

木质部导管空穴化研究中的几个热点问题

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摘要 导管的空穴化和栓塞化现象是目前国际上水分生理生态研究的一个热点。该文对导管空穴化和栓塞化研究中出现的几个热点问题进行了概括和总结。1)在研究导管空穴化的实验手段上,超声波传感器探测法具有一定的局限性;目前至少存在4种可能的原因来解释木质部压力探针法(XPP)和压力室法所测得的导管水柱张力不一致的现象,近来出现的核磁共振成像法可以进行导管空穴化的无损检测。2)导管解剖学特征与形成空穴的可能性之间的关系可能与树种相关。3)导管空穴化引起气孔关闭的作用机制目前还不太清楚。4)植物防止空穴化产生的能力与适应干旱能力之间的关系还没有定论。5)单独用根压来解释空穴化导管的重新注水机制是不全面的,还存在其它重新注水机制。

关键词 木质部导管/管胞 空穴化 栓塞化

SEVERAL CONTROVERSIAL VIEWPOINTS IN STUDYING THE CAVITATION OF XYLEM VESSELS

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Abstract Xylem cavitation/embolism, a topic that has received extensive attention, is generally seen as a potential threat for living plants because it lowers the conductivity of the axial water-conducting system. In this paper, several controversial viewpoints about studying the cavitation of xylem vessels were listed, and current efforts and advances in this field were reviewed. Ultrasonic sensors can be used to directly detect the occurrence of xylem cavitation; however, this method has some limitations. Almost all current methods used to study xylem cavitation/embolism, except for the ultrasonic sensor, requires destructive sampling. Recently, a non-invasive method based on high-resolution magnetic resonance imaging technique was introduced. Large discrepancies existed between the results of pressure chamber tests and xylem pressure probe, both of which were used to detect the tension of xylem vessels. There are at least four possible reasons to explain this discrepancy. The relationship between the anatomical characteristics and the ability of xylem vessel to resist cavitation is complex and it may show a species-specific response. The underlying mechanism of stomatal closure induced by xylem cavitation is still unclear. There is no general conclusion about the relationship between xylem vessel resistance to cavitation and the capacity of plants to adapt to water-stress. What about the embolized vessels refilled by water? It is risky to attribute this process solely to the mechanism of root pressure, because there is now some evidence that other mechanisms are involved. In general, further efforts are needed to clarify and resolve these uncertainties and discrepancies in order for us to better understand the cavitation of xylem vessels and the water-conducting system of plants.

Key words Review, Xylem vessels, Cavitation, Embolism

水分在植物体内的传输主要通过木质部的管道系统(被子植物的导管和裸子植物的管胞)。目前普遍认为水分运输的内聚力-张力学说可以解释水分向上传输的机理。然而,导管的空穴化和栓塞化现象却对该学说提出了挑战。

一般而言,当导管水势降低时,会造成导管(包括根、茎和叶脉)水柱张力变大,如果超过一定的范

围(如导管水势降低到 -0.8 到 -1 Mpa以下),会在导管内形成空穴,空穴的形成导致该条输水通道栓塞化从而失去运输水分的功能(Tyree & Sperry, 1989a)。栓塞化会导致活性导管数量减少(Edwards & Jarvis, 1982),从而使木质部导管水分导度下降,进而影响到叶片气孔的导度,造成落叶和植株缺水死亡。因此,这种空穴的形成可能极大地影响植物对

水分胁迫的适应能力(Tyree & Sperry, 1989a)。当叶片水势恢复正常后,这种空穴化现象逐渐消失,栓塞的导管开始修复并重新开始运输水分。

导管的空穴化形成的原因以及这种现象与植物对水分胁迫的适应能力之间的关系是十分复杂的。导管空穴化和栓塞化现象是目前植物水分生理生态研究的一个热点问题。

1 空穴化现象的检测

空穴化会导致液体张力的迅速松弛,产生了声波发射(Acoustic emissions, AEs)(Pena & Grace, 1986)。AEs可以被高频率的声波传感器和放大器检测到。如蓖麻(*Ricinus*)叶片在萎蔫时产生了3 000 Hz AEs。在叶柄处加上一滴水,可以减缓或停止 AEs的产生。

