



# 木本植物木质部的冻融栓塞应对研究进展

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**摘要** 冻融栓塞在中高纬度地区木本植物中普遍存在。抗冻融栓塞能力对在寒冷环境中木本植物的生长和安全越冬十分关键, 这直接决定植物分布范围。冻融栓塞是由于冰中气体溶解度低, 木质部水分在低温下冷冻, 使之前水中溶解的气体逸出到导管中, 随后木质部中的冰融化又使气泡扩张而引发的栓塞现象。木质部解剖结构的差异会影响植物的抗冻融栓塞能力, 植物还可以通过调节木质部正压、代谢耗能等方式主动修复冻融栓塞, 也可通过增加树液溶质含量等逃避冷冻, 以减少低温损伤。然而, 与干旱栓塞相比, 目前对木质部冻融栓塞的形成以及植物响应和调节机制的理解不足。为此, 该文首先综述了木质部冻融栓塞的形成机制和植物的逃避、忍耐、修复等3种冻融栓塞的应对策略, 然后总结了木质部抗低温胁迫能力的生理表现、影响因子和评价指标, 并在此基础上讨论了低温抗性、干旱抗性和水力效率之间的多元权衡关系, 最后提出今后该领域中的5个优先研究问题: (1)不同植物冰冻的最低温度阈值; (2)是否存在应对低温胁迫的水力脆弱性分割机制; (3)冻融栓塞修复与代谢消耗的关系; (4)低温抗性、干旱抗性和水力效率之间的权衡关系; (5)抗冻融栓塞性状是否能够纳入经济性状谱系。

**关键词** 冻融栓塞; 栓塞修复; 水力效率; 权衡; 水力特征

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## Research progress on responses of xylem of woody plants to freeze-thaw embolism

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### Abstract

Embolism induced by the freeze-thaw commonly occurs in the woody plant in mid- and high-latitude regions. In cold environments, the resistance capacity to freeze-thaw embolism of woody plants is critical for their growth and successful survival throughout winter, which directly determines their distribution in the earth. During freeze-thaw cycles, the freeze-thaw embolism of vessels is induced by the bubbles that are from dissolved frozen water because of the low solubility of ice. The resistance capacity to freeze-thaw embolism varies from plants with different anatomical structures. Plants can also reduce potential damages of freeze-thaw embolism through adjusting the xylem positive pressure by refilling embolism and metabolism, and/or increasing the sap solute contents to avoid the stress. Compared to embolism induced by drought, however, few studies have been conducted on embolism by freeze-thaw, and the underlying mechanisms of plant responses and regulation are poorly understood. In this paper, we first reviewed the process of formation and repair of freeze-thaw embolism of xylem, including the strategies of escaping freezing, tolerance, and repairing freeze-thaw cavitation. Then we summarized physiological characteristics of plant resistance to low-temperature stress, influencing factors and evaluating criteria, based on the multiple trade-offs between low-temperature resistance, drought resistance, and hydraulic efficiency. Finally, we proposed five priorities for future study in this field: (1) the threshold of freezing temperature for different plants; (2) the vulnerability segmentation of frost-induced embolism; (3) the relationships between freeze-thaw cavitation repair and metabolism exhaustion; (4) the potential trade-offs between low-temperature resistance, drought resistance and hydraulic efficiency; and (5) integration of the traits of freeze-thaw embolism resistance into the economic spectrum of plants.

**Key words** freeze-thaw embolism; embolism repair; hydraulic efficiency; trade-off; hydraulic characteristic

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北方森林和温带森林几乎占全球森林总面积的1/3 (Reich *et al.*, 2016), 其植物面临的最主要环境胁迫之一是冬季低温。低温使植物地上器官木质部中的水分逐步冻结(Niu *et al.*, 2017), 所以植物如何最大程度减少低温胁迫引起的损伤对其安全越冬(Hacke *et al.*, 2015; Kreyling *et al.*, 2015; Charrier *et al.*, 2017)、生长、生存以及分布均具有重要作用(Schreiber *et al.*, 2013; Charrier *et al.*, 2015; Niu *et al.*, 2017)。低温时期冻融诱导形成的栓塞是低温胁迫对植物产生损伤的重要因素(Zanne *et al.*, 2014; Zhang *et al.*, 2018)。许多研究发现, 植物抗冻融栓塞能力不仅影响其在低温时期的损伤程度和碳消耗(Bowling *et al.*, 2018; Yin *et al.*, 2018), 还显著影响随后生长季中的水分供应能力(冷冻疲劳, Feng *et al.*, 2015; Zhang *et al.*, 2018)。但与干旱栓塞相比, 目前对木质部冻融栓塞的形成以及植物响应和调节机制的理解不足(Choat *et al.*, 2011; Yin *et al.*, 2018)。为了推进该领域的研究, 本文先综述木质部冻融栓塞的形成机制和植物的逃避、忍耐、修复等3种冻融栓塞的应对策略, 然后总结植物低温抗性的生理表现、评价和影响因子, 在此基础上讨论低温抗性、干旱抗性和水力效率之间的多元权衡关系, 最后提出今后该领域中的优先研究问题。

