植物-土壤系统中水分再分配作用研究进展

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摘要：在过去100多年里，植物与土壤之间水分关系的研究多侧重于植物本身的水分利用方式、水分利用效率及其植物根系对水分的吸收等。然而进入20世纪80年代后期，植物生理生态学研究人员开始将注意力转移到植物根系对土壤水分的调节作用，即水分再分配（hydraulic redistribution）作用，具体地讲是在水势差的驱动下水分由根系向土壤中释出的一种双向和被动的水分运转过程，其中既包含水分由深层土壤向表层土壤的释出，也包括由表层土壤向深层土壤的流动，同时还涵盖了水分在水平方向上的侧向运输过程。伴随着研究手段的不断提高和对生态系统水平衡问题的关注，水分再分配逐渐成为近代植物生态学和水文学的交叉学科生态水文学（ecohydrology）的核心研究内容之一。目前该领域的研究已经阐明水分再分配作用在不同程度上对植物个体蒸腾、碳同化速率有很大贡献，有利于提高根系生活力和土壤养分；另外，在不断扩展的生态系统生态学研究中，也加强了对制约水分再分配作用发生的外部因子的认识。回顾和分析了水分再分配的研究历史、生态学意义、影响因素、测定方法等，特别提出阐述浅根系植物对水分再分配作用的依赖性与依赖程度，从植物进化学角度解释水分再分配作用发生的生理学基础和意义及水分再分配作用对土壤微生物活性的影响等方面将是未来研究的几个重点方向。

关键词：水分再分配；水分平衡；根系；生态恢复

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Hydraulic redistribution in plant-soil systems

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Abstract: For much of the past century, researches on water relations of plant-soil systems mostly focued on the mode and efficiency of plant water use and water movement in soils. Although hydraulic redistribution of soil water by plant roots was first reported as early as the late 1920's, the importance of the process in regulating soil water and associated ecological processes was not widely recognized by plant physiologists and ecologists until the late 1980's. The term "hydraulic redistribution", known also as "hydraulic lift" as reported in many studies, refers to the phenomenon of soil water redistribution by plant roots through passive processes of water uptake and release driven by water potential gradient in the root-soil interface. However, hydraulic lift has been used more specifically to describe the transportation of soil water from deep wetter layers to shallow drier layers. Recent measurements of sapflow in taproots and lateral roots of trees have demonstrated that roots can also redistribution water either downward or laterally from moist surface soils to drier bottom soil layers. Because of the bidirectional movement of the transported water, "hydraulic redistribution" has been proposed as a more comprehensive term than "hydraulic lift" to describe the phenomenon.

Hydraulic redistribution usually occurs at night when transpiration has diminished sufficiently, or during periods when transpiration is substantially reduced, to allow the water potential of the roots to exceed that of the drier parts of soil layers. To

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date, much progress has been made in understanding the role of hydraulic redistribution in maintaining water balance of plant community under drought conditions, and in identifying the internal and external factors that regulate the occurrence and magnitude of hydraulic redistribution. Three techniques have been commonly used in the hydraulic redistribution research: the first involves determination of the direction and rate of sapflow in roots using heat pulse or heat dissipation sapflow measurement sytems; the second is to measure the deuterium content of neighbor species when deuterated water is supply to deep roots of the target trees to trace the movement of water to shallow roots of grasses; and the third is to measure changes in soil water potential and/or soil water content. There have been more than 60 cases of hydraulic redistribution reported for plant species across diverse habitats, and it is expected that the hydraulic redistribution is widespread wherever conditions are conductive to its occurrence. Nevertheless, more efforts are needed in exploring the ecological function and significance of the hydraulic redistribution, especially its significance in ecosystem restoration of degrading ecosystems in arid and semi-arid environments.