Tyree等(Tyree & Dixon, 1983; Tyree *et al.*, 1984; Tyree & Sperry, 1989b)认为在张力的作用下固体和液体断裂时,会在裂缝附近产生快速的张力松弛,并形成频率范围很宽的 AEs(50 Hz ~ 1 000 KHz)信号。因此对于树干而言,只要产生固体或液体的断裂,都会产生 AEs。对于阔叶树,在大部分水分传输能力丧失时仍会产生 AEs,这可能是由于木质纤维、薄壁细胞和射线细胞产生的空穴化所致,因此,由 AEs 大小可能不能推断什么类型的细胞产生了空穴化现象(Tyree *et al.*, 1984)。如果细胞壁为刚性细胞壁,则一个 AEs 的产生对应于一次空穴化事件。但是由于信号衰减的原因,可能大部分的 AEs 不能被检测到(Sandford & Grace, 1985)。此外,由于钟效应(当一次 AEs 事件撞击到传感器时,传感器会发出频率幅度很宽的信号),AEs 的频率组成含有很复杂的信息。而且,超声波传感器的灵敏度针对不同频率的响应不同(Borghetti *et al.*, 1989)。因此,目前超声波传感器主要用于针叶树和环孔树种的空穴化检测,并最好结合脆弱性曲线进行分析^①。

目前普遍采用以下3种方法来研究导管的空穴化和栓塞化现象。1)采用高压注入溶液方式(如175 kPa)去除栓塞化现象(Sperry *et al.*, 1988a),测量去除和未去除栓塞化的木质部导管的水分传输能力差异,这样就可以测量所有空穴化产生的累计效应(Sperry *et al.*, 1987; Cochard *et al.*, 1992)。2)利用外界注射空气的方法、离心方法和电子显微镜法可以研究这种气泡的产生机理以及重新注水的机制

(Cochard *et al.*, 1992; 2000; Alder *et al.*, 1997; Canny, 1997; Cochard, 2002)。3)用某些染料(如番红精, Sperry & Tyree, 1990)对木质部进行染色,由于空穴化的导管不会被染上色,因此可以测量空穴化导管所占木质部面积大小(Phillips *et al.*, 2001)。然而以上这3种方法均为破坏性采样方法, Holbrook等(2001)报道了用核磁共振成像法研究自然状态下葡萄茎的空穴化和栓塞化修复现象,精确地探知了干旱处理时间内产生的空穴化的导管数量以及空穴化的导管重新注水的过程,取得了一些很有意思的结果。

木质部压力探针法(Xylem pressure probe, XPP)(Zimmermann & Steudle, 1978)压力室法和外界注射空气的方法(Alder *et al.*, 1997)可以用来探测导管的水柱张力。然而, XPP 检测到的导管水柱张力总是不低于-0.5 ~ -1.0 MPa(Balling & Aimmermann, 1990; Sperry & Pockman, 1993; Tyree, 1997; Wei *et al.*, 1999)。而压力室法可以检测到-10 MPa以下的水柱张力(Tyree, 1998)。在水分胁迫过程中, XPP 法测定的木质部水势上升而压力室法测定的水势下降,二者所测定的结果出现不一致。产生这种现象的可能原因之一是 XPP 测定的是单一的导管水柱张力,而压力室测定的是全部导管的一种平均化的结果(Zimmermann *et al.*, 1993);第二个原因可能是压力室法需要过高的压力去克服导管水分运输中产生的流体阻力(Balling & Aimmermann, 1990);第三个原因可能是 XPP 法主要用来测定叶片和小叶柄的导管水柱张力,可能光合产物的渗透势调节对导管水柱张力产生了影响(Melcher *et al.*, 2001);第四个原因也有可能是 XPP 法的装置设计上的问题(Wei *et al.*, 2001)。XPP 法所得的实验结果在一定条件下并不反对水分运输的内聚力-张力学说。

2 导管形成空穴的方式

当导管内负水压克服了导管纹孔膜空气-水界面的毛细管拉力后,充水的导管内出现一个小的气泡,这种小气泡会迅速扩大并导致导管栓塞,失去运输水分的功能。Crombie等(1985)首先提出相邻的空穴化导管内的空气通过导管间的纹孔膜进入非空穴化的导管内,这种空穴化的形成方式称为“气穴形成”(Air seeding)。目前认为“气穴形成”有4种模式(Tyree, 1997),这4种方式分别为:气泡从纹孔处进