## 1 木质部冻融栓塞的形成机理

栓塞是降低木质部内水分运输效率的关键因子(Choat *et al.*, 2012; 金鹰等, 2016), 主要包括干旱栓塞和冻融栓塞(Améglie *et al.*, 2002; Willson & Jackson, 2006; Venturas *et al.*, 2017)。两种栓塞形成的主要机理均为空气进入导管或管胞, 从而阻断木质部水柱, 形成栓塞(Sperry & Sullivan, 1992), 而不同之处在于引发空气进入的过程(Hacke & Sperry, 2001)。根据内聚力-张力理论, 木质部导管内水分持续运输动力主要来自叶片蒸腾失水引起的拉力, 因此导管中的水分始终处于亚稳态(Sperry & Love, 2015)。当蒸腾加剧和/或土壤水分供应不足而使木质部导管内负压超过一定阈值时, 就会造成其水柱断裂, 致使周围组织中的气体进入导管, 从而形成干旱栓塞(Choat *et al.*, 2018)。而冻融栓塞主要发生在木质部经历多次冻融循环的过程中(Sperry &

Sullivan, 1992; Feild & Brodribb, 2001; Charra-Vaskou *et al.*, 2016)。当木质部水分冰冻时, 水中原有溶解气体因在冰中的溶解度很低而逸散到导管中(Lintunen *et al.*, 2014)。而当冰冻融化时, 导管中的留存气体或者重新溶进水中(气泡压力大于大气压时, Hacke & Sperry, 2001), 或者由于冰冻压力的释放(冰融化后体积减小)等使气体在导管中扩大(Lemoine *et al.*, 1999; Mayr *et al.*, 2002; Pittermann & Sperry, 2006), 多次冻融交替之后, 导管中气体不断增加和扩张, 最终引发冻融栓塞, 该现象也被称为“融化-扩张假说”(Mayr & Sperry, 2010; Mayr & Améglie, 2016)。干旱栓塞和冻融栓塞均会阻碍植物水分从土壤到叶片的运输, 从而降低叶片的光合速率(Brodribb *et al.*, 2007; Reich, 2014; Jin *et al.*, 2016), 导致植物生产力降低甚至死亡(McDowell *et al.*, 2008; Hoffmann *et al.*, 2011; McDowell, 2011; Choat *et al.*, 2018)。

## 2 植物应对木质部冻融栓塞的策略

在长期的进化过程中, 植物(尤其是中高纬度、高山和亚高山木本植物)面对冻融栓塞, 逐渐形成了不同的应对策略(Lintunen *et al.*, 2018; Wang *et al.*, 2018; Willick *et al.*, 2018; Yin *et al.*, 2018), 主要包括逃避、忍耐和修复等3种应对策略(图1)

### 2.1 逃避策略

冬季落叶是植物常见的逃避低温的策略之一(Preston & Sandve, 2013; Hoermler *et al.*, 2018)。乔木和灌木树种通过凋落叶片, 切断水力功能, 减少低温胁迫损伤(Vitasse *et al.*, 2014)。草本植物则通过衰老地上组织, 以种子或者地下储存器官的形式, 在土壤和雪的保护下越冬(Zanne *et al.*, 2014)。此外, 环孔材树种在低温时期直接使冻融栓塞的导管失去生理功能, 而通过春季形成的新导管来运营其水分运输功能, 这也是一种逃避低温策略(Cochard & Tyree, 1990; Brodersen & McElrone, 2013)。环孔材树种的木质部水力效率较高, 其导管直径和长度也显著大于散孔材树种, 故其栓塞抗性较低(殷笑寒和郝广友, 2018)。

