根-土界面水分再分配研究现状与展望

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摘要：对根-土界面水分再分配的研究背景（概念、发现及证据）、普遍性与再分配的水量及其生理生态学意义（对相邻植物利用水分、根际活动、土壤-植物-大气系统水分传输和根系可塑性发育的促进效应）等进行了深入论述，对水分再分配的认识和研究方法进行了探讨，并对未来的相关研究进行了展望。

关键词：根-土界面；水分再分配；水分提升；生理生态学意义；现状；展望

The present situation and prospect of researches on hydraulic redistribution between the interface of root and soil

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Abstract: Based on our own research work, the following aspects of hydraulic redistribution (HR) between the interface of roots and soil are discussed.

HR usually occurs at night when transpiration has diminished sufficiently to allow the roots' water potential to exceed the drier soil water potential (Ψ_s) in the soil profile. Although the direction of water movement in the process of root HR is typically upward, towards drier, more shallow soil layers, recent measurements of sap flow in taproots and lateral roots of trees have demonstrated that roots can also redistribute water either downward or laterally from moist surface soils to drier regions of soil. "Hydraulic redistribution" has been proposed as a more comprehensive term than "hydraulic lift" to describe this phenomenon in considering that it can be bi-directional and is apparently passive. Water released from roots into drier soil layers may be reabsorbed when transpiration exceeds water up-take by deep roots only. Redistribution of soil water through root systems has been demonstrated in greenhouses, laboratories and field experiments. The first strong evidence for HL occurring in the field was observation of diurnal fluctuations in Ψ_s that gradually increased at night and sharply declined during the day, associated with the shrub *Artemisia tridentata*. Our own observations of HL in the half-shrub *Gutierrezia sarothrae* with a shallow roots system indicates that the HL improved water uptake during the day when evaporation is high and less water is available in the topsoil.

So far HR has been reported in forty -three woody and sixteen herbaceous species distributed over different climatic regions, which indicates that the phenomenon of HR is not restricted to only arid and semiarid environments.

The quantities of water redistributed by roots were affected by many factors, such as daily evapotranspiration (*ET*) and root length densities. A considerable amount of water is lifted by roots each night. Estimates of hydraulically lifted water range from 14% of daily ET for the suffrutescent shrub *G. sarothrae* to roughly one-third of daily ET for the shrub *A. tridentata*.

From 3% to 60% of the redistributed water can be utilized by neighboring plants, as many of these species are in close proximity to one another. In addition, the reoccurrence of HR over significant periods of time in dry upper soil layers has

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several implications for rhizosphere processes and plant nutrient acquisition. These include prolonging the activity and life span of fine roots, improving nutrient ion mobility, and potentially smoothing spatial heterogeneity of nutrients. HR can facilitate water movement in the soil-plant-atmosphere system by improving ET for plants. The root plasticitally adapting itself towards very dry soil or sand below its depth might be facilitated by the water transfer from the moist surface soil to dry deep soil following a precipitation event. The process of water moving from upper to lower drier soil layers along an inverted water potential gradient in the soil profile was termed "inverse hydraulic lift".

Although much progress in research on HR has been made, there are still some contradicting points of views about HR. There are a few reports on alfalfa and cotton which show that roots of some species largely prevent reverse water flow. Some studies have concluded that the quantities of water redistributed by this process are minute.

Three methods to measure HR were tested, but measuring the changes of soil water content and soil water potential(Ψ_s) around plant rhizosphere proved to be the most convenient. In addition, the reduction in transpiration can serve as an indirect measurement of the quantity of hydraulically lifted water.

Though several challenging studies on HR have been conducted, further investigation into the effects of HL on the water balance of neighboring plants and the influence of HR on water movement in the soil-plant-atmosphere system needs to be done.

We propose further studies on HR based on the above discussion: the magnitude of HR in perennial and annual crop systems is still not well known, but if HR is present, it would have implications for irrigation, fertilization practices, and intercropping. Further field experimentation to investigate the contribution of HR in community level phenomena such as plant population dynamics, facilitation of neighboring species, ET, nutrient acquisition, and biogeochemical processes needs to be done. Additionally, further research work will focus on species-specific, tree-size specific, seasonal, and substrate-related differences in the magnitude of HR of soil water across climatic gradients.