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入导管形成空穴;驻留在导管内疏水区域的小气泡膨胀形成空穴;液体流动过程中自然发生的微小气核膨胀形成空穴;以及导管壁上微小气核与疏水区脱离形成空穴。“气穴形成”模式为许多实验所证明,如葡萄(*Vitis*)(Sperry *et al.*, 1988a)、红树(*Rhizophoraceae*)(Sperry *et al.*, 1988b)、泥炭藓(*Sphagnum*)(Lewis, 1988)、几种裸子植物(香脂冷杉 *Abies balsamea*、红云杉 *Picea rubens*、北美圆柏 *Juniperus virginiana*)(Sperry & Tyree, 1990)、两种丛林灌木(Jarbeau *et al.*, 1995)等。

3 影响导管空穴形成的因素

目前认为导管直径的大小与形成空穴的可能性之间的关系可能与树种相关。对于某些树种,导管直径越大越容易形成空穴(Salleo & Lo-Gullo, 1989; Hargrave *et al.*, 1994; Pockmen & Sperry, 1997; Harvey & van den Driessche, 1997; Sperry & Ikeda, 1997; Harvey & van den Driessche, 1999; Linton *et al.*, 1998);而另外一些树种导管直径与形成空穴的可能性之间并不相关(Cochard, 1992; Sperry & Saliendra, 1994; Alder *et al.*, 1996; Hacke & Sauter, 1996)。此外其它因素还包括:导管纹孔膜的尺寸(Jarbeau *et al.*, 1995)、纹孔膜的弹性以及木材密度等解剖学特征(Hacke *et al.*, 2001b)。如美国生长的一种杨树(*Populus trichocarpa*)尽管其中抗旱品种较不抗旱品种其导管的直径和导度均要大,但抗旱品种的纹孔膜的强度要高,高强度的纹孔膜会防止膜的损坏,提高抗旱品种对空穴化的抵抗能力(Tyree *et al.*, 1993)。当然,纹孔大小与导管大小具有一定的关系。

一些落叶树种的根较茎的木质部导管的空穴化脆弱性程度要高(Sperry & Saliendra, 1994; Alder *et al.*, 1996; Hacke & Sauter, 1996; Sperry & Ikeda, 1997; Sperry *et al.*, 1998; Kolb & Sperry, 1999; Ewers *et al.*, 2000; Hacke *et al.*, 2000)。对于一种蒿属植物(*Artemisia tridentata*)根水势低于 -4.0 Mpa时,大部分根导管产生空穴化现象,而茎水势要低于 -7.8 MPa(Kolb & Sperry, 1999)。小枝的空穴化脆弱性程度要高于大枝(Tyree & Sperry, 1989a; Mencuccini & Comstock, 1997)。叶脉在一天的早些时候出现空穴化现象,而枝稍迟出现空穴化现象(Salleo *et al.*, 2000)。Zimmermann(1983)提出了脆弱性区隔化(Vulnerability segmentation)的概念,认为在极端干旱的情况下,次要的小枝和叶片叶脉较主干易于产

生导管空穴化,这样只导致部分叶片的萎蔫。部分叶片的萎蔫可以防止进一步的水分丧失,以防止对植物生命极为重要的器官如主干导管产生空穴化的现象(Tyree *et al.*, 1993)。干旱导致植物树梢导管空穴化的产生,并与树梢的枯死联系紧密,空穴化使树梢枯死会降低植物蒸腾作用强度,保证其它枝条的水分的平衡关系,是一种适应干旱气候的表现(Rood *et al.*, 2000)。

植物茎节及分叉处形成空穴的可能性较小,秋材导管形成空穴的可能性小于春材,这是因为秋材的导管较窄所致。植物导管细胞壁的弹性回缩可能也是植物防止导管形成空穴的原因之一(Marshall & Dumbroff, 1999)。

此外,外界环境条件也可以改变植物防止空穴化产生的能力,如:外加氮素可以降低这种能力,而外加磷素则增加这种能力。这是因为外加氮素导致植物叶面积/根面积比率的增加,增加叶片的总蒸腾作用,增加导管直径,从而加剧木质部导管张力,易于导致空穴化的形成;而外加磷则有可能减小纹孔膜的尺寸,从而提高植物防止空穴化产生的能力(Harvey & van den Driessche, 1997; 1999)。土壤成分的不同也会造成这种能力的差异。沙质土壤可以使火炬松(*Pinus taeda*)防止空穴化产生的能力降低(Hacke *et al.*, 2000)。

