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湿地土壤种子库与地上植被相似性关系研究评述

刘庆艳[1,2], 姜　明[1,*], 吕宪国[1], 王国栋[1,2]
(1. 中国科学院湿地生态与环境重点实验室,中国科学院东北地理与农业生态研究所,长春　130102;2. 中国科学院大学,北京　100049)

摘要:土壤种子库与地上植被的关系是土壤种子库研究的重要组成部分。当前,湿地生态系统面临严重威胁,研究湿地土壤种子库和地上植被关系既可以加强对土壤种子库和植物群落特征的认识,又可以为湿地保护与管理提供理论指导。检索了科学引文索引扩展版(SCIE)数据库中收录的 1900—2012 年间研究湿地土壤种子库与地上植被关系的文献,通过分析土壤种子库与地上植被的 Sørensen 相似性系数,结果发现:不同湿地类型的土壤种子库和地上植被的相似性存在显著差异,河流湿地中两者的相似性最小;不同植被类型中土壤种子库与地上植被的相似性差异显著:草本群落的相似性大于乔木群落;不同气候带的湿地中两者的相似性也存在显著差异,其中亚热带地区相似性最小。总结了湿地种子库与地上植被相似性关系的时空变化特征。二者的相似性通常随着植物群落的演替而减小,在空间上也随着环境梯度而变化。分析了两者关系的影响因素,如种子传播、环境条件和繁殖策略等。对研究中存在的问题及发展方向提出建议。

关键词:土壤种子库;地上植被;湿地;相似性

A review of similarity between soil seed bank and aboveground vegetation in wetlands

LIU Qingyan[1,2], JIANG Ming[1,*], LÜ Xianguo[1], WANG Guodong[1,2]
1 *Key Laboratory of Wetland Ecology and Environment, Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun* 130102, *China*
2 *University of Chinese Academy of Sciences, Beijing* 100049, *China*

Abstract: The relationship between soil seed banks and aboveground vegetation is one of the most important components of soil seed bank research. It provides critical information on the nature of vegetation regeneration in ecosystems and ultimately guides the conservation and management of wetland biodiversity. In order to explore this relationship, using the Sørensen similarity index we reviewed the literature on the study of wetland soil seed banks and vegetation from 1900 to 2012, based on the Science Citation Index Expanded (SCIE). The results indicate that the similarity between soil seed banks and the vegetation of different wetland types varies significantly. Riverine wetlands had the lowest similarity between aboveground vegetation and seed banks compared with marshy wetland, lacustrine wetland and coastal wetland. Similarity varied significantly among different vegetation types, and herbaceous plant communities had a higher similarity than forested communities. A significant difference in the similarity index was also found among climatic zones, with the lowest in subtropical zones. This paper also reviewed the temporal and spatial characteristics of the relationship between wetland soil seed banks and vegetation. Similarity varied among seasons and years. Generally, the similarity index decreases with plant community succession; however, it varies in proportion to environmental factors, especially water disturbance. Most of the

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* 通讯作者 Corresponding author.E-mail: jiangm@ neigae.ac.cn

studies were conducted on a local scale using the space-for-time method. Long-term observational and landscape scale studies have become a new trend. Factors influencing their relationships were discussed in terms of seed dispersal, environmental conditions and reproductive strategy. Seed dispersal by wind, water and animals changes the species composition of the seed bank, making it different from the aboveground vegetation. Seeds that accumulate in persistent seed bank remain viable for a long period, which might otherwise perish in aboveground vegetation—one of the reasons for low similarity at the late successional stage. Environmental conditions, such as light, temperature and water conditions, are another mechanism driving plant community composition, affecting seed germination and seedling survival. The similarity is high in conditions suitable for seed germination and establishment, and low in unsuitable conditions. Differentiation in reproductive strategy between sexual reproduction and vegetative reproduction also resulted in a difference in species abundance in seed banks and in the similarity between seed banks and aboveground vegetation. The relationship between seed banks and vegetation can provide an insight into how the composition of plant communities changes in respect to disturbances, succession and restoration. A high similarity between seed banks and aboveground vegetation is more likely with the regeneration of vegetation on wetlands. In terms of wetland conservation and management, it is necessary to carry out assessments of targeted species and environmental evaluations of seed banks. For a comprehensive understanding of plant community structure and dynamics, it is proposed that future research should focus on the relationship between the soil seed bank and aboveground vegetation in wetlands. Long-term observation of wetland ecosystems and improved methods are suggested. At the same time, research suggests that there should be far more focus on how seed banks and aboveground vegetation influence each other and whether there is a threshold of similarity index indicating changes in plant community characteristics based on statistics. More studies should focus on the conservation and management of wetlands due to global climate change and human activity.

