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根皮层结构和组织化学分化及生理功能研究进展

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摘要:维管植物根的皮肤具内皮层和外皮层,这两者之间的中间皮层分为内侧皮层、外侧皮层、厚壁层和皮下层,有的植物缺乏外侧皮层、厚壁层和外皮层。皮层具额外细胞分裂、细胞器状结构、“O”“C”“Φ”状和均匀增厚或木质化等结构分化。这些皮层结构分化与适应水湿寡营养环境和陆生干旱、附生或气生环境密切联系;具有调节和限制离子自由出入的屏障保护功能,并与矿质营养吸收和超聚集重金属离子功能有关。皮层木质化可能是作物高亲和/高容量矿质养分吸收转运系统的结构性状,这可以为作物选育高效利用水和矿质营养的品种提供理论依据,可以为选择高效修复离子污染环境的植物提供结构特征依据,也为研究入侵植物的入侵机制等生态学问题提供新思路。

关键词:根皮层;皮层分化;生态适应;离子吸收;生态修复

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植物群落、种群或表现型及其可塑性在相对较长的时间尺度上与自然环境协同进化,对环境的变化和干扰处于动态变化状态,根系由胚根发育来的主根和营养体产生的不定根组成,以适应各种特定或者复杂多变的生态环境^[1-7]。植物主要依靠根尖及根毛区吸收水和矿质营养,完成个体发育生活史,实现作物耐低磷和低肥增效,减轻农业排放对环境的污染^[8-11]。

维管植物(vascular plant)根解剖结构的维管柱(vascular cylinder or stele)、皮层(cortex)、表皮(rhizodermis)和根冠(root cap)由其顶端分生组织分化而来^[12-17]。根尖顶端分生组织(root apical meristems)分化发育过程主要有开放型根尖组织(open patterns)、封闭型根尖组织(closed patterns)以及介于这二者之间的过渡类型^[15,18-20]。

本文综述皮层随物种、生态环境等因素变化,径向和切向壁具有“O”“Φ”“C”状和均匀增厚或木质化,细胞器状结构分化,细胞层数变化,分裂形成新外皮层(exodermis)等结构和组织化学特征;并具机械保护、耐淹没适应水湿环境、耐盐胁迫和离子

超积累等生理功能,对今后水体和土壤离子污染的生态修复有指导意义^[21-30]。关于内皮层、外皮层和通气组织的结构和生理功能已有综述报道^[17,27-29,31-34],在此就不再赘述。

1 维管植物根尖顶端分生组织分化类型

被子植物根尖顶端分生组织细胞分化发育过程可以分为开放型根尖组织和封闭型根尖组织。开放型根尖组织为祖先类型,即皮层、表皮和根冠之间缺乏明确的界限;封闭型根尖组织即皮层、表皮和根冠之间具有明确的界限^[15,18-19]。菖蒲(*Acorus calamus*)根尖顶端分生组织介于开放型和封闭型根尖组织之间^[18]。现存石松类植物根尖顶端分生组织细胞分化发育过程相对于被子植物更为复杂,在石松类植物和茎叶植物类中进化了好几次,大致分为3种类型,其中2种类型与被子植物的开放型和封闭型有类似构造^[20]。根维管柱与表皮之间为薄壁组织皮层,皮层最内侧的内皮层(endodermis)和表皮下的外皮层常有凯氏带、栓质化和木质化特点而被称为质外体屏障结构(apoplastic barriers),能够阻碍水和矿质离子自由出入^[12-17,35-36]。根据凯氏带蛋白分子发育证据和组织化学特征,现在认为内皮层和外皮层为独立的结构单元并行使其相应生理功能^[17,37-39]。封闭型根尖组织的皮层组织由共同的原始细胞分裂而来,表皮由独立的原始细胞分裂而来^[15,19,40-42]。

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2 皮层的解剖结构和组织化学

以水稻 (*Oryza sativa*) 模式植物为例, 根据免疫化学和组织化学研究结果, 其根皮层从内到外依次为内皮层、邻近内皮层的内侧皮层 (inner cortex or peri-endodermal)、邻近厚壁层的外侧皮层 (outer cortex)、厚壁层 (sclerenchyma ring) 和仅 1 层细胞的外皮层^[33,43-49]; 其木质化厚壁层与菰 (*Zizania latifolia*) 类似, 而不同于德国鸢尾 (*Iris germanica*) 和藨草 (*Phalaris arundinacea*) 等的多层细胞外皮层^[32-33,50-51]。因物种不同, 如拟南芥 (*Arabidopsis thaliana*) 和壶瓶碎米荠 (*Cardamine hupingshanensis*) 只有无凯氏带分化的皮下层 (hypodermis) 而无外皮层^[17,27,37-38,40-42]。水稻、德国鸢尾、香蒲属植物 (*Typha* spp.) 和玉米 (*Zea mays*) 等主根、不定根及次级侧根的中间皮层具有 1 层到数层细胞^[48-50,52-55]。因此, 本文提出根的皮层, 除了明显分化的内皮层和外皮层, 这两者之间的中间皮层 (middle cortex) 包含内侧皮层、外侧皮层、厚壁层和皮下层, 或缺乏外侧皮层、厚壁层和外皮层^[17,25,27,40-42,49]。