植物还可以通过木质部过冷却的方式避免低温及冰冻损伤(Arias *et al.*, 2017)。过冷却指植物使细

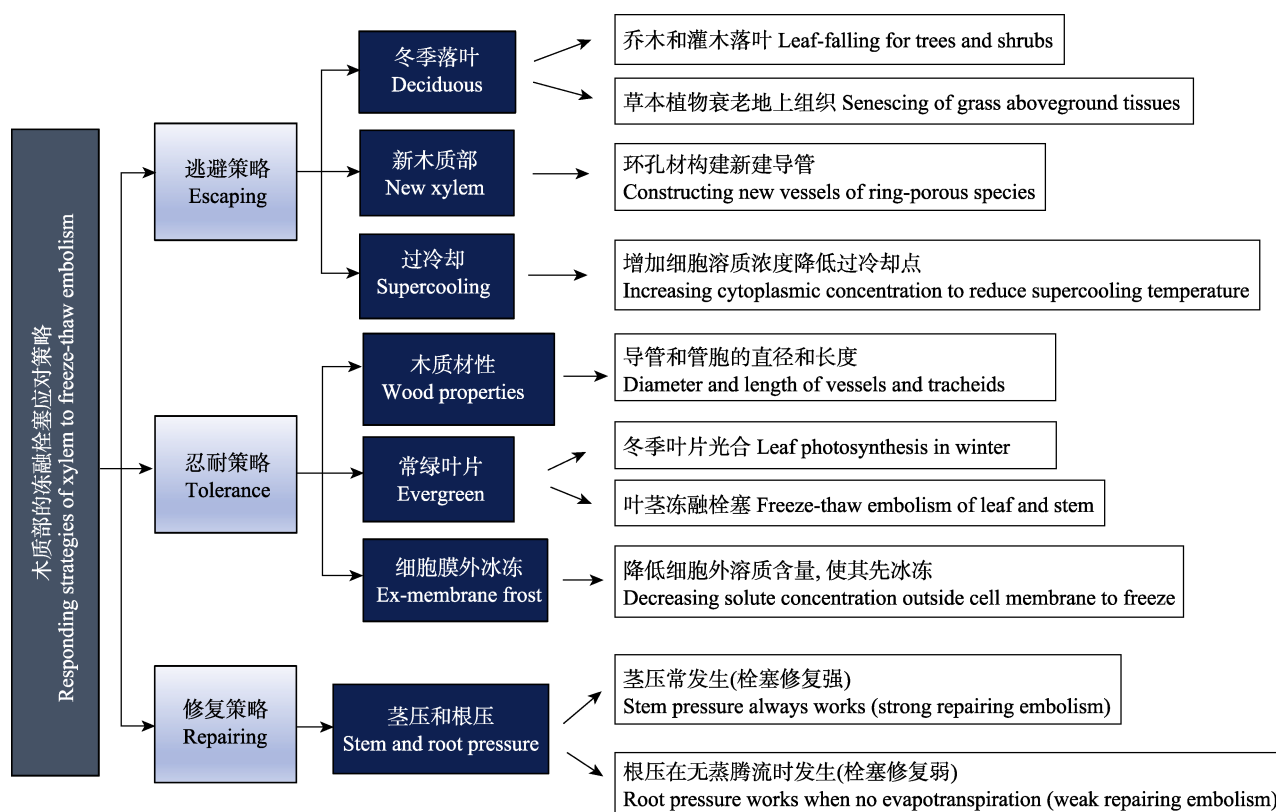


图1 植物木质部的冻融栓塞应对策略。

Fig. 1 Three responding strategies of xylem to freeze-thaw embolism.

胞中液体的冰点温度远低于液态水冰点的能力 (Arias *et al.*, 2015)。Rasmussen和MacKenzie (1972) 指出, 没有任何结晶核的纯水结冰温度低至  $-38.1^{\circ}\text{C}$ 。因此, 植物细胞内异质结晶核含量影响其过冷却点的高低 (Losso *et al.*, 2018)。过冷却能力对植物应对突发性的冰冻事件 (如热带植物遭遇突发性寒流) 十分重要 (Reyes-Díaz *et al.*, 2006)。Arias等 (2015) 发现, 在寒冷环境中驯化过的油橄榄 (*Olea europaea*) 栽培种, 其叶片冰点温度低至  $-13^{\circ}\text{C}$  (远低于环境最低温度), 而且有更高的叶密度和细胞壁刚性, 从而使其溶质渗透性和组织可塑性更高, 质外体水分含量更低; 进一步研究发现, 从夏季到冬季该树种茎最低冰点逐渐降低, 而且其木质部抗空穴化能力与叶片和茎的过冷却能力之间存在权衡 (Arias *et al.*, 2017)。

## 2.2 忍耐策略

与动物不同, 植物的固定性使得其更多地采用“被动”的忍耐策略, 例如不同的木质结构、调整组织水分含量和溶质含量等, 以减少低温损伤 (Mayr *et al.*, 2014; Arias *et al.*, 2015; Lintunen *et al.*, 2018)。被子植物和裸子植物解剖结构的差异, 使二者对低

温胁迫的忍耐能力不同 (Pittermann & Sperry, 2003; Lintunen *et al.*, 2016)。被子植物的导管比裸子植物的管胞结构具有更高的水力效率, 但是其木质部抗冻融栓塞能力较低 (Feild & Brodribb, 2001; Lintunen *et al.*, 2018)。Davis等 (1999) 报道, 当导管直径大于  $40\ \mu\text{m}$  时, 一次冻融交替使木质部栓塞程度高达 95%; Feild和Brodribb (2001) 也发现, 常绿针叶植物和导管较小的被子植物经历一次冻融交替后, 其茎水力导度降低最少 (几乎为0), 而其他被子植物则平均降低 18%–70%。可见, 被子植物木质部忍耐低温能力远低于裸子植物。植物经过多次冻融交替后, 导管或周围组织中产生的气泡可能在整个冬季留存, 直到春季才能重新进入融化水中或者气泡扩张形成栓塞 (Hacke & Sperry, 2001; Venturas *et al.*, 2017; Medeiros & Danielson, 2018), 所以导管内水分含量直接影响植物冻融栓塞程度 (Choat *et al.*, 2011)。而水分含量与导管直径紧密相关 (Lens *et al.*, 2013)。因此构建直径更小的导管是最直接增加抗冻融栓塞能力的方法。裸子植物直径较小的管胞结构能够在很大程度上减少冻融栓塞的形成, 不仅因为在管胞中形成的气泡更小, 而且小气泡更容易在融化期重新

溶解进入水中(Hacke *et al.*, 2015)。Pittermann和Sperry等(2006)报道, 管胞越窄的裸子树种气泡形成的空穴化越小, 并且得出冻融栓塞引起的木质部负压随着管胞直径的增加而增加。之后, Choat等(2011)对11种被子植物的研究也发现, 导管直径越大、长度越长的植物, 冻融引起的水力导度丢失量(PLC)越多、造成的栓塞越大。这可能是因为直径较大的导管具有更少的单位长度导管末端, 造成其纹孔数量减少、栓塞抗性降低(Choat *et al.*, 2006)。因此, 构建直径更小的导管(或管胞), 是植物应对冻融栓塞最直接的方式(Pittermann & Sperry, 2006; Jiménez-Castillo & Lusk, 2013; Hacke *et al.*, 2017; Gleason *et al.*, 2018)。

