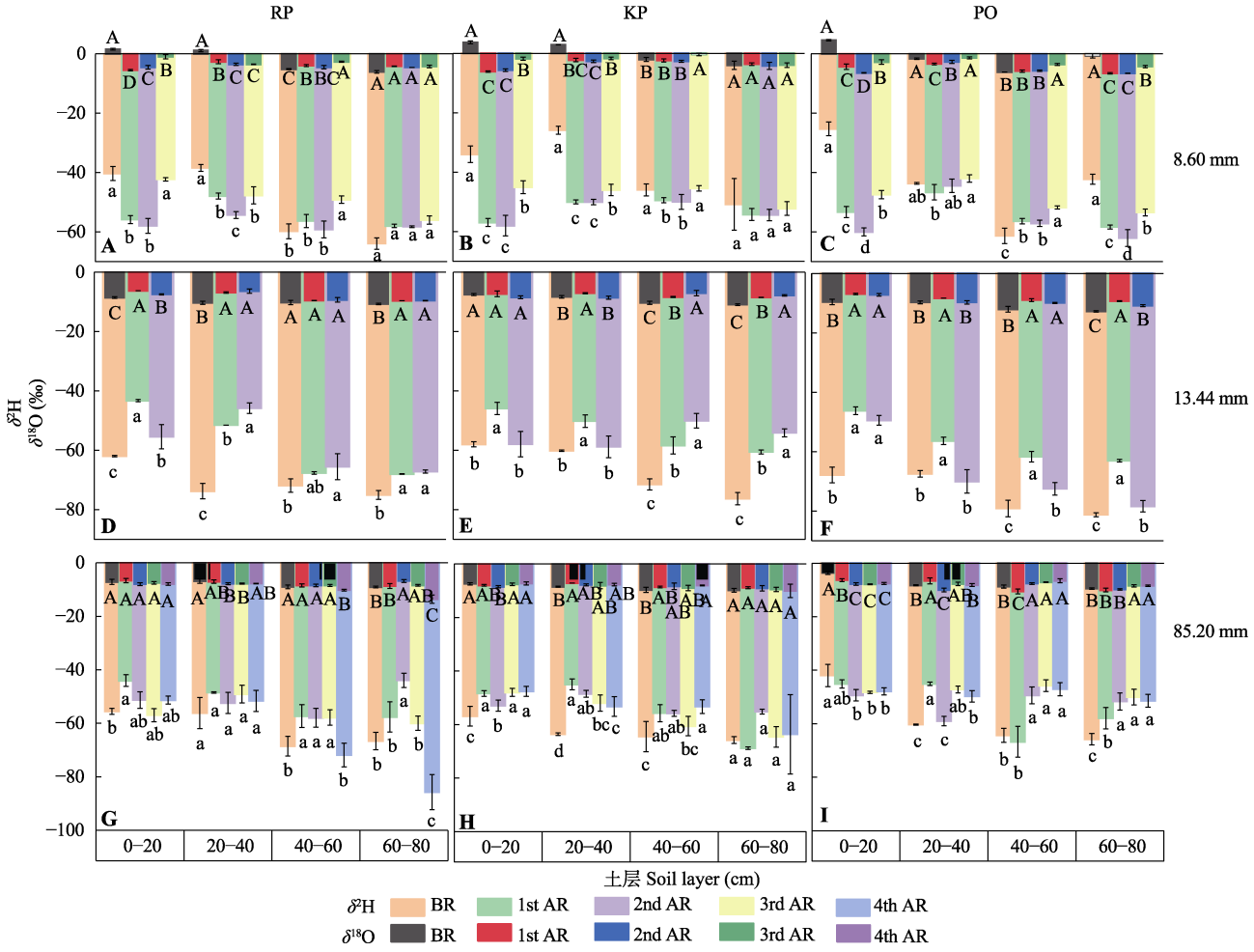


图4 不同降雨量降雨前后不同林分土壤水氢氧同位素组成(δ^2H和δ^{18}O)的变化(平均值±标准差)。KP, 栾树林; PO, 侧柏林; RP, 刺槐林。降雨量, 8.60、13.44和85.20 mm; BR, 雨前; 1st AR, 雨后第1天; 2nd AR, 雨后第2天; 3rd AR, 雨后第3天; 4th AR, 雨后第4天。不同大写字母表示不同采样时间土壤水δ^{18}O值存在显著差异, 不同小写字母表示不同采样时间土壤水δ^2H值存在显著差异($p < 0.05$)。