3 皮层的结构分化类型

3.1 皮层额外细胞分裂和细胞器状结构

野艾蒿 (*Artemisia lavandulaefolia*) 和藜蒿 (*A. selengensis*) 根的皮层细胞继续分裂扩大通气组织的体积, 并在破坏的外皮层内侧形成新的外皮层^[24]。水生水杉 (*Metasequoia glyptostroboides*) 根的中间皮层细胞继续分裂扩大通气组织体积, 也有“Φ”状木质化增厚^[28], 把野艾蒿、藜蒿和 水生水杉根的皮层称为分裂型皮层 (dilated cortex)。龙胆草 (*Gentiana asclepiadea*) 根的内、外皮层细胞分裂增加根周径^[56]。但是椴树 (*Tilia americana*) 和水花生 (*Alternanthera philoxeroides*) 根的次生韧皮部薄壁细胞分裂扩大根的周径和通气组织体积^[14,29], 把这种分裂方式称为韧皮部薄壁细胞分裂 (dilated parenchyma)。这些根中额外细胞分裂主要是扩大通气组织的体积, 是植物适应和耐水淹的结构特征^[17,27-29,31-34,51]。

千里光属植物 *Senecio coronatus* 超聚镍基因型内侧皮层具明显球形细胞器状细胞质 (organelle-rich cytoplasm), 并富含生物碱; 而其非超聚镍基因型内侧皮层极少有细胞器状细胞质, 含少量生物

碱, 外皮层凯氏带较明显, 推测该结构强烈阻挡镍离子进入根内^[57-58]。

3.2 皮层“O”状增厚

蕨类植物二歧鹿角蕨 (*Platycerium bifurcatum*)、黑心蕨属植物 *Doryopteris triphylla*、*Pleopeltis macrocarpa* 等根中内侧皮层具有 1 层或数层纤维素“O”状增厚的厚壁细胞层, 增强了机械强度, 可以适应陆生干旱或附生环境^[59-67]。伏贴石杉 (*Lycopodium appressum*) 和小翠云 (*Selaginella kraussiana*) 根内侧皮层细胞壁有明显的“O”状木质化增厚, 外侧皮层均匀木质化增厚^[60]。

3.3 皮层均匀木质化增厚

水生水花生根皮层明显均匀木质化, 而且黄连素不能透过; 陆生水花生根仅有微弱木质化或无木质化^[29]。黄花柳 (*Salix caprea*)、簇根类植物 (cluster roots) 的银桦 (*Grevillea robusta*) 和荣桦属植物 *Hakea prostrata* 根皮层为均匀木质化^[68-70]。超聚硒植物壶瓶碎米荠外侧皮层和皮下层主要为均匀木质化, 兼有少量较小“Φ”状木质化增厚^[27]。凤梨科根皮层中部和皮下层具木质化厚壁层, 而不同于水稻和菰的根只有外皮层为木质化厚壁层^[33,43-45,71]。

3.4 皮层“C”状增厚

南美楸 (*Feijoa sellowiana*) 根内侧皮层具“C”状增厚^[72]。超积累锌和镉山萆薢属植物 *Nocca caerulea* 根内侧皮层富含果胶木质化“C”状增厚, 染料不能透过该结构, 与“Φ”状增厚功能类似; 但非超积累锌和镉的 *N. arvense* 的根缺乏“C”状增厚; 1% 蔗糖溶液可以诱导 *N. caerulea* 根皮层“C”状增厚^[21,30,73-74]。在旱生条件下, 杨梅 (*Myrica rubra*) 和石榴 (*Punica granatum*) 根内侧皮层具“C”状木质化增厚^[75-76]。在水淹条件下, 洋蒲桃 (*Syzygium samarangense*) 根内侧皮层具“C”状木质化增厚^[23,77]。

3.5 皮层“Φ”状木质化增厚

按照 Aleamotu'a 等的观点, 种子植物根皮层“Φ”增厚类型 I 是内侧皮层木质化增厚最为普遍的^[25], 本文认为该类型发生在内侧皮层或者外侧皮层, “Φ”状增厚程度由内而外逐渐减小, 主要包括一些裸子植物、木榄 (*Bruguiera gymnorrhiza*)、附生兰科、蔷薇科和十字花科植物^[22,27,78-88]。附生兰科植物根皮层富含果胶、木栓质, “Φ”状木质化增厚有助于水和矿质的吸收、机械支持和保护作用^[89]。根

“Φ”状增厚类型Ⅱ是根皮下层木质化增厚,天竺葵(*Pelargonium hortorum*)根从皮下层向内部皮层细胞壁有由大到小的“Φ”状木质化增厚^[50,78,90-92],并能透过并结合荧光染料 cellufluor^[92]。根“Φ”状增厚类型Ⅲ是根皮层中部木质化增厚,见于花生(*Arachis hypogaea*)、欧洲桤木(*Alnus glutinosa*)、加拿大黄桦(*Betula alleghaniensis*)和美洲红树(*Rhizophora mangle*)中^[93-97]。

水生水杉根皮层细胞继续分裂不仅扩大通气组织体积和其细胞层数,从内皮层外侧到外皮层以内细胞壁依次有由大到小的“Φ”状木质化增厚;而旱生水杉根仅有内侧皮层的“Φ”状木质化增厚^[28]。水淹环境诱导云实属植物 *Caesalpinia peltophoroides* 根皮层“Φ”状木质化增厚,其机械保护能力得到增强^[98]。适应陆生的日本柳杉(*Cryptomeria japonica*),在压实或者压实水淹土壤环境中根皮层“Φ”状木质化增厚程度略减轻和细胞层减少,诱导效果不显著^[82]。