In this article we reviewed our state of knowledge on hydraulic redistribution, and examined the significance of the process in water balance of plant-soil systems. Based on our review of literature and synthesis of existing information, we stressed the need for further research to evaluate the contribution of hydraulic redistribution to the water balance of plant community and ecosystem restoration in arid and semi-arid areas or in regions experiencing the stage of frequent droughts. Specific questions that should be addressed in future research may include, but not limited to: (1) How dependent are the plants with shallow roots on hydraulic redistribution by plants with deep roots in arid ecosystems? (2) What are the biological basis and significance of hydraulic redistribution from perspective of plant evolution? (3) What is the significance of hydraulic redistribution to maintaining soil microbial activities? (4) Do the mode and magnitude of hydraulic redistribution differ among different types of vegetation? Moreover, quantitative information on the threshold of soil water potential and/or soil water content for inducing hydraulic redistribution in different ecosystems would be useful in elucidating the plant water relations in arid and semi-arid regions.

Key words: hydraulic redistribution; water balance; roots; ecosystem restoration

植物在生长发育过程中,根系需要不断地从土壤中吸收水分,又通过叶片蒸腾作用将水分散失到大气中去。在植物强烈的蒸腾拉力作用下,土壤中的水分从高水势向低水势区输送,同时地面蒸发也使水分在热辐射的作用下从土壤中散失。然而,当植物蒸腾、地面蒸发减弱或停止时,植物根系仍可从深层较湿土壤中吸收水分,再由侧根释放到表层较干燥的土壤中;或侧根从表层湿润的土壤中吸收水分,通过主根向下运输在深层较干燥的土壤中释出,从而改善表层土壤水分状况或将水分贮藏在深层土壤中[1~3],这种现象被称为水分再分配(hydraulic redistribution)作用。本文系统回顾了水分再分配的研究历史、测定方法及其生态学意义,以方便国内同行开展相关研究。

1 水分再分配的研究历史

通常认为植物根系的功能是吸收水分、养分及稳定植株个体,而事实上,它还可以释放水分,调节根际的水分分布状况。早在20世纪20年代末期, Magistad & Breazeale[4]通过对田间作物生长观测提出,植物根系可能有释放水分的功能,随后Breazeale[5]在实验室对小麦幼苗进行了分根实验,发现当干燥土壤的含水量临近萎蔫点时,处于湿润土壤中的根系从土壤中吸收水分,然后运输到处于干燥环境中的根系并将其释放到土壤中,使得干燥土壤的含水量增加。类似的现象在玉米中也有发现,使根系获得土壤水分“平衡器”的称号[6]。随后对水分释出的直接测定已有很多报道[7,8],并将这种现象称作“水分吸收与释放(water uptake and release)”或“水分逆向运输(negative water transport)”[9]。直到20世纪80年代后期,Richards & Caldwell[10]首次在野外实验中对三齿蒿(*Artimisia tridentata*)根系周围的土壤水势(Ψs)日动态观察发现Ψs在夜间增加而白天下降,但当用不透明的塑料袋罩住植物阻止蒸腾作用后,Ψs随之增加;相反如果在夜间给予植物光照,Ψs就表现下降的趋势。这种变化证实了水分的逆向流动,并第1次将这种现象定义为hydraulic lift,指当蒸腾作用减弱或停止时,植物根系从深层土壤中吸收水分,通过主根向上运输,再由浅层侧根释放到表层较干的土壤中,从而改善表层土壤水分状况,保持这些植物自身的浅层根系或周围其他植物根系的水分供给。Hydraulic lift的进

一步证实是用同位素示踪法，当给三齿蒿深层根系浇以重水(即氧化氘，分子符号 D_2O)后，在相邻的沙生冰草(*Agropyron desertorum*)茎中也发现了氘，表明三齿蒿的根系吸收水分后又释放到浅层土壤中而被相邻植物吸收[11]。中文文献曾将这种作用译为"水力提升"[12]、"提水作用"[13~15]，或"根水倒流"[16]。