常绿树种茎抗低温胁迫能力可能还与叶片低温抗性有关(Ball *et al.*, 2004; Fernández-Pérez *et al.*, 2018; Verhoeven *et al.*, 2018)。“脆弱性分割假说”指出, 植物面临胁迫时, 其叶片(或小枝)可能比其茎表现得更为脆弱, 通过牺牲“造价低廉”的末端器官保护“造价昂贵”的茎干, 以避免栓塞发生(Zimmermann, 1983; Tyree & Ewers, 1991)。已存在大量有关干旱胁迫下的“脆弱性分割假说”验证研究(Hao *et al.*, 2008; Johnson *et al.*, 2012; Pivovarov *et al.*, 2014; Zhu *et al.*, 2019), 但还不清楚低温胁迫下是否也会发生该现象。Fernández-Pérez等(2018)发现, 6个松属(*Pinus*)树种的针叶低温抗性对其分布范围的预测能力大于茎干木质部抗冻融栓塞能力。在北半球温带森林中, 冬季留存叶片因日间光照而使其日间温度高于0 °C, 从而可能延长光合作用的时间(Feild & Brodribb, 2001; Sevanto *et al.*, 2006; Lindfors *et al.*, 2015; Bowling *et al.*, 2018), 生产的有机物可用于早春修复冻融栓塞和细胞损伤。不过, 此时树干仍处于冰冻状态, 导致叶片可能比茎经历更多次的冻融循环, 从而加剧叶片的冻融栓塞(Feild & Brodribb, 2001; Charra-Vaskou *et al.*, 2016), 降低茎干的冻融栓塞程度, 在一定程度上对主茎起到保护作用(Charrier *et al.*, 2017)。

植物还有一种忍耐低温胁迫的策略是, 通过改变细胞膜内外的溶质浓度, 使细胞内溶质浓度增加(形成低水势), 从而降低细胞外溶质浓度(Mayr *et al.*, 2007; Lintunen *et al.*, 2016)。当冰冻发生时, 细胞外水分首先冻结(主要发生在细胞壁表面、纤维、导

管内或者细胞外的空间)(Willick *et al.*, 2018), 冰形成的低水势使细胞内水分进一步流出, 细胞内溶质浓度增加, 从而避免细胞内冰冻导致的细胞死亡(McCully *et al.*, 2004), 能够暂时保护细胞不受冰冻损伤(Mayr & Améglio, 2016)。

### 2.3 修复策略

修复是植物应对冻融栓塞的又一重要策略(Preston & Sandve, 2013; Wang *et al.*, 2018)。有研究表明, 采用正压(主要包括根压和茎压)恢复水力功能的植物可能具有更强的抗冷冻疲劳能力(即木质部冰冻后对水力功能丢失更敏感的现象)(Niu *et al.*, 2017; Yin *et al.*, 2018), 这是植物对冻融栓塞的一种主动修复。Hao等(2013)发现, 早春纸桦(*Betula papyrifera*)树干水分含量明显高于生长季, 表明根压在修复冻融栓塞导管的过程中具有重要作用。Améglio等(2002)报道, 冬季胡桃(*Juglans regia*) PLC可高达100%, 但是由于冬季和春季茎压修复, 木质部冻融栓塞程度有一定的降低。另外, 近期研究表明, 能产生木质部正压的植物, 其抗冻融栓塞能力可能不受导管直径的影响(Niu *et al.*, 2017)。根压和茎压主要来源于糖类水解成的蔗糖被运输到栓塞导管中而产生渗透浓度梯度(Nardini *et al.*, 2011; Cao *et al.*, 2012), 从而使水分流向栓塞导管, 即渗透调节假说(金鹰等, 2016)。两者的不同之处在于: 根压主要在无蒸腾流情况下产生作用(Swaef *et al.*, 2013), 且修复栓塞作用较小(Salleo *et al.*, 2004), 特别是对高大植物上层木质部栓塞的修复作用很小(Westhoff *et al.*, 2008)。而茎压产生的渗透梯度可能来自韧皮部的糖类(韧皮部卸载假说, Salleo *et al.*, 2004; Hölttä *et al.*, 2018), 因此在多数情况下均有茎压存在, 这也被称为“新的再冲水”(novel refilling)假说(Brodersen & McElrone, 2013; 金鹰等, 2016)。Améglio等(2004)发现, 胡桃在深冬时茎中淀粉含量最低, 在发芽前茎中再次合成淀粉, 这不仅表明胡桃在冬季低温下进行淀粉和蔗糖的转换, 而且蔗糖累积是其冻融栓塞修复中的关键。张海燕等(2013)也发现, 12个温带树种老枝的淀粉含量变化具有相同趋势。