Fig. 4 Variations of hydrogen and oxygen isotopes composition (δ^2H and δ^{18}O) of soil water in different stands and rainfall amounts before and after rainfall (mean ± *SD*). RP, *Robinia pseudoacacia* forest; KP, *Koelreuteria paniculata* forest; PO, *Platycladus orientalis* forest. AR, after rain; BR, before rain. Rainfall amounts, 8.60 mm, 13.44 mm and 85.20 mm. Different uppercase letters indicate significant differences in δ^{18}O values of soil water at different sampling times, and different lowercase letters indicate significant differences in δ^2H values of soil water at different sampling times ($p < 0.05$).

的δ^2H和δ^{18}O影响不显著(图4A–4C)。

与雨前相比, 13.44 mm降雨显著增加刺槐0–40、 60–80 cm和栾树40–80 cm土壤水的δ^2H和δ^{18}O, 同时也显著增加了侧柏0–20 cm和40–80 cm土壤水的δ^2H和δ^{18}O。85.20 mm降雨后, 栾树样地60–80 cm土壤水的δ^2H和δ^{18}O与雨前差异不显著(图4H), 雨后第2天至第4天侧柏样地表层土壤(0–20 cm)水的δ^2H和δ^{18}O显著低于雨前, 而40–80 cm土壤水的δ^2H和δ^{18}O均显著高于雨前(图4I)。

2.3 降雨前后木质部水同位素的变化特征

植物木质部水的δ^2H和δ^{18}O随植物种类和采样时间不同而发生变化(图5)。除侧柏外, 不同降雨类型下刺槐和栾树林下灌木木质部水的δ^2H和δ^{18}O均大于乔木。在同一类型降雨下, 降雨前后采样时间变化影响木质部水同位素组成(图5)。干旱小雨(8.60 mm)后, 刺槐林下荆条和侧柏林下荆条木质部水的δ^2H和δ^{18}O随降雨天数增加呈增加趋势(图5A、5D)。湿润中雨(13.44 mm)后, 刺槐、刺槐林下荆条和侧柏林下荆条木质部水的δ^2H和δ^{18}O随降雨天数增加呈增加趋势(图5B、5E)。干旱暴雨(85.20 mm)后, 乔木木质部水的δ^2H和δ^{18}O随降雨天数增加呈增加趋势, 侧柏林下荆条雨后木质部水的δ^2H和δ^{18}O显著高于雨前, 而刺槐林下荆条水的δ^2H和δ^{18}O在降雨前后差异不显著(图5C、5F)。

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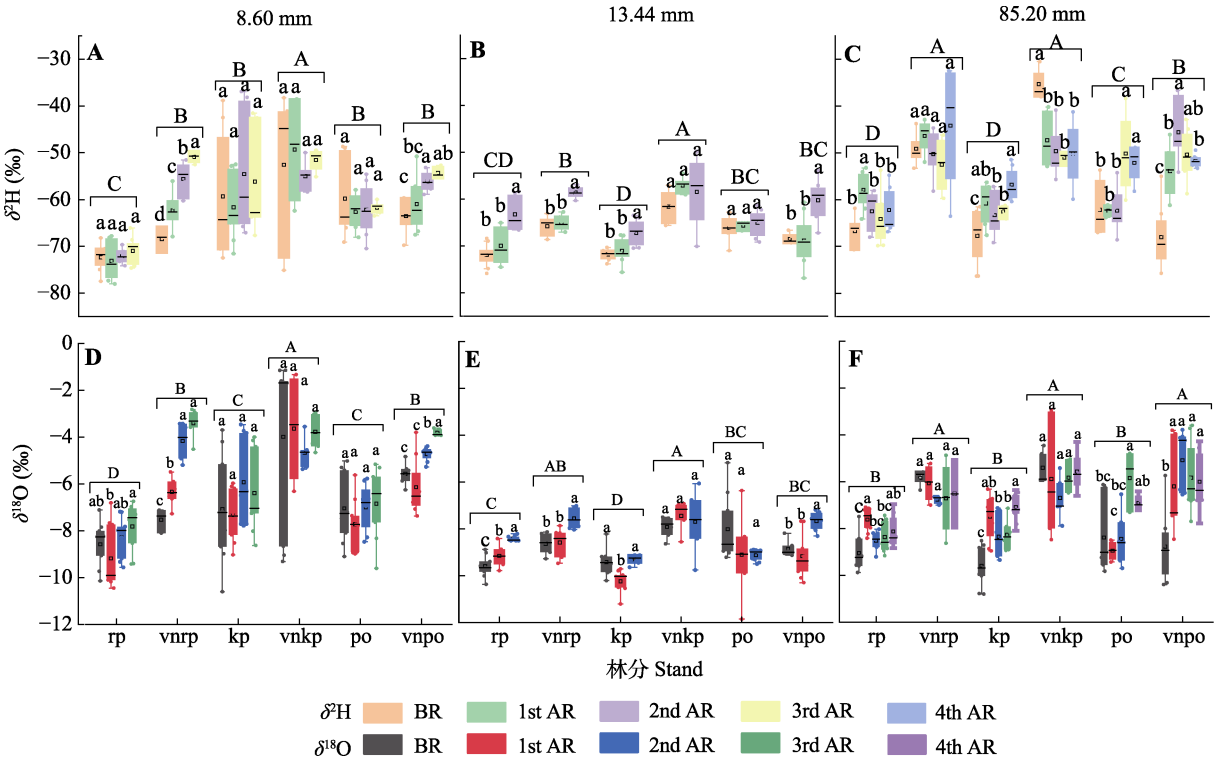