4 气孔关闭与空穴产生之间的关系

普遍认为干旱诱导气孔关闭过程主要是脱落酸的信号传递过程,与水分传输机理无关(Crocker *et al.*, 1998)。但导管空穴化也可能是引起气孔关闭的因素之一(Tyree & Ewers, 1991; Cochard *et al.*, 1996)。因此,气孔关闭的原因可能是化学信号传导和水分运输共同作用的结果(Salah & Tardieu, 1997; Thompson *et al.*, 1997; Pena & Grace, 1986)。一般认为,干旱导致根部产生ABA化学信号,通过树液传导到叶片,ABA作用于叶片气孔的保卫细胞,从而导致气孔关闭(Liang & Zhang, 1999)。然而有证据表明在根部不缺水的情况下,植物叶片气孔关闭与叶片叶脉的导管空穴化相关(Tyree & Ewers, 1991)。对于一种蔷薇科树种(*Prunus laurocerasus*),干旱导致叶片空穴产生的时间和气孔关闭的时间基本同步(Nardini & Salleo, 2000)。另一项研究发现枝条导管产生空穴化现象10 min的时间之内,叶片气孔大部分明显关闭,随后气孔导度和临界空穴化的叶片水势之间形成负反馈关系,避免进一步的空穴化和气

孔的关闭(Salleo *et al.*, 2000; Nardini *et al.*, 2001)。这说明枝条而非叶片导管产生的空穴极大影响叶片气孔的运动。当然,叶片气孔水平的调控可以预防张力增大,有利于防止空穴的产生(Tyree & Sperry, 1988)。

根部导管的空穴化是否对气孔关闭造成影响?对于这一问题目前仍有争议。如有研究者认为花旗松(Douglas fir)根的空穴化是影响叶片气体交换更为重要的因素之一(Sperry & Ikeda, 1997)。

5 植物防止空穴化产生的能力与适应干旱能力之间的关系

一般认为植物防止空穴化产生能力与适应干旱能力之间的关系紧密,植物防止空穴形成的能力部分是由遗传决定的,但是,具有相似抗旱能力的种之间的空穴化临界水势值并不一致(Kavanagh & Zaerr, 1997; Tyree *et al.*, 1998; Kavanagh *et al.*, 1999; Kolb & Sperry, 1999)。Pockman 和 Sperry (2000)认为干旱地区生长的植物对空穴化的抵抗能力要高于湿润地区生长的植物;Cochard 等(1992)在对某些针叶树“脆弱性曲线”进行分析时发现,耐旱品种防止形成空穴的能力大于不耐旱品种。

但是,也有一种意见认为植物导管防止形成空穴化的能力和植物对水分的利用效率无明显关系,或呈相当弱的正相关。对多个松属树种的研究发现,干旱可以诱导边材面积/叶面积比率(A_R/A_L)增加、气孔控制能力增加、水分导通能力加强,而不一定使导管防止形成空穴化的能力加强。如欧洲赤松(*Pinus sylvestris*) (Jackson *et al.*, 1995; Piñol & Sala, 2000)、火炬松(Ewers *et al.*, 2000)、西黄松(*Pinus ponderosa*)和 *Pinus menziesii* (Maherali & DeLucia, 2001)。对于一种蔷薇科树种(*Prunus laurocerasus*)的叶片,切断中脉只降低了 30% 的水分导通性,说明由于叶片内传输水分的通道数量相当多,水分可以绕过中脉进行运输,暗示植物导管防止形成空穴化的能力和植物的抗旱性的关系并不明显(Nardini *et al.*, 2001)。部分研究者认为部分导管的空穴化甚至有利于植物利用水分(Lo Gullo & Salleo, 1993; Borghetti *et al.*, 1998; Melcher *et al.*, 2001)因为空穴化的产生导致同一管道上其它未空穴化的导管水势升高,从而有利于附近细胞暂时利用这些导管的水分。

综合以上两种不同观点,Sperry 等研究者认为在不同土壤、不同根/叶横截面积比率条件下,根系

周围水分通导性和木质部水分通导性在植物水分利用关系上重要性不同(Sperry *et al.*, 1998; Sperry *et al.*, 2002)。如:在高 A_R/A_L 、黏土、防止空穴化产生能力低的情况下,木质部导管的空穴化起到了限制植物利用水分的主要作用。

普遍认为木质部水分运输能力和防止空穴化形成的能力之间存在一种矛盾的关系(Tyree, 1997)。也即当植物处于干旱情况下(导管水势降到导管形成空穴时的临界水势),部分导管的空穴化导致叶片气孔关闭,降低蒸腾的拉力,并保持适当的水分运输速度,避免植株整体过分失水(Stratton *et al.*, 2000; Domec & Gartner, 2001)。因此,研究者认为植物抗旱能力的重要标志之一是植物控制导管水柱张力的能力,既避免形成大量空穴又保持适当的水分运输能力(Bond & Kavangh, 1999)。这种控制能力可能与植物对气孔的控制能力强烈相关,至少在地中海性气候(Borghetti *et al.*, 1998)和非季节性气候区域是如此(Tyree *et al.*, 1998),但也有不同观点(Phillips *et al.*, 2001)。这种控制能力还可能与树干储水能力(Tyree & Yang, 1990; Tognetti *et al.*, 1996; Domec & Gartner, 2001)以及脆弱性区隔化能力相关。