Key words: interface of root and soil; hydraulic redistribution; hydraulic lift; significance of physiological ecology; present situation; prospect

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根-土界面水分再分配(hydraulic redistribution)能促进发生水分再分配植物本身及其相邻植物的水分平衡[1]。由于根系释放到干燥土壤中的水分在蒸腾超过深层根系吸收水分的情形下能被重新利用[2],水分再分配能促进上层土壤中细根对养分的吸收[3],有助于维持干燥土壤中菌根及固氮菌的活性[4]。目前根-土界面水分再分配已成为国际植物生理生态学术界十分关注的研究领域之一[3,5,6],开展了相关研究并取得了一定进展,但也存在一些争议[7~10]。本文将对根-土界面水分再分配进行探讨,并对该领域以后的研究作出展望。

1　根-土界面水分再分配的研究背景

1.1　水分再分配的概念

水分再分配的概念源于水分提升。水分提升是当夜间蒸腾降低后根系将深层土壤水分向干燥上层提升的水分运动过程[2,11,12]。由于水分通常是向表层的干燥土层运动,Richards 和 Caldwell[2]用"hydraulic lift"描述这一过程。根-土界面水分再分配通常发生在蒸腾减小到足以使根系水势超过干燥土壤水势(Ψ_s)的夜间[7]。根系再分配所释放的水分能被同种或其它种植物重新吸收利用[2,11]。一般认为水分被提升的方向是从湿润的深层土壤到干燥的浅层土壤。但最近对几种乔木主根及侧根液流(sap flow)的研究表明,只要土壤水势存在一定梯度[4],根系也能对土壤水分在垂直方向进行向下(从湿润表土层到深层)[13~15]或在水平方向进行横向的水分再分配[13,16~19]。由于水分再分配是被动和双向的,Burgess[13]认为"水分再分配"比"水分提升"能更好地表述根-土界面这一水分传输现象。

1.2　水分再分配的发现及其证据

根系水分再分配现象在温室、实验室及野外条件下均有发现[20],其证据是当蒸腾降低到木质部水势高于干燥土壤水势时,水分从根系到土壤发生被动运动[1,3,20,21]。在温室,分根(split-root)系统土壤水分的变化为根系水分再分配提供了证据[22]。在实验室条件下,Breazeale[23,24]首次观察到生长在凋萎含水率以下土壤中小麦幼苗的根系如果能接触到水源,则上层干燥土壤能被湿润。后来 Schippers[25]发现在蒸腾减弱时豆科植物下胚轴中有水分向上的传输现象。Hansen[26]发现水分可以从一株植物的根系转运到另一株植物的根系。McCully[27]观察到单子叶植物有水分提升现象。在野外条件下,水分提升的最初发现来自土壤水势的昼夜波动,即 Ψ_s 在夜间缓慢上升,而在白天快速下降[1,2,5,28,29]。Richards 和 Caldwell[2]发现深根系灌木三齿蒿 *Artemisia* *tridentata*（根深2.2m）的Ψ_s在昼夜尺度上波动（夜间升高；白天降低），*A. tridentata*在相当干燥的土壤（−5.0 MPa）仍能进行持续的水分提升，首次有力证明野外条件下植物存在水分提升现象。随后他们[5]又发现如果在白天将*A. tridentata*用塑料袋罩住以阻止蒸腾，Ψ_s在2d中持续上升直到*A. tridentata*重新接受日照。相反，如果在夜间照射*A. tridentata*，则Ψ_s的增高受到抑制。表明Ψ_s的升高与蒸腾被抑制有关。金雀花拳参（*Gutierrezia sarothrae* Britt et Rusgy）是北美的一种浅根系半灌木。在许多草本植物处于休眠的干旱夏季，发现*G. sarothrae*依然保持绿色[30,31]，而且它的气孔保持开张状态。将*G. sarothrae*盆栽，再将盆埋在野外试验地（其根系通过盆底部的孔能延伸到盆下的土壤），发现盆中土壤水分含量有增加现象。如果在白天遮盖*G. sarothrae*抑制蒸腾超过3h，则土壤湿度增加，证明蒸腾减弱可导致*G. sarothrae*提升水分。*G. sarothrae*对干旱胁迫有较强的适应性，在土壤水势为−3.4MPa（叶水势为−8.19MPa）时它仍有净光合积累[32]。对*G. sarothrae*水分提升发现的重要性在于首次证明浅根系植物也能进行水分提升。