图5 不同降雨量降雨前后不同林分木质部水的氢氧同位素组成(δ^2H和δ^{18}O)变化(平均值±标准差)。kp, 栾树; po, 侧柏; rp, 刺槐; vnkp, 栾树林下荆条; vnpo, 侧柏林下荆条; vnrp, 刺槐林下荆条。降雨量, 8.60、13.44和85.20 mm; BR, 雨前; 1st AR, 雨后第1天; 2nd AR, 雨后第2天; 3rd AR, 雨后第3天; 4th AR, 雨后第4天。不同大写字母表示不同植被间木质部同位素数值存在显著差异, 不同小写字母表示不同采样时间的木质部同位素数值存在显著差异($p < 0.05$)。

Fig. 5 Variations of hydrogen and oxygen isotopes composition (δ^2H and δ^{18}O) of xylem water in different stands and rainfall amounts before and after rainfall (mean ± *SD*). kp, *Koelreuteria paniculata*; po, *Platycladus orientalis*; rp, *Robinia pseudoacacia*; vnkp, *Vitex negundo* under *Koelreuteria paniculata*; vnpo, *Vitex negundo* under *Platycladus orientalis*; vnrp, *Vitex negundo* under *Robinia pseudoacacia*. AR, after rain; BR, before rain. Rainfall amounts, 8.60, 13.44 and 85.20 mm. Different uppercase letters indicate significant differences in xylem isotope values among different vegetations, and different lowercase letters indicate significant differences in xylem isotope values at different sampling times ($p < 0.05$).

2.4 降雨前后植物对土壤水分的利用

不同降雨类型下, 乔木和灌木的水分利用策略随降雨前后采样时间的不同而发生变化(图6)。干旱小雨(8.60 mm)前, 刺槐和林下荆条主要从地下水获取水分, 其贡献率分别为69.4%和50.0%; 栾树同样主要依赖地下水获取水分, 而林下荆条水分来源不同, 其主要从40–60 cm土壤水获取水分, 占比分别为60.6%和41.9%; 与栾树林分获取水分来源的趋势一致, 侧柏也主要从地下水获取水分, 其林下荆条主要从40–60 cm土壤水吸收水分, 占比分别为52.5%和57.8%。干旱小雨后, 3个林分的乔木和灌木均增加了对0–40 cm表层土壤水的吸收, 其中刺槐仍以地下水为主要水分来源, 而林下荆条以0–60 cm土壤水为主要来源, 其占比分别为68.5%和66.7%; 同样, 栾树主要依赖地下水获取水分, 而林下荆条以0–40 cm土壤水为主要来源, 占比分别为34.9%和40.2%; 与栾树林分获取水分来源的趋势一致, 侧柏也主要从地下水获取水分, 其林下荆条主要从0–40 cm土壤水吸收水分, 占比分别为43.3%和41.7%。