进入20世纪90年代，Burgess 等人[1]在西澳大利亚地中海气候区用热脉冲的方法对银桦(*Grevillea robusta*)和赤桉(*Eucalyptus camaldulensis*)根系中的液流流量和方向进行了监测研究，发现在上层土壤湿润而底层土壤干燥的情况下，水分会沿着根系由上层土壤向深层流动或侧向运输，并建议以"hydraulic redistribution"取代"hydraulic lift"。同一时期，Schulze 等人[2]在美国的卡拉哈里(Kalahari)沙漠用同位素示踪法监测了灌木 *Acacia haematoxylon*、小乔木骆驼树(*Acacia erioloba*)和3种多年生草本植物(*Stipagrostis amabilis*, *Stipagrostis obtuse*, *Centropodium glauca*)根系吸收水分模式，同样观测到当表层土壤湿润后由根系将水分向深层运输的现象，这反映了根系对水分运输的双向性，如图1所示。这一发现使水分再分配研究跨越了一个新的台阶，由原来只认为水分再分配对浅层细根作用、对浅层土壤养分的有效性等有明显作用，沿伸到考虑水分再分配对深层根系的作用。目前学术界已基本倾向于以"hydraulic redistribution"取代"hydraulic lift"的提法[3,17~21]。"Hydraulic redistribution"，即"水分再分配"，较之"hydraulic lift"更客观和科学地描述植物根系对土壤水分分布的调控作用。

到目前为止，全世界已有60多个研究实例证实了水分再分配作用的存在[22]，而其中具有水分再分配作用的植物有深根系的，也有浅根系的；有乔木、灌木，也有草本，而它们的共同特点是分布在干旱、半干旱地区[23~25]或有阶段性土壤干旱的湿润地区[26]。由此推论，水分再分配作用可能是自然界植物普遍存在的一种现象，然而，是否干旱半干旱区的所有植物都具有水分再分配作用尚无定论。

2 水分再分配的生态功能研究

大多数生态系统中，土壤水分状况普遍存在时空异质性，导致植物根系的分布呈明显分层现象。水分再分配作用可以在一定程度上改变水分供给的空间格局，从而调节生态系统水分平衡和促进养分循环，提高群落地上部分同化作用效率，改善地下部生态环境，提高生态系统生产力[27]。水分再分配的生态功能的总体框架可简示为图2。

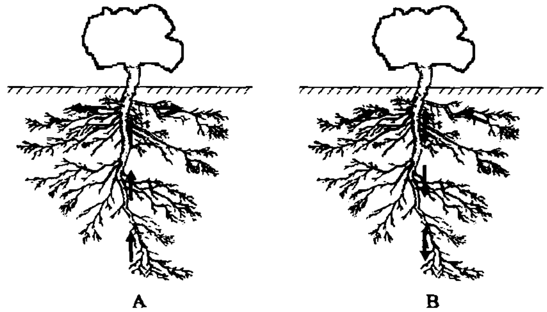

图1 根据水分再分配发生的原理，在蒸腾作用减弱或停止时，水分在根系和土壤中的流动模式图

Fig.1 Pattern of water movement through the root systems under the influence of hydraulic redistribution

箭头表示水分流动方向；A，表层土壤干燥而深层土壤湿润；B，表层土壤湿润而深层土壤干燥 The arrow indicates water movement. A, water moves from tap-root through lateral roots when the shallow soil layers are drier than the deep layers; B, water moves from lateral roots to the tap-root when the shallow soil layers are wetter than the deep layers

2.1 对土壤水分的调节作用

通常认为降水是由重力驱动下的渗透作用到达深层土壤。在高渗透的沙土中，平均每年的水分下渗深度不过几米；而对于紧实度较高的粘土，水分每年下渗仅有几厘米[28]。反过来，贮藏于高渗透性土壤中的水分又由于微弱的毛细管作用而很难到达表层土壤中，因此根系成为不同土壤层之间水分运输的主要通道，已有的研究表明根系的水分再分配作用对土壤含水量有较大调节作用，如北美黄杉(*Pseudotsuga menziesii*)群落和美国黄松(*Pinus ponderosa*)群落中，2m内土壤层中分别有28%和35%的水分来自根系水分再分配[18]。水分再分配作用可使 *Sebania rostrata* 的根系在一夜间释放到表层土壤中22.5g水[17]，使降水在三齿蒿群落中1d内可下渗到1.5m的深度[19]，从而将水分贮藏在深层土壤中以便当表层土壤干燥时保证植物的水分获取。对其它植物的大量研究阐明水分再分配对调节土壤水分平衡方面有重要的作用[29~32]。尽管有些研究认为水分再分配的数量较小，其生态学作用不显著[33]，但这种结论或许与研究区域的极端自然环境和观测时间有关。