甘蓝(*Brassica oleracea*)和欧洲油菜(*Brassica napus*)根在琼脂培养基添加盐或蔗糖,或者田间栽培环境诱导皮层形成强烈的“Φ”状木质化增厚,并具有调节和限制离子自由出入的屏障保护功能,是该物种响应水和盐胁迫的结构基础^[22,75,85,99]。在旱生条件下,枇杷(*Eriobotrya japonica*)根皮层迅速形成“Φ”状木质化增厚,可能与响应水分胁迫有关^[83,100]。

美堇兰属(*Miltoniopsis*)植物根在去离子水中诱导出现“Φ”状增厚,但无质外体屏障保护功能;在琼脂培养基和潮湿土壤中根无“Φ”状增厚;在有良好排水基质和缺水胁迫时形成“Φ”状增厚,表明其适应附着气生环境^[26]。此外,玉米在矿渣培养条件下,诱导根表皮“Φ”状木质化增厚,而在水培和通气水培条件下则没有“Φ”状增厚^[101]。

4 皮层木质化组织化学染色法和细胞发育生物学

细胞壁木质化,以往常用盐酸-间苯三酚对染呈现櫻桃红色;现在用硫酸氢黄连素-苯胺兰对染、fluorol yellow-Congo red 对染、Fluorol yellow-acridine orange 对染、Acridine orange 等荧光染料染色,皮层木质化细胞壁与木质部显色一致,即认为细胞壁木质化^[89,91,102-105],同时这些荧光染料也作为离子示踪剂。因此,笔者认为黄花柳、银桦和 *Hakea prostrata* 根皮层发生了木质化,尽管原文作者没有指出这一点^[68-69]。

附生美堇兰属植物皮层生活细胞次生壁“Φ”状木质化、“Φ”状增厚形成经历3个阶段,早期微管纵向对齐将增厚的位置,过渡期胼胝质类似微管对齐将要增厚的位置,随后微管、胼胝质和小麦胚凝集素(wheat germ agglutinin)标记都消失,最后皮层“Φ”状木质化增厚^[22,25,106]。

5 皮层结构分化与适应环境关系

根分裂型皮层的野艾蒿、藜蒿和生生水杉扩大气腔,同时野艾蒿和藜蒿外侧皮层产生新的外皮层保护空气不外泄;黄花柳和疏花水柏枝皮层均匀木质化;水淹洋蒲桃根呈“C”状增厚,木榄和水杉水生根具“Φ”状木质化增厚增强机械强度忍耐水力冲刷,也可能在寡营养水体易于获得矿质离子,而适应水湿寡营养环境^[22-24,28,31,45,70,76,89]。

蕨类植物根皮层呈“O”状增厚或者发生木质化^[60-67];凤梨科皮层木质化厚壁层^[77];南美椴、杨梅和石榴皮层具“C”状木质化增厚^[73,74-75];种子植物根皮层有“Φ”状木质化增厚类型Ⅰ、Ⅱ、Ⅲ,如日本柳杉、天竺葵、花生、枇杷以及附生兰科、蔷薇科和十字花科植物^[25-27,79,82-83,91,100],增强机械强度适应陆生干旱、附生或气生环境。

甘蓝、欧洲油菜和 *Caesalpinia peltophoroides* 在响应水和盐胁迫下,诱导皮层发生“Φ”状木质化增厚,具有调节和限制离子自由出入的屏障保护功能^[22,30,73,85,98-99]。簇根植物银桦和 *Hakea prostrata* 皮层均匀木质化;附生兰科植物根皮层的果胶、木栓质和“Φ”状木质化增厚利于吸收水和矿质离子^[68-71,89,107]。

Senecio coronatus 超聚镍基因型的根皮层具球形细胞器状细胞质和富含生物碱^[57-58],超积累锌和镉的 *Noccea caerulea* 根皮层富含果胶和“C”状木质化增厚^[21,30,74,108],超聚硒和镉的壶瓶碎米茅皮层具“Φ”状和均匀木质化增厚^[27,109-110],推测这些物种皮层结构和组织化学分化可能与其超聚集重金属离子功能有关^[22,30,73,89,108]。此外,十字花科植物芜菁(*Brassica rapa*)和 *Stanleya pinnata* var. *pinnata* 也有超聚硒功能^[111-112]。

著名入侵植物水花生^[113-120]易于入侵富营养化水体,并具有较强的去除氮磷和重金属离子能力,与本土物种竞争中占有明显优势,可能是它们根皮层的木质化而使根具有较强的离子吸收能力^[22,29-30,71,87,105]。因此,水花生与本土植物相比,根的较强离子吸收能力是其重要入侵机制之一。

6 皮层结构研究展望

研究植物根系及解剖结构特征,明确其适应复杂多变的生态环境,更好服务农业生产和改善生态环境,一是改善作物高效吸收水和矿质营养,减少农业排放对环境的污染,二是高效植物修复土壤重金属离子污染和水体离子污染。本文主要探讨了根皮层结构分化类型与其适应各种环境的关系,皮层木质化具有调节和限制离子自由出入的屏障结构功能,有利于吸收水和矿质营养,超积累重金属离子及与入侵植物的入侵机制有密切关系。在植物高效修复污染环境实践中,本文为选择适合的植物种类及结构特征提供了参考依据,也为研究入侵植物的入侵机制提供新思路。根皮层木质化或许就是作物育种中高亲和力/高容量的矿质养分吸收转运系统的结构性状,可以实现低肥增效和减少农业污染^[1-4,6-9,11,13,17,25,35]。