## 3 植物木质部低温胁迫抗性和影响因子

木质部结构是影响植物忍耐低温胁迫的主要因

素(Hacke *et al.*, 2015, 2017; Lintunen *et al.*, 2018)。被子植物采用多个细胞死亡后相互连接构成的导管进行水分运输, 长度在1 mm到几米不等; 裸子植物则依靠单个细胞伸长形成的管胞进行水分运输, 长度在2–6 mm之间(Tyree & Ewers, 1991), 而且管胞直径一般小于导管(Sperry *et al.*, 2006)。这种木质部结构差异导致裸子植物和被子植物响应冻融栓塞时产生显著PLC差异(Feild & Brodribb, 2001; Feng *et al.*, 2015; Fernández-Pérez *et al.*, 2018)。以往研究表明, 植物在入冬前PLC逐步增加(Zhang *et al.*, 2018), 而导管或管胞的直径差异是植物PLC不同的主要原因(Pittermann & Sperry, 2003; Hacke *et al.*, 2015, 2017)。在所有季节中, 裸子植物的PLC均小于被子植物(Granda *et al.*, 2014)。例如, 被子植物葡萄牙栎(*Quercus faginea*)抗空穴化能力较差, 夏季PLC达到80%, 冬季进一步达到90%, 而裸子植物香桧(*Juniperus thurifera*)和欧洲黑松(*Pinus nigra*)夏季PLC几乎为0, 冬季仅增加到3%–9% (Granda *et al.*, 2014)。

经典气泡扩张理论认为, 冻融栓塞的形成取决于融化时木质部张力( $P_x$ )和气泡压力( $P^*$ )之间的关系(Domec, 2011; Charrier *et al.*, 2017);  $P^*$ 受气泡表面张力( $t$ )和气泡中气液混合物压力( $P_b$ )的共同影响,  $P^*$ 还与气泡直径( $D_b$ )大小相关。因此,

$$P^* = -4t/D_b + P_b \quad (1)$$

只有当 $P_x$ 小于 $P^*$ 时, 气泡才有可能扩大并形成空穴。由公式(1)可知, 木质部导管越大, 越容易形成直径较大的气泡, 气泡压力越小, 在较低张力下气泡越可能扩大, 因而对冻融栓塞的抵抗更加脆弱(Feild & Brodribb, 2001; Choat *et al.*, 2011; Hacke *et al.*, 2017)。裸子植物管胞直径一般比被子植物导管直径小(Hacke *et al.*, 2017), 因此裸子植物的抗冻融栓塞能力较强。但在管道直径相同时, 裸子植物与被子植物具有相似的抗冻融栓塞能力(Pittermann & Sperry, 2003, 2006; Hacke *et al.*, 2015)。

木质部水分含量是影响植物抗冻融栓塞能力的又一因素。因为导管直径与木质部水分含量正相关(Lens *et al.*, 2013), 因此, 裸子植物管胞的含水量一般低于被子植物导管, 从而使裸子植物的冻融栓塞程度较低。冬季日间太阳直射使留存的植物叶片和/或小枝中冰冻水分融化, 引起蒸腾失水, 但下部冰

冻的树干(Charrier *et al.*, 2017)无法及时补充水分丢失(Bowling *et al.*, 2018), 从而使植物叶片和小枝的木质部含水量降低。另外, 含水量变化还可能会引起质外体组织冰冻时的体积发生变化(Lintunen *et al.*, 2016)。低温胁迫使木质组织首先脱水收缩, 再经历液态水冰冻时的体积膨大(+9%)(Améglio *et al.*, 2001)。在冰冻前, 植物主动降低质外体含水量, 增加溶质浓度, 此时脱水引起的体积减小能够降低过冷却点(Lintunen *et al.*, 2013; Willick *et al.*, 2019)。因此, 冰冻前含水量越低(体积越小), 植物对低温胁迫的忍耐力越强(Lintunen *et al.*, 2018)。当冰冻发生时, 由于水分由液态转为固态的体积增加, 对周围细胞壁产生机械压力, 植物需构建更强健的细胞壁(Zhang *et al.*, 2016; Ployet *et al.*, 2018)和改变细胞壁上蛋白组分(Willick *et al.*, 2018)来抵御低温胁迫, 因此, 质外体较高的水分含量可能对植物产生更严重的低温损伤。研究表明, 木质部通过寒冷驯化后其直径少量收缩(Améglio *et al.*, 2001; Charra-Vaskou *et al.*, 2016; Lintunen *et al.*, 2016)。例如, 欧洲赤松(*Pinus sylvestris*)和欧洲山杨(*Populus tremula*)木质部直径经寒冷驯化后分别收缩了0.5%和1.0%, 小于渗透胁迫和干旱胁迫引起的收缩量(Lintunen *et al.*, 2016)。此外, 植物通过寒冷驯化, 可以降低质外体的含水量, 并将水分转移到冰储存位点, 同时不同冰区之间形成隔离带(Willick *et al.*, 2019), 从而尽可能减少低温损伤。

#### 4 评价植物抗低温胁迫能力的生理指标

评价植物抗冻融栓塞能力最直接的指标是冻融栓塞引起水力导度丢失的百分比, 即木质部最大水力导度与低温下水力导度之差和最大水力导度之比(Charrier *et al.*, 2013; Niu *et al.*, 2017), 与干旱PLC类似。冻融栓塞常常会引起植物水力导度丢失现象。Granda等(2014)整合75个研究中的210个记录发现, 植物PLC从夏季到冬季逐步增加。Charrier等(2013)也发现, 冬季植物PLC最高, 且PLC可能受海拔限制。然而, Fernández-Pérez等(2018)报道, 低温胁迫引起的6个松属树种的PLC较低, 而且没有发现PLC与低温损伤(叶黎明前水势)之间的关系。