2　根-土界面水分再分配的普遍性

迄今已发现[1,3,5,11,20,30,33~41]近60种植物（43种木本，16种草本）有水分再分配现象（表1）。这些生活型不同的植物分别属于不同的科属，分布于不同的地理气候区域，可以推测水分再分配现象是广泛存在的[3,7,42]。

表1　一些具有水分再分配现象的植物

Table 1　Some species exhibiting hydraulic redistribution

科 Family	属 Genus	种 Species	生活型 Life form	参考文献 Reference
松科 Pinaceae	松属 *Pinus*	*Pinus ponderosa* Dougl. ex Laws	乔木 Tree	[7]
	黄杉属 *Pseudotsuga*	*Pseudotsuga menziesii* (Mirb.)Franco	乔木 Tree	[7]
柏科 Cupressaceae	圆柏属 *Sabina*	沙地柏（叉子圆柏）*Sabina vulgaris* Ant.	灌木 Shrub	[35]
壳斗科 Fagaceae	栎属 *Quercus*	蓝栎 *Quercus douglasii* Hook. et Arn.	乔木 Tree	[20]
豆科 Leguminosae	苜蓿属 *Medicago*	紫花苜蓿 *Medicago sativa* L.	多年生草本①	[11]
桃金娘科 Myrtaceae	桉属 *Eucalyptus*	*Eucalyptus viminalis*	乔木 Tree	[3]
蒺藜科 Zygophyllaceae	*Larrea*	墨西哥三齿拉瑞阿 *Larrea tridentata*	灌木 Shrub	[3]
仙人掌科 Cactaceae	仙人掌属 *Opuntia*	印榕仙人掌 Opuntia ficus-indica (L.)Mill.	灌木 Shrub	[37]
茄科 Solanaceae	番茄属 *Lycopersicon*	番茄 *Lycopersicon esculentum* Mill.	1年生草本②	[3]
菊科 Compositae	蒿属 *Artemisia*	黑沙蒿 *Artemisia ordosica* Kraschen.	半灌木③	[35]
	蒿属 *Artemisia*	三齿蒿 *Artemisia tridentata*	灌木 Shrub	[2,42]
	Guttierrezia	金雀花拳参 *Gutierrezia sarothrae*	半灌木	[30,31]
禾本科 Gramineae	玉蜀黍属 *Zea*	玉米 *Zea mays* L.	1年生草本	[3]
	狗牙根属 *Cynodon*	狗牙根 *Cynodon dactylon* (L.)Pars.	多年生草本	[3]
	冰草属 *Agropyron*	沙生冰草 *Agropyron* desertorum (Fisch.)Gaertn.	多年生草本	[3]
	狗尾草属 *Setaria*	谷子（Millet）*Setaria italica* (L.)Beauv.	1年生草本	[38~41]

① Perennial herb；② Annual herb；③ Subshrub

3　根-土界面再分配的水量

根系再分配水量的多少受多种因素影响，如向上提升的水量与蒸发蒸腾（*ET*）相关[3]，而水平方向再分配的水量则主要决定于根长密度[7]。多数研究[2,3,7,28,30]表明，根系在根-土界面再分配的水量相当可观，如*A. tridentata*提升的水量相当于它*ET*的1/3[2]。Brooks和Meinzer[7]在北美用氢同位素法测得1种冷杉（*Pseudotsuga menziesii*（Mirb.）Franco）和1种重松（*Pinus ponderosa* Dougl. ex Laws）在8月份2m深土壤范围内根系提升的水量占其日总利用水量的比例分别是35%和28%。Emerman和Dawson[28]发现成熟糖槭（*Acer saccharum*）夜间平均提升的水量是102±54 L，相当于其日总吸收水量的25%。Ludwig和Dawson[43]估计1棵*Acacia tortilis* 1夜提升的水量约为70～235 L。作者[30,44]估计*G. sarothrae*提升的水量相当于它*ET*的14%。