参考文献:

- [1] Gratani L. Plant phenotypic plasticity in response to environmental factors[J]. *Advances in Botany*, 2014(4):1-17.
- [2] Pham B, McConaughay K. Plant phenotypic expression in variable environments[M]//Monson R. *Ecology and the environment*. New York:Springer, 2015:1-19.
- [3] Steffens B, Rasmussen A. The physiology of adventitious roots[J]. *Plant Physiology*, 2016, 170(2):603-617.
- [4] Gonin M, Bergounoux V, Nguyen T D, et al. What makes adventitious roots? [J]. *Plants*, 2019, 8(7):240.
- [5] Mittelbach G G, McGill B J. *Community ecology* [M]. 2nd ed. Oxford:Oxford University Press, 2019.
- [6] Rasmussen A, Dobrijevic D P, Ola A, et al. Aerial root physiology: reaching for the sky or down to earth? [J]. *Annual Plant Reviews*, 2019, 2:1-32.
- [7] van Veen H, Sasidharan R. Shape shifting by amphibious plants in dynamic hydrological niches[J]. *The New Phytologist*, 2021, 229(1):79-84.
- [8] Lynch J P. Roots of the second green revolution[J]. *Australian Journal of Botany*, 2007, 55(5):493-512.
- [9] Lynch J P. Root phenotypes for improved nutrient capture: an underexploited opportunity for global agriculture [J]. *The New Phytologist*, 2019, 223(2):548-564.
- [10] Paez - Garcia A, Motes C M, Scheible W R, et al. Root traits and phenotyping strategies for plant improvement[J]. *Plants*, 2015, 4(2):334-355.
- [11] White P J. Root traits benefitting crop production in environments with limited water and nutrient availability[J]. *Annals of Botany*, 2019, 124(6):883-890.
- [12] Fahn A. *Plant anatomy* [M]. 4th ed. Oxford, UK: Pergamon Press, 1990.
- [13] Lux A, Luxová M, Abe J, et al. Root cortex: structural and functional variability and responses to environmental stress [J]. *Root Research*, 2004, 13(3):117-131.
- [14] Evert R F. *Esau's plant anatomy: meristems, cells, and tissues of the plant body: their structure, function, and development* [M]. 3rd ed. Hoboken, New Jersey, USA: Wiley - Interscience, 2006.
- [15] Seago J L, Fernando D D. Anatomical aspects of angiosperm root evolution[J]. *Annals of Botany*, 2013, 112(2):223-238.
- [16] Crang R, Lyons - Sobaski S, Wise R. Periderm: a concept - based approach to the structure of seed plants [M]//*Plant anatomy*. Gewerbestrasse, Switzerland: Springer, 2018:553-575.
- [17] 杨朝东, 张霞, 刘国锋, 等. 植物根中质外体屏障结构和生理功能研究进展[J]. *植物研究*, 2013, 33(1):114-119.
- [18] Soukup A, Seago J J, Votrubová O. Developmental anatomy of the root cortex of the basal monocotyledon, *Acorus calamus* (Acorales, Acoraceae) [J]. *Annals of Botany*, 2005, 96(3):379-385.
- [19] Heimsch C, Seago J L. Organization of the root apical meristem in angiosperms[J]. *American Journal of Botany*, 2008, 95(1):1-21.
- [20] Fujinami R, Yamada T, Nakajima A, et al. Root apical meristem diversity in extant lycophytes and implications for root origins[J]. *The New Phytologist*, 2017, 215(3):1210-1220.
- [21] Zelko I, Lux A, Czibula K. Difference in the root structure of hyperaccumulator *Thlaspi caerulescens* and non - hyperaccumulator *Thlaspi arvense* [J]. *International Journal of Environment and Pollution*, 2008, 33(2/3):123-132.
- [22] Fernandez - Garcia N, Lopez - Perez L, Hernandez M, et al. Role of phi cells and the endodermis under salt stress in *Brassica oleracea* [J]. *The New Phytologist*, 2009, 181(2):347-360.
- [23] Tuladhar A, Nii N. Anatomical studies on Myrtaceae roots[J]. *Acta horticulturae*, 2017, 1166:55-62.
- [24] Zhang X, Yang C D, Seago Jr. J L. Anatomical and histochemical traits of roots and stems of *Artemisia lavandulaefolia* and *A. selengensis* (Asteraceae) in the Jiangnan Floodplain, China [J]. *Flora*, 2018, 239:87-97.
- [25] Aleamotu'a M, McCurdy D W, Collings D. Phi thickenings in roots: novel secondary wall structures responsive to biotic and abiotic stresses [J]. *Journal of Experimental Botany*, 2019, 70(18):4631-4642.
- [26] Idris N, Collings D A. The induction and roles played by phi thickenings in orchid roots[J]. *Plants (Basel, Switzerland)*, 2019, 8(12):574.
- [27] Xiang J Q, Ming J J, Yin H Q, et al. Anatomy and histochemistry of the roots and shoots in the aquatic selenium hyperaccumulator *Cardamine hupingshanensis* (Brassicaceae) [J]. *Open Life Science*, 2019, 14(1):318-326.
- [28] Yang C D, Zhang X, Wang T, et al. Phenotypic plasticity in the structure of fine adventitious *Metasequoia glyptostroboides* roots allows adaptation to aquatic and terrestrial environments [J]. *Plants*, 2019, 8(11):501.
- [29] Yang C D, Yang X L, Zhang X, et al. Anatomical structures of