虽然植物通过逃避、忍耐、修复等方式应对冻融栓塞, 但冻融过程中导管细胞壁和纹孔膜的损伤会显著降低植物再次应对冻融栓塞的能力, 该现象



被称为“冷冻疲劳”(Christensen-Dalsgaard & Tyree, 2013)。此概念最初源于木质部在经历多次干旱栓塞后,再次面临干旱时会增加栓塞敏感性,降低植物抗干旱栓塞能力(Stiller & Sperry, 2002; Hillabrand *et al.*, 2016)。同样,冷冻疲劳指木质部经过多次冻融交替后对水力丢失更为敏感(Yin *et al.*, 2018)。通常采用自然条件下导水率丢失50%时所对应的水势( $P_{50}$ )与经过一次(或多次)冻融交替后的 $P_{50}$ 之差表示冷冻疲劳(Christensen-Dalsgaard & Tyree, 2014; Feng *et al.*, 2015; Zhang *et al.*, 2018)。Christensen-Dalsgaard和Tyree (2014)发现,经过一个自然条件下冬季后,散孔材树种的栓塞抗性显著降低,导水率丢失25%时所对应的水势( $P_{25}$ )比 $P_{50}$ 降低更多,这表明散孔材树种表现出显著的冷冻疲劳。Yin等(2018)发现,在模拟冻融交替下,不同功能型树种的冷冻疲劳(根压、根压+茎压、无根压、茎压)差异显著,且与木质密度、导管密度和单个纹孔特性有关。与茎压相比,能够产生根压和根压+茎压的树种所具有的更高木质密度,可以增加其忍耐木质部被拉长(冰冻体积增加)的能力(Yin *et al.*, 2018)。Zhang等(2018)报道,五角槭(*Acer mono*)冷冻疲劳具有循环周期性,表现出冬季最弱、夏季最高。上述研究结果表明,冷冻疲劳可能是温带森林中普遍存在的现象(Christensen-Dalsgaard & Tyree, 2013),并且显著影响植物抗冻融栓塞能力。

另一种评价植物低温耐性的生理特征是低温对植物的损伤程度,即将经过低温处理后的植物置于适宜环境中生长,之后观察枯落叶(或者死根)的百分比,以此来判断植物低温忍耐能力(Carles *et al.*, 2011; Rorato *et al.*, 2018)。Toca等(2018)报道,经历冬季(低温处理)后的松树幼苗,其小枝低温忍耐能力明显增加,且氮添加显著影响植物低温忍耐能力,但正负效应均存在。土壤养分是否影响植物低温耐性还有待于深入研究。

常绿植物保证叶片安全越冬对其之后的生长具有关键作用(Ball *et al.*, 2004),因此我们还可以通过分析叶片抗低温胁迫能力来评价植物的低温耐性。目前评价叶片抗低温胁迫能力的指标主要有:叶片电解质渗出率(Climent *et al.*, 2009; Hoermiller *et al.*, 2018)、可溶性糖含量(Fernández-Pérez *et al.*, 2018)、黎明前叶水势(Taneda & Tatenno, 2005)、叶细胞弹性

模量(细胞壁刚性越高,细胞弹性模量越大)(Zhang *et al.*, 2016)等。Fernández-Pérez等(2018)报道,伊比利亚半岛6个松属树种的分布与其叶片低温忍耐能力有关,生长在寒冷环境中的针叶的电解质渗出率和可溶性糖含量较低,且黎明前叶水势对针叶低温损伤有影响。Martínez-Vilalta等(2016)整合分析全球尺度121个研究中177个物种非结构性碳(淀粉和可溶性糖)数据发现,北方和温带生物区系物种叶片非结构性碳含量最高,而且在入冬过程中逐步增加。Zhang等(2016)发现,叶片细胞壁强度的增加,降低了质外体冰冻对细胞膜的物理损伤,使植物在较低的温度下得以存活。上述几个评价指标中,电解质渗出率是最常用的评价植物组织损伤的指标(Charrier *et al.*, 2013; Arias *et al.*, 2015; Mayr & Améglio, 2016)。通常采用电解质渗出率达50%时所对应的温度( $LT_{50}$ )来评价植物的低温抗性: $LT_{50}$ 越低,则低温抗性越强(Kreyling *et al.*, 2015; Bachofen *et al.*, 2016; Arias *et al.*, 2017)。例如,Arias等(2017)报道,油橄榄的 $LT_{50}$ 从夏季到冬季呈现逐步降低的趋势,这表明随着温度的降低,通过不断驯化,油橄榄的低温抗性逐步增强。

## 5 木质部低温抗性、干旱抗性和水力效率的权衡

木质部的水力效率-安全权衡是植物适应环境和进化的结果(Blackman *et al.*, 2010; Jin *et al.*, 2016),影响植物的竞争力和生产力(Nardini & Luglio, 2014)。水力效率一般用植物水力导度表示,而水力安全常用抗干旱栓塞能力( $P_{50}$ )表示(Santiago *et al.*, 2018)。Nardini等(2012)报道,来自温带的6种植物(槭属(*Acer*)和栎属(*Quercus*)各3种)的水力导度、 $P_{50}$ 和比叶质量之间存在显著相关性,支持水力效率-安全权衡,且增加叶碳投入可以提高水力丢失的忍耐能力。Nardini和Luglio (2014)整合130个木本被子植物叶片水力数据后也发现存在叶水力效率-安全权衡关系,而且生长在低降水量地区的植物的 $P_{50}$ (负值)和叶水力导度均较低。Gleason等(2016)综合分析335种被子植物和89种裸子植物的茎水力数据,发现虽然水力导度和抗干旱栓塞能力之间存在弱相关性(支持水力效率-安全权衡),但没有发现高效率和高安全性的植物。因此,植物普遍存在不同程度