湿润中雨(13.44 mm)前, 刺槐主要吸收0–80 cm土壤水, 各层土壤水利用较均匀, 而林下荆条主要吸收0–20 cm土壤水(占比为61.8%); 栾树主要吸收40–80 cm土壤水, 林下荆条主要吸收0–20 cm土壤水, 占比分别为68.3%和60.5%; 侧柏和林下荆条主要吸收0–40 cm土壤水, 占比分别为82.9%和78.0%。雨后第1天, 刺槐和林下荆条均以40–60 cm土壤水为主(占比分别为45.7%和47.1%); 栾树以地下水为主(占比为88.0%), 林下荆条以0–60 cm土壤水为主(占比为63.9%); 侧柏也以地下水为主(占比为56.6%), 林下荆条以40–60 cm土壤水为主(占比为43.7%)。雨后第2天, 不同林分的乔木和灌木均以表层0–40 cm土壤水为主要吸收来源。

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干旱暴雨(85.20 mm)前, 刺槐以40–80 cm土壤水和地下水为主要水分来源(占比为79.7%), 林下荆条主要吸收土壤0–40 cm土壤水(占比为85.8%); 栾树也以40–80 cm土壤水和地下水为主要水分来源(占比为74.4%), 林下荆条主要吸收土壤0–20 cm土壤水(占比为65.5%); 侧柏也以40–80 cm土壤水和地下水为主要水分来源(占比为70.8%), 林下荆条主要吸收40–80 cm土壤水(占比为65.7%)。雨后, 不同林分的乔木均增加了0–40 cm土壤水分吸收, 使得不同土层吸水量趋于均匀, 而灌木的主要水分来源均为0–40 cm浅层土壤水, 其占比分别为57.0%、67.8%和46.7%。

2.5 降雨前后水分生态位的变化特征

不同降雨类型下, 乔木和灌木的水分生态位宽度随降雨前后采样时间的不同而发生改变(图7)。干旱小雨(8.60 mm)前后, 刺槐林下荆条和栾树林下荆条生态位宽度显著大于对应乔木(图7A)。8.60 mm降雨增加了刺槐、栾树和对应灌木生态位宽度, 随

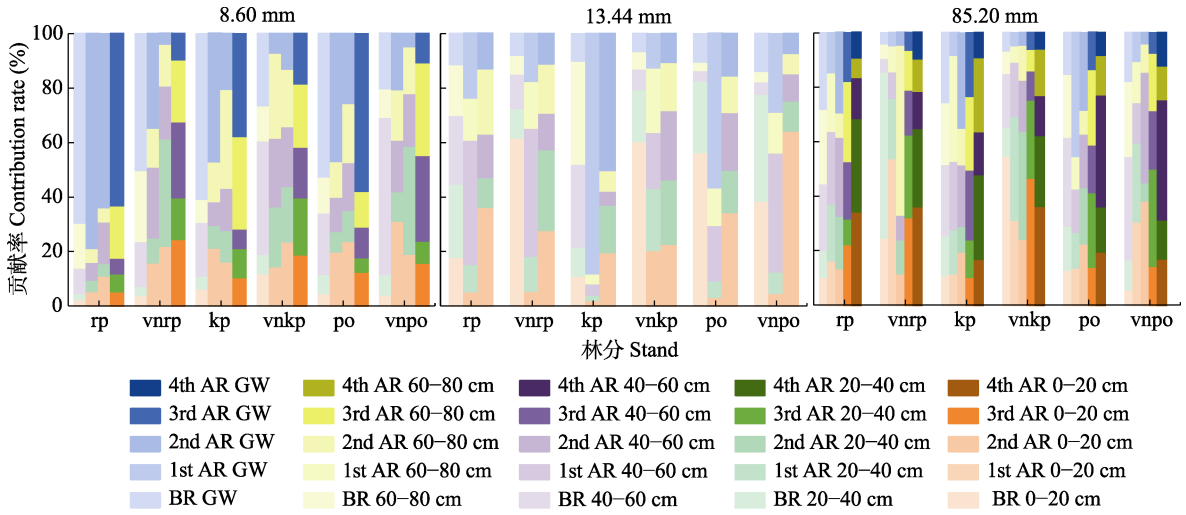


图6 不同降雨量降雨前后不同林分乔木和灌木对各层土壤水分的利用比例。kp, 栾树; po, 侧柏; rp, 刺槐; vnkp, 栾树林下荆条; vnpo, 侧柏林下荆条; vnrp, 刺槐林下荆条。降雨量, 8.60、13.44和85.2 mm。BR, 雨前; 1st AR, 雨后第1天; 2nd AR, 雨后第2天; 3rd AR, 雨后第3天; 4th AR, 雨后第4天; GW, 地下水。

Fig. 6 Absorption proportion of soil water in each layer for trees and shrubs in different stands and rainfall amounts before and after rainfall. kp, *Koelreuteria paniculata*; po, *Platycladus orientalis*; rp, *Robinia pseudoacacia*; vnkp, *Vitex negundo* under *Koelreuteria paniculata*; vnpo, *Vitex negundo* under *Platycladus orientalis*; vnrp, *Vitex negundo* under *Robinia pseudoacacia*. Rainfall amounts, 8.60, 13.44 and 85.2 mm. AR, after rain; BR, before rain. GW, groundwater.