- alligator weed (*Alternanthera philoxeroides*) suggest it is well adapted to the aquatic – terrestrial transition zone [J]. *Flora*, 2019, 253: 27 – 34.
- [30] Kováč J, Lux A, Soukup M, et al. A new insight on structural and some functional aspects of peri – endodermal thickenings, a specific layer in *Nocca caerulescens* roots [J]. *Annals of Botany*, 2020, 126 (3): 423 – 434.
- [31] Seago J J, Marsh L C, Stevens K J, et al. A re – examination of the root cortex in wetland flowering plants with respect to aerenchyma [J]. *Annals of Botany*, 2005, 96 (4): 565 – 579.
- [32] Yang C D, Zhang X, Zhou C Y, et al. Root and stem anatomy and histochemistry of four grasses from the Jiangnan Floodplain along the Yangtze River, China [J]. *Flora*, 2011, 206 (7): 653 – 661.
- [33] Yang C D, Zhang X, Li J K, et al. Anatomy and histochemistry of roots and shoots in wild rice (*Zizania latifolia* Griseb.) [J]. *Journal of Botany*, 2014: 181727.
- [34] Yang C D, Zhang X, Seago Jr. J L, et al. Anatomical and histochemical features of *Brasenia schreberi* (Cabombaceae) shoots [J]. *Flora*, 2020, 263: 151524.
- [35] Enstone D E, Peterson C A, Ma F S. Root endodermis and exodermis: structure, function, and responses to the environment [J]. *Journal of Plant Growth Regulation*, 2002, 21 (4): 335 – 351.
- [36] Lux A, Rost T L. Plant root research: the past, the present and the future [J]. *Annals of Botany*, 2012, 110 (2): 201 – 204.
- [37] Roppolo D, De Rybel B, Dénervaud T V, et al. A novel protein family mediates Casparian strip formation in the endodermis [J]. *Nature*, 2011, 473 (7347): 380 – 383.
- [38] Geldner N. The endodermis [J]. *Annual Review of Plant Biology*, 2013, 64: 531 – 558.
- [39] Barberon M. The endodermis as a checkpoint for nutrients [J]. *The New Phytologist*, 2017, 213 (4): 1604 – 1610.
- [40] Pauluzzi G, Divol F, Puig J, et al. Surfing along the root ground tissue gene network [J]. *Developmental Biology*, 2012, 365 (1): 14 – 22.
- [41] di Mambro R, Sabatini S, Dello I R. Patterning the axes: a lesson from the root [J]. *Plants*, 2018, 8 (1): 8.
- [42] di Ruocco G, di Mambro R, Dello I R. Building the differences: a case for the ground tissue patterning in plants [J]. *Proceedings Biological Sciences*, 2018, 285 (1890): 20181746.
- [43] Krishnamurthy P, Ranathunge K, Franke R, et al. The role of root apoplastic transport barriers in salt tolerance of rice (*Oryza sativa* L.) [J]. *Planta*, 2009, 230 (1): 119 – 134.
- [44] Krishnamurthy P, Ranathunge K, Nayak S, et al. Root apoplastic barriers block Na⁺ transport to shoots in rice (*Oryza sativa* L.) [J]. *Journal of Experimental Botany*, 2011, 62 (12): 4215 – 4228.
- [45] Kotula L, Ranathunge K, Schreiber L, et al. Functional and chemical comparison of apoplastic barriers to radial oxygen loss in roots of rice (*Oryza sativa* L.) grown in aerated or deoxygenated solution [J]. *Journal of Experimental Botany*, 2009, 60 (7): 2155 – 2167.