4　根-土界面水分再分配的生理生态学意义

4.1　促进相邻植物利用水分

荒漠生态系统中植物对水分和养分的竞争在何种程度上影响群落的结构和动态，仍在争议之中[45~47]。温带荒漠和冷荒漠植物存在激烈的种内和种间水分竞争[48,49]，而且对水分竞争的强度激烈于对养分（N）的竞争[12,45]。土壤在遭受长期干旱后，只有深层的水分能被植物利用[50]。由于大部分植物的根长密度随土壤深度指数式减少[51]，因而即使植物根系能够接近深层土壤的水分，在土壤深层较低的根长密度却制约了根系对水分的吸收。因此，水分胁迫是限制荒漠植物生长代谢的主要因子[52,53]。根-土界面水分再分配对干旱系统水分胁迫的缓解提供了一种途径。如发现[2,5]深根系植物*A. tridentata*能从湿润深层土壤吸收并提升水分释放到干燥表层土壤，所提升的水分可被根深1.3m的沙生冰草（*Agropyron desertorun*（Fisch.）Gaertn）再吸收。

实验表明[33]，水分再分配不仅对再分配水分植物的本身，而且对相邻植物均有助于实现水分平衡。据报道[1]林木下层种及小幼苗可能受益于再分配水分。相邻植物利用再分配水分的量存在较大潜力[5]，据研究[1]在植物个体彼此相当靠近的情况下相邻植物利用提升水分的比例，其范围在 3%～60%。以上事实说明植物-植物之间不总存在负的相互作用（如对水分竞争等），从而支持了植物个体相互促进作用是影响植物群落动态变化重要生态过程的观点[42,54,55]。

4.2 促进根际活动

养分通常富集在土壤上层，水分依赖的分解、矿化和氮硝化等生物地球化学循环过程在土壤上层有较高的活性[56]。然而，干旱胁迫下土壤上层中离子的移动将变慢。水分再分配能通过促进细根对养分的吸收，从而提高土壤养分的有效性[3,57]。同时，水分再分配能延长细根和根毛的活动并提高与其相伴生的微生物（如菌根）的活性[58]。*A. tridentata* 的根系在相当程度的干旱胁迫下仍能保持吸收养分的能力，似与其提升水分有关[59]。水分提升有利于糖槭幼苗碳固定，促进根及枝条的生长，这种促进效应与根际高的 NH_4^+、可溶性有机氮及 K^+ 富集有关[2]。

4.3 促进土壤-植物-大气系统的水分传输

在景观尺度下，深根系植物通过水分提升，促进与其相伴生的浅根系植物的 *ET*。在开花期对玉米耐干旱种（TAES176 和 P3223）和对干旱敏感种（P3225）水分提升进行的研究表明，耐干旱种土壤体积水含量（ϕ_v）有增加现象，而干旱敏感种则没有 ϕ_v 的增加[50]。提示耐干旱种由于水分提升能够避免土壤水分的消耗。本试验首次揭示了中午遮荫后由于水分提升导致蒸腾的激增[60]。

在上层土壤干燥时，水分提升对 *ET* 的直接贡献决定于土壤在垂直方向的湿度和根长密度的分布。在蒸发需求低时，深根系获得的水分能够满足蒸腾耗水；在蒸发需求高时，夜间获得的和提升的水分有助于支持植物 24h 的蒸腾需水。水分提升通过提高植物个体的水分利用效率，促进土壤-植物-大气系统水分的传输[1]。