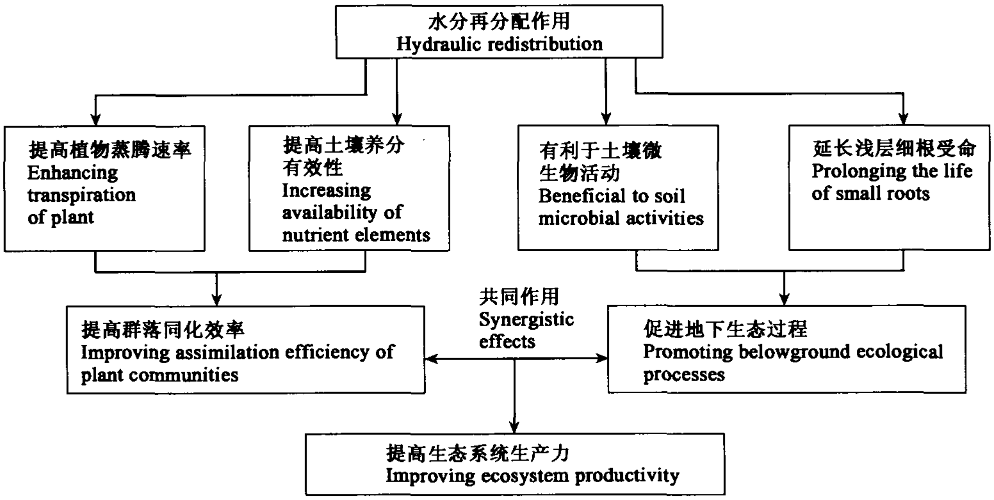

图 2　水分再分配生态学功能的总体关系图

Fig.2　Schematic diagram illustrating the ecological function of hydraulic redistribution

2.2　对植物碳同化的影响

土壤含水量的改变直接影响植物的碳同化速率和蒸腾速率,尤其是在蒸腾强烈的情况下其影响显著。水分再分配作用可以调节不同土层间的土壤含水量,使植物根系相互补偿水分以供给叶片蒸腾耗水。能利用再分配水分的植物通常具有较高的叶片水势、气孔导度和地上生物量等特征。Caldwell & Richards[11] 在对三齿蒿水分再分配作用的研究中发现,如果通过切根阻止了水分再分配作用的发生,将导致蒸腾速率下降 25% ~ 50%,最大气孔导度下降 17% ~ 47%。同时,三齿蒿根系的水分再分配还将降雨均匀地分布在土壤中,延长土壤湿润的时间,这些贮藏在土壤中的水分在干旱期间可使群落冠层蒸腾速率提高 3.5%,最大可达 20.5%[30]。与糖槭(Acer saccharum)相邻的浅根系植物在白天蒸腾消耗的水分中 60%来自糖槭根系水分再分配[34]。具有水分再分配功能的植物根系,处于不同水势的土层中而互相补充供给地上部分的蒸腾耗水需要,可以认为是植物适应环境协同进化的表现。水分再分配作用不仅对具有这种功能的植物本身的蒸腾有促进作用,而且可以促进相邻不具有此功能的浅根系植物的蒸腾,在植物抵抗干旱和提高水分利用效率方面具有重要意义。因而在干旱区植被恢复建设中,应注意将具有水分再分配作用的深根系物种和不具有水分再分配作用的浅根系物种进行合理搭配。

2.3　对土壤养分及微生物的作用

水分再分配作用能使表层土壤含水量增加,因而对植物的水分吸收、养分吸收,植株间的竞争作用,土壤中大量和微量元素的养分有效性有重要的意义。多项研究表明水分再分配作用明显活化了表层土壤中的氮、磷、钾等养分元素的肥效,特别是磷的吸收[14,15,35,36];也促进了上层土壤中硝化和矿化等生化过程[37],并有利于植物从土壤中吸收微量元素[38]。水分再分配可保持上层干燥土壤中细根的活性,延长细根的寿命,以继续从养分丰富的表层土壤中吸收养分,充足的水分也有利于微生物的活动[23,39,40]。然而,水分再分配对影响土壤微生物多样性的维持有多大作用?提高的土壤养分元素的吸收利用对生态系统生产力的贡献有多大?这些方面仍值得深入探讨。