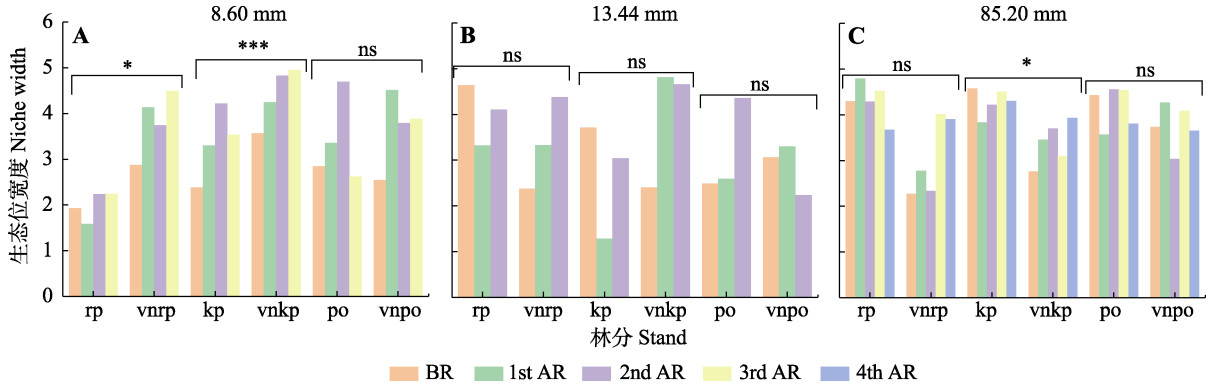


图7 不同降雨量降雨前后不同林分上层乔木和下层灌木水分生态位宽度变化特征。kp, 栾树; po, 侧柏; rp, 刺槐; vnkp, 栾树林下荆条; vnpo, 侧柏林下荆条; vnrp, 刺槐林下荆条。降雨量, 8.60、13.44和85.20 mm。BR, 雨前; 1st AR, 雨后第1天; 2nd AR, 雨后第2天; 3rd AR, 雨后第3天; 4th AR, 雨后第4天。***, $p < 0.001$; *, $p < 0.05$; ns, $p > 0.05$。

Fig. 7 Variations of water niche width of overstory arbors and understory shrubs in different stands and rainfall amounts before and after rainfall. kp, *Koelreuteria paniculata*; po, *Platycladus orientalis*; rp, *Robinia pseudoacacia*; vnkp, *Vitex negundo* under *Koelreuteria paniculata*; vnpo, *Vitex negundo* under *Platycladus orientalis*; vnrp, *Vitex negundo* under *Robinia pseudoacacia*. Rainfall amounts, 8.60, 13.44 and 85.20 mm; AR, after rain; BR, before rain. ***, $p < 0.001$; *, $p < 0.05$; ns, $p > 0.05$.

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降雨天数增加而增加。湿润中雨(13.44 mm)前，刺槐和栾树生态位宽度大于其林下荆条，而侧柏小于林下荆条(图7B)。13.44 mm降雨增加了刺槐林下灌木和栾树林下灌木生态位宽度，降低了刺槐和栾树生态位宽度。干旱暴雨(85.20 mm)前后，栾树的生态位宽度高于林下荆条(图7C)。与雨前相比，85.20 mm降雨增加刺槐林下荆条和栾树林下荆条生态位宽度(图7C)。侧柏在不同降雨类型中表现一致，雨后第1天侧柏林下荆条生态位宽度陡增，雨后第2天侧柏生态位宽度陡增。

不同林分水分生态位重叠的变化随降雨类型发生变化(图8)。刺槐林分生态位重叠在降雨8.60 mm前后最小，随降雨天数增加而递减(图8A)。栾树林分生态位重叠在降雨13.44 mm前后显著最小(图8B)。侧柏林分水分生态位重叠在3场降雨后第1天均有降低，在降雨8.60 mm和13.44 mm后第2天增加(图8C)。