的水力效率-安全权衡关系,但其关系的紧密程度受导管特征(Lens *et al.*, 2011; Hajek *et al.*, 2014)、木质材性(金鹰和王传宽, 2016)、树高(Prendin *et al.*, 2018)等因素的影响。

与干旱栓塞类似,冻融栓塞也阻断木质部的水分运输,由此推测水力导度随着抗冻融栓塞能力的增加而降低,然而,以往研究结果并不一致。例如,Choat等(2011)研究发现,温带树种水分运输能力与冻融栓塞之间存在权衡,且该权衡影响光合作用。但Feild和Brodribb (2001)报道,低温PLC与茎水力导度无关,不支持抗冻融栓塞能力与水力导度之间的权衡。Niu等(2017)也发现,散孔材树种能产生木质部正压,不存在水力效率和抗冻融栓塞能力的权衡现象,而其他功能型树种则存在这种权衡关系,这表明根压或茎压会影响该权衡。因此,抗冻融栓塞能力与水力导度之间的权衡是否普遍存在,尚需进一步研究。

木质部低温抗性、干旱抗性和水力效率三者间是否存在多元权衡现象?目前对此问题的综合研究较少,但已有研究指出,干旱显著增加植物的低温抗性(Kreyling *et al.*, 2012; Walter *et al.*, 2013; Sierra-Almeida *et al.*, 2016; Sperling *et al.*, 2017)。这是因为植物通过驯化改变了细胞对脱水的忍耐能力(Buchner & Neuner, 2011),其中包括基因表达的改变导致的细胞膜结构变化或者细胞化学成分变化(Verhoeven *et al.*, 2018)。例如,Medeiros和Pockman (2011)报道,在-15 °C环境中干旱处理使*Larrea tridentate*植株细胞死亡减少、叶留存量增加、水力导度和气体交换速率升高,这表明干旱处理显著增加了其低温抗性。Hoffman等(2012)也发现,干旱处理能够显著增加黑麦草(*Lolium perenne*)的低温抗性。然而,Kong和Henry (2016)研究发现,早春低温处理的草地早熟禾(*Poa pratensis*)的抗旱性显著增加(生物量和存活率增加),但夏季干旱处理并未增加其低温抗性,这表明干旱处理对植物低温抗性无影响的现象也存在。同样,Bachofen等(2016)也发现,干旱处理没有增加地中海松属3个树种的低温抗性,而且推测该现象可能仅在短期极端条件下发生。Yin等(2018)同时对低温抗性、干旱抗性和水力效率进行研究发现,抗干旱栓塞与水力效率存在权衡,抗冷冻疲劳与水力效率间也存在权衡现象,支持多元

权衡现象。然而,当植物同时面对干旱和低温胁迫时(如高山树线植物)(Mayr *et al.*, 2007; Charrier *et al.*, 2017),多次冻融交替结合干旱胁迫可能引起PLC增加(Mayr *et al.*, 2003; Charrier *et al.*, 2014)。Mayr等(2006)报道,生长在林线处的针叶树种,每个冬季经历至少100次冻融交替,再加上干旱胁迫,二者共同引起欧洲云杉(*Picea abies*) PLC高达100%。因此,生长在低温和干旱胁迫共存环境中的植物,其PLC可能更高,间接表明三者间存在一定程度的权衡。综上所述,我们构建了低温抗性、干旱抗性和水力效率之间多元权衡概念图(图2)。

## 6 研究问题和展望

许多研究表明,植物木质部在环境温度低于0 °C后没有立即发生冰冻现象。植物应对低温的忍耐策略(过冷却能力和降低水势等)能够降低形成冰冻的最低温度。因此,明确不同植物冰冻的最低温度阈值能够提高在全球气候变化条件下对植物分布的预测能力。

植物不同器官对于干旱胁迫的响应存在差异,叶片(或小枝)比主茎抗干旱栓塞能力更弱,即“脆弱性分割假说”。冻融栓塞和干旱栓塞均能阻碍水分运输。因此,植物不同器官间的抗冻融栓塞能力是否也存在分割现象,这如何影响植物抗低温胁迫能力等相关问题仍需进一步研究。

植物主动修复冻融栓塞的过程是将溶质主动运输到栓塞导管中以形成渗透势梯度,这会产生碳消耗,因此,该过程可能与CO<sub>2</sub>释放有关。随着全球温度升高,低温胁迫对植物的损伤可能减轻,从而降低植物用于修复冻融栓塞的代谢消耗,这可能会影响植物的碳固定量,但需要更多的实验验证。

探索木质部低温抗性、干旱抗性和水力效率间的多元权衡,深入了解干旱和低温胁迫对植物生理特征的影响,特别是植物如何调整生理结构和代谢来适应干旱和低温胁迫共存的环境。这对植物应对不断加剧的全球气候变化的研究具有重要意义。

Reich (2014)提出植物体中存在“快-慢”谱系的普适性规律,包括碳、氮和水分性状的耦合关系,但没有明确包含植物低温时期的生理特征。植物抗低温胁迫能力是否能够纳入经济性状谱系,与其他经济性状是否相关等问题亟待解决。