4.4 促进根系的可塑性发育

虽然一般认为[51]根系生物量的大部分出现在土壤深度 50cm 的范围之内，但全球陆地生态系统中根系在地下垂直分布的最深记录是 68m（在干旱的 Kalahari 沙漠）[61,62]。在 Kalahari 沙漠，少于 300mm 的降水量最多能湿润数米深的土壤，根系必须在湿润界面以下的干燥土壤中向下生长延长数十米才能接触到土壤深层的水分。在如此干旱的沙土中促进根生长的机制是通过根系从降水后湿润表层土壤到深层土壤进行水分转移。在野外条件下用氢同位素示踪法证明水分有从湿润上层到干燥下层的逆向提升（inverse hydraulic lift）现象。水分逆向提升是当 Ψ_s 在土壤深层（如湿润锋下的干燥土层）比土壤上层更负时（如降雨后），将土壤上层的水分逆向提升到土壤深层的过程[17]。

在干旱陆地生态系统，资源（养分，尤其是水分）以脉冲方式供应，即在大的降雨后，植物经历一个资源供应量相对高却短暂的资源供应期，接下来是一个资源匮乏的高胁迫脉冲间歇期[6]。逆向水分提升使植物有效利用脉冲式资源（尤其是降水）成为可能[13]。据 Smith[15]估计，通过侧根向土壤深层逆向提升的水分可占植物日吸收水分的 26%，对土壤水分平衡产生实质性影响。因此，水分逆向提升使植物能够快速利用聚集在土壤表层的降水，是植物对干旱胁迫的一种适应性对策。在水分胁迫生态系统中根系具有向下生长穿越干土层的能力，逆向水分提升允许根系穿过干土层[13]，可能就是根在土壤深层发生的机制[17]。比如，室内研究发现生长于湿润浅层土壤中金合欢属的一种植物（*Acacia greggii*）其根系能穿过石蜡层而向深层干燥土壤生长。根系在深层干燥土壤中进一步生长的结果使深层干土中的水分含量有所增加，表明 *A. greggii* 根系将湿润上层土壤的水分向干燥下层土壤进行了逆向转运（水分逆向提升），而这种水分逆向提升反过来促进 *A. greggii* 根系的生长发育[3]。

5 讨论

对水分再分配的争议　尽管大多数研究者[3,7,63]的研究均证明许多植物在根-土界面能再分配相当量的水分，对缓解相邻植物的干旱胁迫有实际意义；但需要特别关注相反的观点及其实验研究结果，因为目前对水分再分配是否普遍存在及其意义仍然在争议之中[7]。比如，有报道认为苜蓿[9]和棉花[10]一些种的根系阻止水分逆向流动，使这些种不能发生水分提升；而且再分配水分的量也微不足道[8]。对水分逆向提升也有不同认识，如 Burgess[64]就认为水分逆向提升不可能发生在水分传导率高的沙土中，因为沙土在降雨数小时之后不能形成逆向水势梯度（即上层 Ψ_s>下层 Ψ_s）。也有研究[65]未能证明水分提升有助于降低土壤上层养分空间异质性。Caldwell[66]在一次试验中未发现与灌木 *A. tridentata* 相邻的丛生沙生冰草 *A. desertorum* 能利用 *A. tridentata* 提升的水分，究其原因是由于 *A. desertorum* 有足够深的根系而且其自身能提升水分，在这种情形之下禾草对灌木补偿水分的依赖性变得很小。

水分再分配的研究方法及其探讨　目前研究水分再分配的方法主要有 3 种：①测定根系周围土壤含水量和土壤水势的变化[30,37,67]；②用氢同位素法测定植株根幅区不同空间潜水和土壤水中氢稳定同位素的比率[7,17,37]；③ 用微气象能量平衡法测定植株的水分再分配[37]。限于条件，目前根-土界面水分再分配测定多采用第 1 种方法，以下就第 1 种方法着重进行探讨。

根际土壤水分含量可用烘干法、中子仪或 TDR 测定[37,67]。土壤水势可用张力计、电阻块和土壤热电偶湿度计测定[67]。张力

计和电阻块主要测定土壤基质势。张力计能有效测定的土壤水势范围在－0.08～0 MPa之间，电阻块适于测<－0.05 MPa的土壤水势，因而张力计与电阻块可以互为补充。总土壤水势（基质势＋渗透势）可用土壤热电偶湿度计测定，需要注意热电偶湿度计对于干燥土壤（<－0.2 MPa）较为有效。