- [46] Ranathunge K, Lin J X, Steudle E, et al. Stagnant deoxygenated growth enhances root suberization and lignifications, but differentially affects water and NaCl permeabilities in rice (*Oryza sativa* L.) roots [J]. *Plant, Cell & Environment*, 2011, 34 (8): 1223 – 1240.
- [47] Ranathunge K, Schreiber L, Bi Y M, et al. Ammonium – induced architectural and anatomical changes with altered suberin and lignin levels significantly change water and solute permeabilities of rice (*Oryza sativa* L.) roots [J]. *Planta*, 2016, 243 (1): 231 – 249.
- [48] Shiono K, Ogawa S, Yamazaki S, et al. Contrasting dynamics of radial O₂ – loss barrier induction and aerenchyma formation in rice roots of two lengths [J]. *Annals of Botany*, 2011, 107 (1): 89 – 99.
- [49] Henry S, Divol F, Bettembourg M, et al. Immunoprofiling of rice root cortex reveals two cortical subdomains [J]. *Frontiers in Plant Science*, 2015, 6: 1139.
- [50] Meyer C J, Seago J J, Peterson C A. Environmental effects on the maturation of the endodermis and multiseriate exodermis of *Iris germanica* roots [J]. *Annals of Botany*, 2009, 103 (5): 687 – 702.
- [51] Zhang X, Hu L J, Yang C D, et al. Structural features of *Phalaris arundinacea* in the Jiangnan Floodplain of the Yangtze River, China [J]. *Flora*, 2017, 229: 100 – 106.
- [52] Seago Jr. J L, Peterson C A, Enstone D E, et al. Development of the endodermis and hypodermis of *Typha glauca* Godr. and *T. angustifolia* L. roots [J]. *Canadian Journal of Botany*, 1999, 77 (1): 122 – 134.
- [53] Husakova E, Hochholdinger F, Soukup A. Lateral root development in the maize (*Zea mays*) lateral rootless1 mutant [J]. *Annals of Botany*, 2013, 112 (2): 417 – 428.
- [54] Tylová E, Pecková E, Blásková Z, et al. Casparian bands and suberin lamellae in exodermis of lateral roots: an important trait of roots system response to abiotic stress factors [J]. *Annals of Botany*, 2017, 120 (1): 71 – 85.
- [55] Dowd T G, Braun D M, Sharp R E. Maize lateral root developmental plasticity induced by mild water stress. I : Genotypic variation across a high – resolution series of water potentials [J]. *Plant, Cell & Environment*, 2019, 42 (7): 2259 – 2273.
- [56] Šottníková A, Lux A. Development, dilation and subdivision of cortical layers of gentian (*Gentiana asclepiadea*) root [J]. *New Phytologist*, 2003, 160: 135 – 143.
- [57] Mesjasz – Przybyłowicz J, Barnabas A, Przybyłowicz W. Comparison of cytology and distribution of nickel in roots of Ni – hyperaccumulating and non – hyperaccumulating genotypes of *Senecio coronatus* [J]. *Plant & Soil*, 2007, 293: 61 – 78.
- [58] Mesjasz – Przybyłowicz J, Barnabas A, Przybyłowicz W J. Root ultrastructure of *Senecio coronatus* genotypes differing in Ni uptake [J]. *Northeastern Naturalist*, 2009, 16: 351 – 365.
- [59] Chapple C S, Peterson R L. Root structure in the fern *Platycerium bifurcatum* (Cav.) C. Chr. (Polypodiaceae) [J]. *Botanical Gazette*, 1987, 148 (2): 180 – 187.
- [60] Damus M, Peterson R L, Enstone D E, et al. Modifications of cortical cell walls in roots of seedless vascular plants [J]. *Plant Biology*, 1997, 110 (2): 190 – 195.