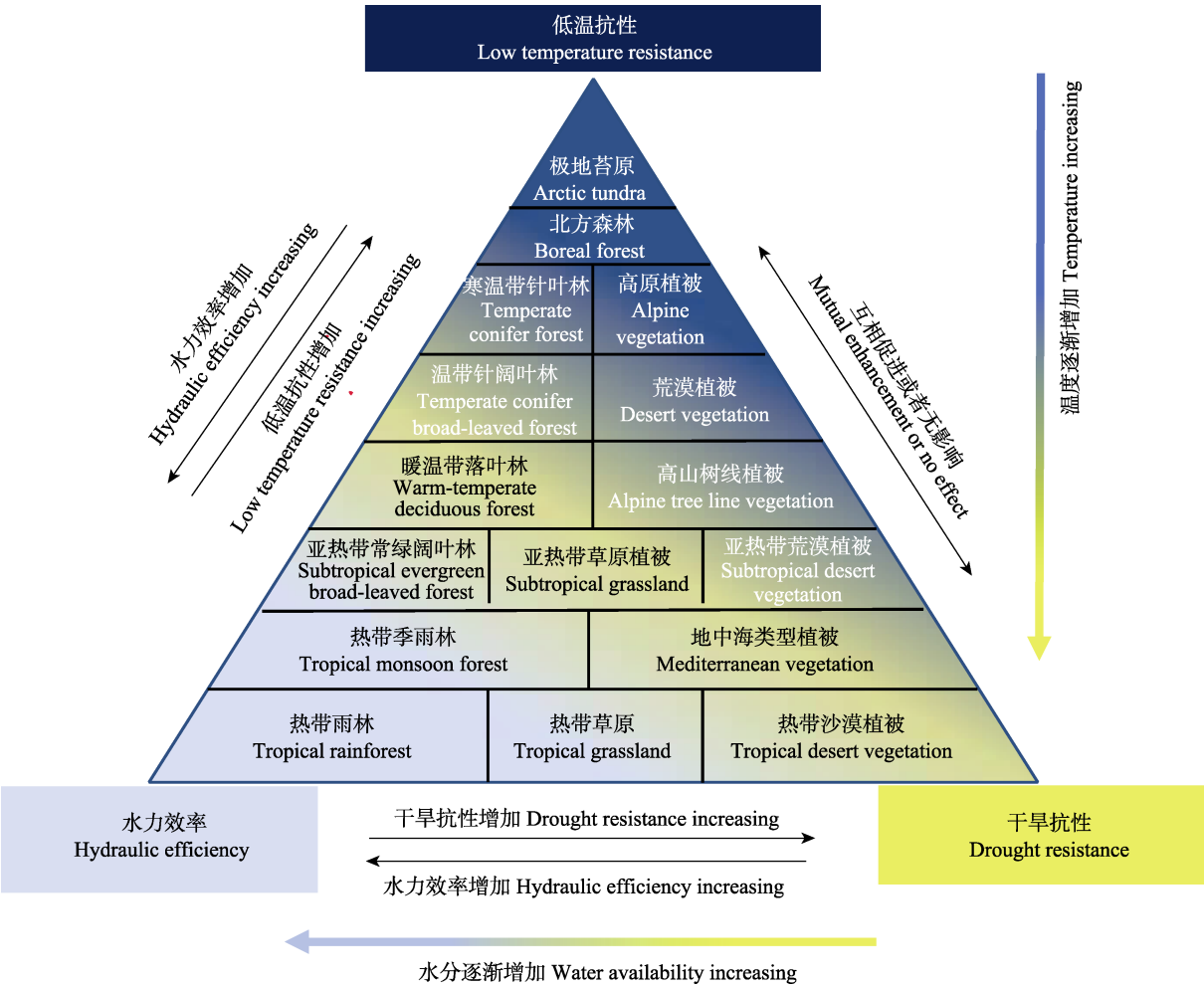


图2 主要植被类型低温抗性、干旱抗性和水力效率之间多元权衡的概念图。高(低)水力效率和低(高)低温抗性相关联,但主动修复可影响该权衡,低温还可影响植物的冷冻疲劳;高(低)水力效率与低(高)干旱抗性相关联,几乎不存在同时高水力效率和高干旱抗性的植物,但具有低水力效率和低干旱抗性的植物;干旱胁迫可增加低温抗性(不同时),反之亦然,干旱和低温同时发生增加水力导度丢失量,但两者对水力系统的影响并不相关。

Fig. 2 A conceptual diagram of multiple trade-offs among low-temperature resistance, drought resistance and hydraulic efficiency of the major vegetation types in the world. High (low) hydraulic efficiency is associated with weak (strong) low-temperature resistance, but the capacity of positive refilling embolism may influence the trade-off between hydraulic efficiency and low-temperature resistance, and low-temperature also affects the plant's frost fatigue. High (low) hydraulic efficiency is associated with weak (strong) drought resistance, but many species have both low hydraulic efficiency and drought resistance rather than high hydraulic efficiency and drought resistance. Drought stress may increase low-temperature resistance (asynchronous), and vice versa; concomitant drought and low-temperature stresses aggravate the loss of hydraulic conductance, but there are no related impacts of drought and low-temperature stresses on the hydraulic system.

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