曾经观察到数种植物的根在水分胁迫下发生萎缩，使根系与土壤之间形成空气间隙，增加了水分运动的阻力，使根系中散失的水分减少[68,69]。根系的这种形态变化在短期内将导致根-土界面水分再分配的减弱，也增加了测定水分再分配的难度[3]。在用TDR测定根际土壤含水量时，由于野外条件下TDR的精确性在于根系与TDR探头接触的紧密程度及根系不同部分组织水分含量对TDR读数影响的敏感程度，因此在使用TDR时应注意它所反映的水分信息其中多少来自于根系，多少来自于土壤[2,3,33]。

实验数据和模型研究均表明，影响水分提升最主要的因素是白天土壤水分的消耗，因为白天土壤水分的消耗能造成驱动次日夜间补充水分的土壤水势梯度。土壤水分的消耗受土壤水分含量变化的影响。因此，除了需要准确区分根系提升的水量与土壤毛管上升的水量外[37]，如何将由降雨引起土壤水分的增加与由降低的*ET*引起土壤水分的增加相区别开来，是一个需要进一步探讨的问题[3]。

作为一种辅助方法，蒸腾降低可以作为一个定量测定根-土界面水分再分配的间接指标[3]。试验依据是在夜间如果给*A. tridentata*光照，通过迫使其气孔开张而阻止发生水分提升（Ψ_s停止升高），发现次日*A. tridentata*整株的蒸腾比正常条件下整株的蒸腾减少25%～50%。如果以后给*A. tridentata*正常的黑夜（停止光照）以重新进行水分提升，次日的蒸腾将恢复到期望的水平。由于夜间光照阻遏了水分提升的发生，植物在次日将得不到用于蒸腾提升的水分。

目前根-土界面水分再分配研究取得了一定进展，但在下列诸方面的研究尚有待于加强：

（1）不同植物的细根（直径<2mm）对小-中等规模降水形成的异质性土壤水分采取不同的觅养策略（foraging strategies）[70,71]。沙漠异质性土壤水分使灌木根系（特别是细根）的生长产生差异，从而导致根系在空间和时间上的分隔，或"生态位分离（niche separation）"，结果在资源相对贫乏的条件下相邻灌木能够得以共存[72]。如北美莫哈维（Mojave）沙漠的4种灌木*Ephedra nevadensis*、*Lycium pallidum*、*Ambrosia dumosa*和*Larrea tridentate*，其吸收水分和养分最为活跃的外周细根的生态位（niche）发生分离，对土壤湿度相异的微生境（microsite）采取不同的觅食策略，以获取自身所需的最大资源[71]。如果将细根的觅养策略与根系可塑性、水分再分配进行关联研究，有可能是阐明不同种灌木共存机制的有效途径。

（2）在荒漠系统灌木再分配水分的时间也值得注意。如果灌木提升水分在季节上太迟，则它所提升的水分不易为草本植物所利用。这需要研究环境因素对水分提升的调控作用，但目前对此知之甚少[20]。

（3）虽然植物对生态系统水分平衡的影响日益受到重视[61]，但水分提升对土壤-植物-大气连续体水分传输的贡献较少受到注意[5,33]。可能原因是尽管目前发现近60种植物有水分再分配现象，但尚不足以预测水分再分配对生态系统水分变化的影响趋势[20]。

（4）由于植物的结构和功能高度复杂，而目前直接测定水分流动驱动力的恰当技术有限[73]，因此迄今对与重力反向的水分提升发生的机理远未搞清楚[73～75]。

越来越多的实验证据表明水分再分配是植物根系的一种普遍现象。对多年生和1年生作物水分提升的研究在作物灌溉、施肥及套种等方面均有指导意义。因此，有必要在野外条件下进一步探索水分再分配对植物蒸发蒸腾、获得养分、促进相邻植物水分利用以及对生物地球化学过程的影响，并探讨水分提升对植物种群动态甚至对群落和生态系统稳定性的影响等[3]。将来的相关研究应该注意在不同气候梯度下，探讨水分再分配与种特异性、植物个体（等级）大小、季节变化以及土壤基质特性等的相关性[7]。今后需要进一步深入开展根-土界面水分再分配的机理研究[74～78]。

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