2.4　对植物群落稳定的作用

土壤水分状况是制约植物群落结构与功能的最重要因素之一[41]。在许多生态系统中,深根系与浅根系植物交错分布,共同维持生态系统的稳定性。水分再分配作用是植物的一种生存机制,是深层根系和浅层根系互相协调使植物适应环境的过程[42,43]。当干旱期来临时,浅根系植物所需求的水分需要由深根系植物的水分再分配作用来满足[44]。研究表明,在干旱期的夜间,银桦和赤桉的表层根系均表现为释放水分;而降雨后的夜间,表层根系表现为吸收水分,深层根系则开始释放水分[1,45]。在新热带地区的萨瓦纳群落中, Byrsonima crassa 和 Styrax ferrugineus 的侧根在白天表现为从土壤中吸收水分，而在夜间向土壤中释放水分，主根在24h内匀表现为吸收水分；另一植物种 Dalbergia miscolobium，不论主根还是侧根系，昼夜均表现为从土壤中吸收水分。而 Blepharocalix salicifolius 的细根则昼夜向土壤中释放水分，主根则表现为吸收水分[26]。可见在同一群落中，不同植物种根系水分再分配作用有一定的差异，它们吸收不同来源的水分，它们之间存在一种非常默契的互利共存的水分利用机制，从而维持自然生态系统中物种多样性和群落稳定性。

3 影响水分再分配因子的研究

只有在特定环境条件下，水分再分配作用才可以发生。因此在自然界中，它受到许多因素的限制。主要的限制因子归纳如下：

(1)土壤水分　水分再分配作用依赖于土壤水势差，只有当湿土层和干土层之间存在一定的水势差，水分再分配现象才能发生[31,45]。而土壤水势的变化与土壤温度密切相关，且在干旱年份和湿润年份的变化趋势截然不同[24]。Sakuratani 等人[17]发现在夜间当上层土壤水势降低至 -0.3MPa 时，Sebania rostrata 的根系出现水分再分配作用；而在 Richards&Caldwell 的研究中[10]，当土壤水势低于 -0.5MPa 时，三齿蒿根系才发生水分再分配作用；谷子中的水分再分配作用当土壤水势低于 -10.0MPa 时才可以观测到[46,47]。也有观点认为，尽管水分再分配作用是在土壤干旱条件下发生，但土壤水势不能太低，水势过低时，干土的阻力会限制根系中水分向土壤扩散[47,48]。水分再分配的量与土壤含水量的大小有直接关系，当给予10mm的降水后，魁核桃根系水分再分配的量是蒸腾量的10%～15%；而当降水量增加到22mm时，水分再分配的量是白天蒸腾量的30%～60%[20]。但针对不同类型土壤，水分再分配作用发生的土壤水势或含水量临界值方面仍没有系统的结论，还需进一步探讨。

(2)植物种　在同一生态系统中，不同植物种的水分再分配的量有显著差异。绒毛白蜡(*Fraxinus velutina*)的水分再分配的量为 0～120 $g \cdot h^{-1}$，相同条件下，伴生树种魁核桃的水分再分配量只有 0～18 $g \cdot h^{-1}$[21]。根系形态[49,50]和根系在土壤中的分布[51]也影响水分再分配作用的数量和持续时间。在水平方向上水分再分配的量依赖于根系密度、动力大小、根系表皮对水分穿透的阻力和物质积累[11]。同一植物种在根系密集的情况下，水分再分配将使地上植被蒸腾速率增大，但如果土壤的透水性较高，根系分布比较均匀，根系的导水性较低，水分再分配对蒸腾速率的影响则较小。植株的年龄也会影响水分再分配作用的发生及大小[52]。根系的深度影响水分提升的速率和强度[53]；根系类型(主根侧根都发达或主根发达侧根不发达或侧根发达主根不发达)影响水分再分配作用的发生，如中雨过后，魁核桃的根系表现出水分再分配作用，但将所有的表层侧根损伤后，水分再分配现象突然停止。由此可见，植物种间根系功能的差异对水分再分配作用有显著影响。然而，到目前为止，关于根系特性及其在土层中的分布对水分再分配影响的研究还仅是凤毛麟角。