3 讨论

3.1 降雨对水分利用的影响

本研究结果表明，3个林分中乔木和灌木的水分来源可塑性较强，对不同类型降雨的响应也不同(图6)。在本研究区，旱季恰逢乔木和灌木快速生长期(6月)，导致水分需求和胁迫俱增(张潇等, 2023)。在旱季，深根系乔木从深层土壤或地下水中吸收水分(刘自强等, 2016; Liu et al., 2019; 葛照欣等, 2023; 吴应明等, 2023)，可有效减少水分胁迫(Nie et al., 2011)。干旱小雨(8.60 mm)前，浅层土壤干热条件可能限制了根毛吸水活性(刘自强等, 2017; 祝维等, 2023)，导致刺槐、栾树和侧柏乔木对地下水的依赖较高，贡献率分别为69.4%、60.6%和52.5%。栾树林下荆条和侧柏林下荆条对40–60 cm土壤水有较高需求，其贡献率分别为41.9%和57.8%，但刺槐林下荆条对地下水依赖仍然较高(50%) (图6)。当土壤水分不能满足生长需要时，植被会向更深层次土壤吸收水分(付昕宇等, 2020)或利用更深风化基岩层水分来维持生存(Nie et al., 2011)。在土壤干旱期间，研究区持续高温无降水导致土壤缺水加剧时，乔木和林下灌木相似水分利用模式可能导致激烈水分竞争(Grossiord et al., 2014; Tang et al., 2018; Han et al., 2023)，特别是刺槐与荆条共享相同水分来源。而栾树和荆条、侧柏和荆条不同水分利用模式，减少了对水的竞争，即使在旱季缺水情况下，也能保证其生长，为其形成稳定的森林生态系统提供了基础。

在山地森林中，降水量很可能是影响树木水源关键因素。由于小降雨事件或短脉冲降水只能湿润表层土壤，而乔木无法吸收利用(Liu et al., 2019)，只有当降水增加到一定阈值时，乔木表层根系才能形成并保持吸收表层土壤水分功能(孙守家等, 2014; Dai et al., 2015; 刘自强等, 2016)，而灌木主要依赖最近降水(Nie et al., 2011; 邓文平等, 2014; 赵娜等, 2017; 刘文娜等, 2018)，本研究结果与前人研究相一致。在干旱小雨(8.60 mm)后，3个林分的灌木均从主要利用深层土壤(40–80 cm)水和地下水转变为主

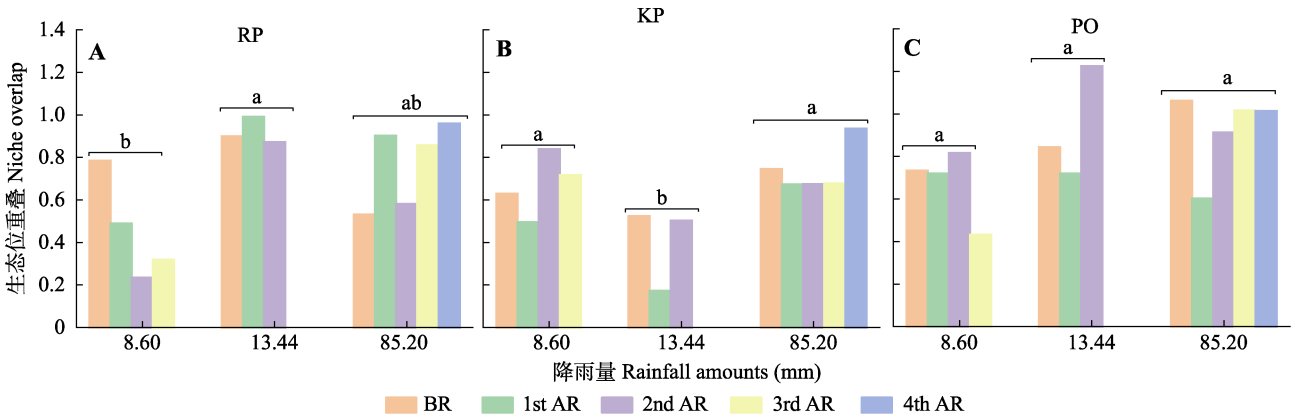


图8 降雨前后不同林分上层乔木和下层灌木水分生态位重叠变化特征。KP，栾树林; PO，侧柏林; RP，刺槐林。BR，雨前; 1st AR，雨后第1天; 2nd AR，雨后第2天; 3rd AR，雨后第3天; 4th AR，雨后第4天。不同小写字母表示降雨类型间存在显著差异($p < 0.05$)。

Fig. 8 Characteristics of water niche overlap of overstory arbors and understory shrubs in different stands before and after rainfall. KP, *Koelreuteria paniculata* forest; PO, *Platycladus orientalis* forest; RP, *Robinia pseudoacacia* forest. AR, after rain; BR, before rain. Different lowercase letters indicate significant difference in different rainfall types ($p < 0.05$).