6 空穴化导管的重新注水机制

在蒸腾很弱的情况下,根木质部导管存在正的压力(称为根压)(Schwenke & Wagner, 1992; Fish *et al.*, 1997)。这种正的压力可能来源于周围活细胞的半透膜性质,也可能来源于根木质部导管存在的渗透势(Canny, 1995; Zhu *et al.*, 1995)。虽然有文献指出玉米(*Zea mays*)根部导管内的溶质浓度很低(McCully *et al.*, 1998; McCully, 1999),但 Zimmermann 等(2002)认为这些实验结果可能存在误差。空穴化的木质部导管在高于大气水汽压的根压下要持续一段时间才会重新注水,导管中的空穴会逐渐消失(Yang & Tyree, 1992)。根压的存在可能有助于空穴化导管的重新注水,特别是夜晚对白天出现的空穴化导管的重新注水(Tyree *et al.*, 1986; Holbrook *et al.*, 2001)。

根压导致正的导管压力对于草本植物空穴化的导管重新注水机制有很好的解释,然而,却不能很好解释高大的木本植物空穴化的修复(Tyree & Sperry, 1989a; Ewers *et al.*, 1997)。比如月桂树(*Laurus nobilis*)的根就缺少根压(Salleo *et al.*, 1996)。此外,对于月桂树的木质部导管重新注水是通过从韧皮部到木质部的通道进行的(Tyree *et al.*, 1999),而根压是

通过木质部到木质部的通道(Fisher *et al.* ,1997)。对于美洲栎树(*Fraxinus americana*)、红花槭(*Acer rubrum*)和红云杉(*Picea rubens*)3种乔木树种木质部水分导通性日变化的研究发现,夜晚可以恢复50%的水分导通性,在木质部导管存在张力的情况下仍然可以对空穴化的导管重新注水(Zwieniecki & Holbrook,1998)。近来研究表明,空穴化的导管重新注水在存在蒸腾的情况下同步发生(Salleo *et al.* ,1996; Canny,1997; McCully *et al.* ,1998; Zwieniecki & Holbrook,1998; Tyree *et al.* ,1999; Salleo *et al.* ,2000)。为解决这种相互冲突的现象,有研究者认为需要重新审查水分传输的机理问题(Canny,1997; Zwieniecki *et al.* ,2001; Zimmermann *et al.* ,2002)。木质部导管伴细胞质膜上存在丰富的水选择通道蛋白(Barrieu *et al.* ,1998)以及导管内腔存在的黏多糖(Zimmermann *et al.* ,2002)可能有助于解决这个矛盾。

Holbrook 和 Zwieniecki (1999)认为空穴化的导管重新注水过程包括以下3个步骤:水进入空穴化的导管;孤立重新充水的导管以便维持正压来溶解气泡;在存在张力的情况下稳定相邻的导管。木质部导管和导管之间的纹孔的特殊形状可能是邻近导管的张力存在的情况下空穴化导管内存在正压的原因之一(Zwieniecki & Holbrook,2000)。

7 展 望

对导管空穴化和栓塞化现象的研究是目前国际上树木生理生态研究领域的研究热点之一,近年来发展十分迅速。导管空穴化研究目前存在许多并不十分清楚的问题,如:1)对于整个输水管道系统,在一定条件下哪个部分最有可能成为输水能力的限制环节(Sperry *et al.* ,2002)?2)导管空穴化是否会产生信号分子(如 ABA)传导到整个植株并影响气孔运动?3)导管空穴化与木质部水分运输能力之间的关系如何?4)导管空穴化的重新注水机制是怎样的,这种重新注水的能力与植物抗旱性的关系如何?5)导管空穴化-注水这种循环造成导管的“疲劳”是否具有普遍性(Hacke *et al.* ,2001a)?通过对这些问题的研究和探讨,对于理解植物长期进化来适应环境的生理生态机制,对于因地制宜制定灌溉和管理措施优化植物的水分利用效率无疑具有十分重要的理论和实践意义。

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