- [61] Schneider H. Root anatomy of Aspleniaceae and the implications for systematics of this fern family[J]. Fern Gazette,1997,15:160–168.
- [62] Leroux O, Bagniewska – Zadworna A, Rambe S K, et al. Non – lignified helical cell wall thickenings in root cortical cells of *Aspleniaceae* (Polypodiales): histology and taxonomical significance [J]. Annals of Botany,2011,107(2):195–207.
- [63] Hernández M A, Teran L, Mata M, et al. Helical cell wall thickenings in root cortical cells of Polypodiaceae species from Northwestern Argentina[J]. The American Fern Journal,2013,103(4):225–240.
- [64] Neira D A, Andrada A R, Páez V D L Á, et al. Anatomical, histochemical and cytogenetic features of *Doryopteris triphylla* (Pteridaceae) [J]. American Journal of Plant Sciences,2017,8(4):907–920.
- [65] Wetzel M L R, Sylvestre L D S, Barros C F, et al. Vegetative anatomy of *Aspleniaceae newman* from Brazilian Atlantic rainforest and its application in taxonomy[J]. Flora,2017,233:118–126.
- [66] Lagoria M Á, Avila G, Neira D A, et al. Morphoanatomical and histochemical characteristics of the epiphytic fern *Pleopeltis macrocarpa* (Polypodiaceae) [J]. Brazilian Journal of Botany, 2018,41(3):739–750.
- [67] Wu D, Li L B, Ma X B, et al. Morphological and anatomical adaptations to dry, shady environments in *Adiantum reniforme* var. *sinense* (Pteridaceae) [J]. PeerJ – Life & Environment, 2020, 8:e9937.
- [68] Skene K R, Sutherland J M, Raven J A, et al. Cluster root development in *Grevillea robusta* (Proteaceae). II. The development of the endodermis in a determinate root and in an indeterminate, lateral root [J]. New Phytologist, 1998, 138(4):733–742.
- [69] Shane M W, Lambers H. Cluster roots: a curiosity in context[J]. Plant and Soil,2005,274(1):101–125.
- [70] Vaculík M, Konlechner C, Langer I, et al. Root anatomy and element distribution vary between two *Salix caprea* isolates with different Cd accumulation capacities[J]. Environmental Pollution, 2012,163:117–126.
- [71] Kowalski V K, de Oliveira F M C, Voltolini C H, et al. Velamen or uniseriate epidermis? Root apices in Bromeliaceae Juss[J]. Flora, 2019,250:9–17.
- [72] Nii N, Ohtsuka S, Ye L H, et al. Formation of endodermis – like cells with Casparian strip and thick wall cells derived from pericycle in the roots of *Feijoa sellowiana* (Myrtaceae) [J]. Journal of the Japanese Society for Horticultural Science,2012,81(4):314–319.
- [73] van de Mortel J E, Almar V L, Schat H, et al. Large expression differences in genes for iron and zinc homeostasis, stress response, and lignin biosynthesis distinguish roots of *Arabidopsis thaliana* and the related metal hyperaccumulator *Thlaspi caerulescens* [J]. Plant Physiology,2006,142(3):1127–1147.
- [74] Aleamotu'a M, Tai Y T, McCurdy D W, et al. Developmental biology and induction of phi thickenings by abiotic stress in roots of the brassicaceae[J]. Plants,2018,7(2):47.
- [75] Song Y, Ye L H, Nii N. Effects of soil water availability on development of suberin lamellae in the endodermis and exodermis and on cortical cell wall thickening in red bayberry (*Myrica rubra* Sieb. et Zucc.) tree roots [J]. Scientia Horticulturae,2011,129(4):554–560.
- [76] Tuladhar A, Ohtsuka S, Nii N. Formation of exclusive pattern during accumulation of ligno – suberic material in cell wall of Myrtaceae root tissues including epidermis, exodermis, endodermis and polyderm[J]. Plant Root,2014,8:24–32.
- [77] Tuladhar A, Ohtsuka S, Nii N. Anatomical study on wax apple (*Syzygium samarangense*) roots under long – term water – logged conditions[J]. Tropical Agriculture Development,2015,59:1–6.
- [78] Mackenzie K. The development of the endodermis and phi layer of apple roots[J]. Protoplasma,1979,100(1):21–32.
- [79] Peterson C A, Emanu M E, Weerdenbu C A. The permeability of phi thickenings in apple (*Pyrus malus*) and geranium (*Pelargonium hortorum*) roots to an apoplastic fluorescent dye tracer[J]. Canadian Journal of Botany,1981,59(6):1107–1110.
- [80] Weerdenburg C A, Peterson C A. Structural changes in phi thickenings during primary and secondary growth in roots. I. Apple (*Pyrus malus*) Rosaceae[J]. Canadian Journal of Botany, 1983,61(10):2570–2576.
- [81] Christodoulakis N S, Psaras G K. A contribution to the root study of the evergreen sclerophyllous anatomy of the primary root of *Quercus coccifera* L. [J]. Flora,1988,180(5/6):445–453.
- [82] Gerrath J M, Matthes U, Purich M, et al. Root environmental effects on phi thickening production and root morphology in three gymnosperms[J]. Canadian Journal of Botany,2005,83(4):379–385.
- [83] Nii N, Pan C X, Ogawa Y, et al. Anatomical features of the cell wall ingrowth in the cortical cells outside the endodermis and the development of the Casparian strip in loquat roots [J]. Japanese Society for Horticultural Science,2004,73(5):411–414.
- [84] Soukup A, Malá J, Hrubcová M, et al. Differences in anatomical structure and lignin content of roots of pedunculate oak and wild cherry – tree plantlets during acclimation[J]. Biologia Plantarum, 2004,48(4):481–489.
- [85] López – Pérez L, Fernández – García N, Olmos E, et al. The phi thickening in roots of broccoli plants: an adaptation mechanism to salinity? [J]. International Journal of Plant Sciences,2007,168(8):1141–1149.
- [86] Bonacorsi N K, Seago J J. Root development and structure in seedlings of *Ginkgo biloba* [J]. American Journal of Botany,2016, 103(2):355–363.
- [87] Song C W, Shen W W, Du L, et al. Development and chemical characterization of Casparian strips in the roots of Chinese fir (*Cunninghamia lanceolata*) [J]. Trees,2019,33(3):827–836.
- [88] Kitin P B, Nakaba S, Hunt C G, et al. Direct fluorescence imaging of lignocellulosic and suberized cell walls in roots and stems [J]. AoB PLANTS,2020,12(4):plaa032.
- [89] Joca T A C, de Oliveira D C, Zotz G, et al. Chemical composition of cell walls in velamentous roots of epiphytic Orchidaceae [J].