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要吸收浅层土壤(0–60 cm)水(图6), 而对3种乔木而言, 降雨虽增加了0–40 cm土壤水利用比例, 但仍以地下水为主要水分来源。其原因一方面可能是8.60 mm的降雨量仅对表层土壤0–40 cm水分产生影响, 而对更深层次的土壤水分影响未达到阈值(图3A–3C); 另一方面可能是植物种类不同, 荆条作为浅根植物(韩烈保等, 2009), 在浅层分布的大量细根提高了对降雨的敏感度(祝维等, 2023), 而降雨未激活乔木土壤表层根系代谢活性(Liu et al., 2019; Tang et al., 2019)。因此, 在土壤干旱阶段面临小雨降落时, 林下灌木具有更强的从深层向浅层转换水源以缓解水分胁迫的能力, 而乔木和灌木对不同土层的水分吸收避免了水分竞争。在干旱暴雨(85.20 mm)后, 不同林分乔木和灌木的水分来源均随土壤含水量升高向浅层土壤(0–40 cm)转变, “可塑性二型根系”灵活转换水分吸收的现象在其他研究中也有报到(Yang et al., 2015; Brinkmann et al., 2019; Mei & Ma, 2022; 张潇等, 2023)。

湿润中雨(13.44 mm)后第1天, 不同林分的乔木和灌木均未增加对表层0–40 cm土壤水分吸收, 反而增加了对40–60 cm土壤水和地下水吸收。相较于另外2次降雨, 这次雨前的采样日期与降雨日期距离较长, 可能导致雨前代表性不强。雨后采样天数的不同可能会导致植被水分来源的不同(Liu et al. 2019; Mei & Ma, 2022)。王艳莉等(2016)研究发现, 与降水后第1天相比, 降水后第7天柠条(*Caragana korshinskii*)与油蒿(*Artemisia ordosica*)均增加了对浅层土壤水的利用比例。与上述研究结果一致, 雨后第2天, 不同林分的乔木和灌木均以表层0–40 cm土壤水为主要吸收来源, 植被可能有足够时间来应对土壤湿度的突然增加(Liu et al., 2019)。

依据降雨量等级划分标准, 近3年(2021–2023)内该区不同降雨量级降雨共235场次。其中小雨183场, 占所有降雨次数的77.87%; 中雨31场, 占比为13.19%; 暴雨10场, 占比4.26%。干旱小雨后, 灌木的水分利用策略对降雨更加敏感, 避免了与乔木的水分竞争。小雨发生频率最高, 乔木和灌木不同的水分利用策略有利于乔木和灌木长期混生。虽然中雨和暴雨次数较少, 但其降雨量大、破坏性较强, 有可能对乔木和灌木的水分利用策略产生重要影响(杨菲等, 2022)。湿润中雨后乔木和灌木竞争0–40 cm土壤水, 而干旱暴雨后乔木和灌木具有不同的水分利用策略, 其差异可能与雨前土壤含水量紧密相关(Mei & Ma, 2022)。

在每个样地选取3个长势良好、生长状况相近的标准木是可行且具有代表性的(Liu et al., 2019; 吴旭等, 2022; Dai et al., 2023; 张潇等, 2023), 其能有效反映该树种在样地的平均生长水平。尽管同株样木采集3个重复样品提高了数据准确性, 但此采样方法也存在很大的局限性, 如选取的样木可能无法全面展现树种的多样性和变异性, 样地内的微环境可能对其结果产生影响等。因此, 鉴于本研究监测降雨次数和采集样品数量有限, 未来应延长监测时间并增加标准木的数量, 以更全面地从时间和空间角度观察其水源变化。同时, 本研究使用双同位素方法计算水分来源, 但尚未探讨木质部氢同位素校正后对其影响, 未来需关注同位素偏移现象(路晨曦等, 2023)。此外, 本研究未深入探讨与植物水分来源密切相关的植物根系、蒸腾作用和生理生态因子等, 这也将是后续研究的重要方向(Zhang et al., 2022)。