(3)土壤结构　在栗钙土分布的地区，土壤中容易形成钙积层。部分植物的根系可以穿透钙积层到土壤深层，而大部分植物的根系分布在钙积层以上。这就很容易造成钙积层上、下土壤水势差，水分再分配作用极易发生[34]。干旱、半干旱地区的沙质土壤的毛细管作用较弱，而大多数植物根系分布较深[54～58]，也有利于水分再分配作用发生。但关于土壤特性对根系水分再分配作用影响的研究还较少，这也将是今后水分再分配作用研究的方向之一。

另外，除以上几种主要因子外，还有其他因子在一定程度上影响着水分再分配的发生。根据最优理论[59]，一种植物付出成本从土壤中吸收水分，又释放到土壤中，为其他植物所利用，这种行为必然有一定的利益回报。也就是说这两种植物之间有进化上的协同互利性。因此从植物进化的角度来阐述水分再分配作用也是未来这一领域研究的重要课题。

4 水分再分配的研究方法

水分再分配的测定从实验室发展到现在的野外直接测定，在技术上取得了很大的进步，目前关于水分再分配的研究方法已基本成熟，也得到广大研究者的认可。主要有3种方法：

(1)利用茎流法(sapflow)的原理[60]，在植物的侧根和主根上分别安装测定茎流的加热和对照探头。由于

根系中液流运动的双向性,与茎杆液流测定不同的是,测定根系茎流量时需要一个加热探头和上下两个对照探头,通过测定加热探头和对照探头的温度差,计算液流速度,从而计算出一定时间内的总液流量[61]。通常使用的有热脉冲法(heat pulse)[53,62,63]和热扩散法(heat dissipation)[64,65]。由于热扩散法的操作简便、成本低,在近几年的研究中得到广泛应用[18,66,67]。

(2)利用同位素示踪法(isotope tracing method),用重水(D_2O)直接浇灌植物的部分根系,然后测定其它根系或相邻植物的根系片断、地上枝条、不同空间土壤中D含量的比率[68,11],从而定量计算水分再分配的量,是目前比较常用的方法之一。并且现在越来越多的研究将同位素示踪法和茎流法结合使用,测量植物根系的资源获取和利用模式[13]。

(3)测量根系周围土壤含水量和水势变化[32,40,46]或直接测定土壤含水量的昼夜变化[69],这种方法只能定性描述某种植物是否具有水分再分配作用,估算水分再分配的范围及水量,结果不够准确;因为在实际操作中很难区分出所测的土壤含水量是真正的土壤含水量,还是根系含水量[49]。如果能结合同位素示踪法[39],结果将更加有说服力。

5 研究展望

阐明植物种群间对水资源的竞争和共享机制是加速生态环境建设、促进生物多样性保护的重要前提。植物根系对土壤水分再分配研究在近二十多年中取得了突破性进展。大量研究验证了水分再分配作用在不同类型生态系统中的存在,并探讨了这一过程的生理学机制及该过程对植被群落水分平衡的影响。但水分再分配的量一直是个受争议的问题,这方面的争议或许是由于研究方法的不同而导致研究结果的差异,或许是在不同生境下水分再分配作用受植被自然演替和进化的影响所致。回顾水分再分配研究进展及其现状,认为该领域研究在未来的发展方向应注重:(1)在干旱环境下的生态系统中,阐明一些浅根系植物对深根系植物水分再分配作用的依赖性与依赖程度;(2)从植物进化的角度来阐述水分再分配作用的生物学基础和意义;(3)水分再分配对土壤微生物活性的影响;(4)采用多个方法结合使用,扩展研究区域,特别是比较研究不同生境下和不同植被类型间水分再分配作用的差异与生态学功能,探讨不同生态系统类型中诱导水分再分配作用发生的土壤水势或含水量临界值的大小。

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