- Protoplasma,2020,257(1):103–118.
- [90] Haas D L, Carothers Z B, Robbins R R. Observations on the phi – thickenings and casparian strips in *Pelargonium* roots [J]. American Journal of Botany, 1976, 63(6): 863–867.
- [91] Peterson R L, Peterson C A, Meiville L H. Teaching plant anatomy through creative laboratory exercise [M]. Ottawa, Ontario: NRC Press, 2008.
- [92] Perumalla C J, Peterson C A, Enstone D E. A survey of angiosperm species to detect hypodermal Casparian bands. I. Roots with a uniseriate hypodermis and epidermis [J]. Botanical Journal of the Linnean Society, 1990, 103(2): 93–112.
- [93] Wilcox H E, Wang C J K. Mycorrhizal and pathological associations of dematiaceous fungi in roots of 7 – month – old tree seedlings [J]. Canadian Journal of Forest Research, 1987, 17(8): 884–899.
- [94] Massicotte H B, Melville L H, Peterson R L, et al. Comparative studies of ectomycorrhiza formation in *Alnus glutinosa* and *Pinus resinosa* with *Paxillus involutus* [J]. Mycorrhiza, 1999, 8(5): 229–240.
- [95] de Menezes N L. Rhizophores in *Rhizophora mangle* L: an alternative interpretation of so – called “aerial roots” [J]. Anais da Academia Brasileira de Ciências, 2006, 78(2): 213–226.
- [96] Tajima R, Abe J, Lee O N, et al. Developmental changes in peanut root structure during root growth and root – structure modification by nodulation [J]. Annals of Botany, 2008, 101(4): 491–499.
- [97] Souza I C, Morozesk M, Duarte I D, et al. Matching pollution with adaptive changes in mangrove plants by multivariate statistics. A case study, *Rhizophora mangle* from four neotropical mangroves in Brazil [J]. Chemosphere, 2014, 108: 115–124.
- [98] Henrique P D C, Alves J D, Goulart P D F P, et al. Physiological and anatomical characteristics of *Sibipiruna* plants under hipoxia [J]. Ciência Rural, 2010, 40(1): 70–76.
- [99] Lopez – Perez L, Fernández – García N, Olmos E, et al. The phi thickening in roots of broccoli plants: an acclimation mechanism to salinity? [J] International Journal of Plant Sciences, 2007, 168(8): 1141–1149.
- [100] Pan C X, Nakao Y, Nii N. Anatomical development of phi thickening and the Casparian strip in loquat roots [J]. Japanese Society for Horticultural Science, 2006, 75(6): 445–449.
- [101] Degenhardt B, Gimmler H. Cell wall adaptations to multiple environmental stresses in maize roots [J]. Journal of Experimental Botany, 2000, 51(344): 595–603.
- [102] Brundrett M C, Enstone D, Peterson C A. A berberine – aniline blue fluorescent staining procedure for suberin, lignin, and callose in plant tissue [J]. Protoplasma, 1988, 146(2): 133–142.
- [103] Brundrett M C, Kendrick B, Peterson C A. Efficient lipid staining in plant material with sudan red 7B or fluoral [correction of fluoral] yellow 088 in polyethylene glycol – glycerol [J]. Biotechnic & Histochemistry, 1991, 66(3): 111–116.
- [104] Ruzin S E. Plant microtechnique and microscopy [M]. New York: Oxford University Press, 1999.
- [105] 张 霞, 胡露洁, 周存宇, 等. 植物细胞壁组织化学定位染色方
- 法和技术的比较研究 [J]. 植物研究, 2017, 37(1): 147–154.
- [106] Idris N A, Collings D A. The Life of phi: the development of phi thickenings in roots of the orchids of the genus *Miltoniopsis* [J]. Planta, 2015, 241(2): 489–506.
- [107] Fajardo A, Piper F I. Cluster root – bearing Proteaceae species show a competitive advantage over non – cluster root – bearing species [J]. Annals of Botany, 2019, 124(6): 1121–1131.
- [108] Milner M J, Mitani – Ueno N, Yamaji N, et al. Root and shoot transcriptome analysis of two ecotypes of *Noccaea caerulea* uncovers the role of *NcNrap1* in Cd hyperaccumulation [J]. Plant Journal, 2014, 78(3): 398–410.
- [109] 白宏锋, 李晓明. 超积累植物壶瓶碎米荠的镉富集 [J]. 江苏农业学报, 2012, 28(1): 76–79.
- [110] 龙胜桥, 邵树勋. 鱼塘坝壩瓶碎米荠超富集镉的地球化学特征 [J]. 矿物学报, 2015, 35(增刊1): 817.
- [111] Li N N, Xie W W, Zhou X B, et al. Comparative effects on nutritional quality and selenium metabolism in two ecotypes of *Brassica rapa* exposed to selenite stress [J]. Environmental & Experimental Botany, 2018, 150: 222–231.
- [112] Wang J M, Cappa J J, Harris J P, et al. Transcriptome – wide comparison of selenium hyperaccumulator and nonaccumulator *Stanleya* species provides new insight into key processes mediating the hyperaccumulation syndrome [J]. Plant Biotechnology Journal, 2018, 16(9): 1582–1594.
- [113] 吴振斌. 水生植物与水体生态修复 [M]. 北京: 科学出版社, 2011.
- [114] 刘海琴, 高运强, 宋 伟, 等. 水花生去除富营养化水体中氮磷及抑藻效果的实验研究 [J]. 现代农业科学, 2008, 15(12): 89–92.
- [115] 朱泽聪, 胡春华, 胡维平. 水花生投放密度对富营养化湖水净化效果影响的试验研究 [J]. 海洋湖沼通报, 2008(4): 49–55.
- [116] Chang R Y, Wang R Q, Zhang Y R, et al. Effects of N : P ratio and nutrient level on the competition between invasive *Alternanthera philoxeroides* and native *Oenanthe javanica* [J]. Advanced Materials Research, 2012, 534: 337–342.
- [117] Liao J X, Tao M, Jiang M X. Spatial arrangements affect suppression of invasive *Alternanthera philoxeroides* by native *Hemarthria compressa* [J]. Acta Oecologica, 2014, 59: 46–51.
- [118] Wang A, Jiang X X, Zhang Q Q, et al. Nitrogen addition increases intraspecific competition in the invasive wetland plant *Alternanthera philoxeroides*, but not in its native congener *Alternanthera sessilis* [J]. Plant Species Biology, 2015, 30(3): 176–183.
- [119] Lu L, Dong B C, Alpert P, et al. Effects of soil substrate heterogeneity and moisture on interspecific competition between *Alternanthera philoxeroides* and four native species [J]. Journal of Plant Ecology, 2016, 10(3): 528–537.
- [120] Wu H, Ismail M, Ding J Q. Global warming increases the interspecific competitiveness of the invasive plant alligator weed, *Alternanthera philoxeroides* [J]. Science of the Total Environment, 2017, 575: 1415–1422.