3.2 降雨对水分生态位的影响

水分生态位反映了植物在时空上如何利用水资源, 及其在长期演化和环境适应过程的水分利用效率, 该效率随水资源量变化而调整。根系生态位作为间接研究植物间水分关系的指标有一定的局限(Chen et al., 2020)。祝维等(2023)发现, 细根生态位重叠和吸水生态位重叠间存在显著差异。此外, 即使垂直根系分布在不同树种间无差异, 但根系吸水时空互补性使植物可获得更多未开发的土壤资源来满足增加的需水量(Kulmatiski et al., 2020)。

水分生态位宽度反映物种对环境适应力及对水资源利用效率(伊力塔等, 2012)。干旱小雨(8.60 mm)前后, 刺槐和栾树生态位宽度低于对应林下灌木, 说明林下灌木适应和利用水分能力强于乔木(图7A), 而在干旱暴雨(85.20 mm)前后, 栾树生态位宽度高于林下灌木(图7C)。其差异可能与土壤水分状况、植被根系形态、水分利用策略和生长阶段紧密相关(Liu et al., 2019)。在小雨前, 土壤一直处于干旱阶段, 而暴雨前1个月土壤经历了湿润(8月), 期间栾树生长旺盛, 其根系垂直分布比灌木更广, 能够吸收更深层次的土壤水分。此外, 乔木叶片和其他结构也可能在湿润条件下可以更有效地保持和利用水分

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(蒋涛等, 2020)。侧柏和林下荆条生态位宽度对不同降雨类型响应一致, 即荆条生态位宽度在雨后第1天陡增, 侧柏生态位宽度在雨后第2天陡增, 说明上层乔木和下层灌木通过不同水分利用策略应对土壤含水量变化, 从而减小两者对同一资源土壤水分竞争, 在长期水资源竞争中形成一种混生机制(杨菲等, 2022)。

生态位重叠度揭示了不同物种在利用相同资源上的相似程度(郝兴明等, 2008; 冯玉超等, 2019)。干旱小雨(8.60 mm)前, 3种优势乔木和林下灌木水分生态位重叠均较高(0.78、0.63和0.73) (图8), 表明乔木和林下灌木利用水分来源相似度高, 存在较为激烈的竞争关系。可能原因是6月土壤含水量低, 而植物生长旺季需水量大, 乔木和灌木均需向土壤深层拓宽水分, 因此增加了水分资源重叠可能性(吴旭等, 2022)。8.60 mm雨后, 刺槐和林下荆条的水分生态位重叠随降雨天数增加而递减, 表明两者由竞争转为互补关系。这与杨菲等(2022)的研究结果相一致。在湿润中雨(13.44 mm)前后, 刺槐和林下荆条、侧柏和林下荆条的水分生态位重叠依然较高, 但由于土壤水分相对充足, 物种间一定的水资源竞争有利于提高水分利用效率(Han et al., 2023)。Sohel等(2021)研究发现, 树木性状(树的大小和木材密度)是影响46种邻近热带植物生态位分离的主要因素。为全面深入地理解水分利用策略和水分生态位特征, 未来的研究应深入探讨影响植物水分来源和水分生态位特征的相关机制。

4 结论

本研究对混生乔灌植物在不同降雨事件下的水分吸收和生态位变化特征进行了分析。干旱小雨后, 灌木的利用水源从深层土壤向上层土壤转移, 而乔木仍以地下水为主; 湿润中雨后, 乔木和灌木均以0–40 cm土壤水为主要水分来源, 这表明两者发生了水分竞争, 但由于土壤水分充足, 其竞争反而有利于土壤水分吸收; 干旱暴雨后, 灌木主要水分来源为0–40 cm浅层土壤水, 而乔木的不同土层吸水量趋于均匀。干旱小雨前, 刺槐和林下荆条水分生态位重叠较大, 雨后其随降雨天数增加而递减。本研究发现, 除干旱小雨前乔木和灌木水分来源相同之外, 两者面对降雨具有不同水分利用策略, 从而避免了彼此间水分竞争。但未来的研究应深入探究影响植物水分来源和水分生态位特征的相关机制。总之, 本研究对评估混生植物在华北土石山区群落的空间配置和森林生态系统恢复管理中的适用性具有指导意义。

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