Key Words: soil seed bank; aboveground vegetation; wetlands; similarity

土壤种子库是指存在于土壤表面和土壤中的全部存活种子的总和[1]。在联系过去、现在以及未来生境中植物种群、群落的结构与动态时,土壤种子库起到了重要的生态、进化上的作用[2]。土壤种子库在群落的演替过程和扩散过程、植被的更新和恢复以及生物多样性的保护等方面都具有重要作用,近年来成为生态学和土壤学等学科的研究热点。

土壤种子库与地上植被的关系是种子库研究的重要内容之一,并成为土壤种子库研究领域的热点问题[3-5]。土壤种子库是植被天然更新的物质基础[6],与地上植被是相互影响的动态关系。一方面,地上植被的种子通过各种途径输入土壤,形成土壤种子库;另一方面,土壤种子库中种子的萌发又在一定程度上决定了地上群落的结构和功能。由于环境因子和时空动态等对种子库物种留存和地上植被生存现状的影响,土壤种子库与地上植被的关系在不同植被类型及其物种组成等方面有不同的表现。研究土壤种子库与地上植被的关系可以预测群落演替方向及未来植被状况[7],对评价种子库的生态恢复功能有重要作用[8-9],并可为植被管理提供理论指导[10]。

湿地具有重要的水文功能、生物地球化学功能和生态功能[11],世界自然保护联盟(IUCN)将湿地生态系统与森林生态系统、农田生态系统并称为全球陆地三大生态系统。全球性的湿地消失和退化引发了严重的生态环境和社会问题,直接威胁到区域、国家乃至全球的可持续发展。随着人们对湿地重要性认识的日益深入,湿地及其恢复与重建逐渐受到广泛重视。土壤种子库是植被群落修复可行性的有用指标[12-15],在湿地修复中起重要作用,已被证实是一种有效的植被修复方法[16-17]。对退化湿地进行植被恢复及湿地的有效管理有必要认识土壤种子库与地上植被的关系[18]。

相比森林和草地生态系统,目前湿地土壤种子库的研究相对较弱[3],湿地土壤种子库与地上植被二者之间关系及相互作用机制尚没有被完全揭示[19]。国内外对土壤种子库与地上植被的关系已经做了大量研究,本文结合国内外湿地种子库研究

的进展,以湿地土壤种子库与地表植被相似性系数为切入点,基于文献中数据资料的整理,对湿地土壤种子库与地上植被关系、时空变化特征及影响因素进行了系统概括和总结,以加强对湿地生态系统的认识,为湿地保护与管理以及湿地恢复提供指导。

1　数据来源及数据处理

研究种子库与植被关系的主要评价指标是种子库与地上植被物种组成的相似性,通常用 Sørensen 相似性系数(SC)[20]表示:

$$SC = 2w/(A + B)$$

式中, A 表示土壤种子库中的物种数, B 表示地上植被的物种数, w 表示种子库和地上植被共有的物种数。

本文在 ISI Web of Science 文献数据库中,以(seed bank OR seedbank OR propagule bank) AND vegetation 为主题词,检索 1900—2012 年间所有文献类型的科学引文索引扩展版(SCIE)文献。在此基础上,依据《Wetlands》[21] 汇总的 marsh、mire、swamp、bog、peatland 等 35 个湿地词汇进行进一步检索,得到 371 篇关于湿地土壤种子库的文献。根据文献是否提供充足数据以计算土壤种子库与地上植被的相似性系数,筛选出 54 篇文献,得到 85 个有效数据[7, 9, 14, 18-19, 22-70]。这些研究分布于 16 个国家 82 个研究区,主要集中在欧洲和北美(占研究区总数的 72%)。我国对湿地土壤种子库与地上植被关系的研究起步较晚,但发展迅速,占研究区总数的 15%。

为了探究湿地生态系统内部土壤种子库与地上植被关系的特征和趋势,对二者相似性按照湿地类型、植被类型和湿地分布的气候带进行了划分:(1)依据国家林业局湿地调查规范对中国湿地类型的划分,将搜集到的文献中的湿地归为沼泽湿地、湖泊湿地、河流湿地以及近海与海岸湿地 4 种类型。沼泽湿地中包括草本沼泽、木本沼泽、泥炭沼泽、沼泽化草甸,湖泊湿地中包括湖、湖滨湿地、干盐湖,河流湿地中包括河岸湿地、洪泛平原湿地,近海与海岸湿地中包括海岸湿地、潟湖以及潮汐淡水沼泽。(2) 依据植物群落优势物种的生活型将湿地植被划分为草本湿地群落、灌木湿地群落和乔木湿地群落三类。(3)比较了不同气候带湿地土壤种子库与地上植被相似性的差异,这些气候带分别是热带、亚热带、温带和寒带。

参考 Hopfensperger[71] 的研究方法,采用单因素方差分析(One-Way ANOVA)、Bonferroni 多重比较分析方法分别对不同湿地类型、不同植被类型以及不同气候带中湿地的 Sørensen 相似性系数的差异性进行检验。对不满足方差齐性的数据采用 Welch 检验及 Games-Howell 多重比较。

2　土壤种子库与地上植被相似性

2.1　不同湿地类型的比较

本文中,湿地生态系统整体的土壤种子库与地上植被的相似性系数为(45.1±2.0)%,接近于 Hopfensperger 的研究结果(47±2.4)%[71],仍介于森林生态系统和草地生态系统之间。单因素方差分析表明,不同湿地类型中土壤种子库与地上植被的相似性系数具有显著差异($F=4.440$, $P=0.006$)。由图 1、表 1 可以看出,沼泽湿地中二者的相似性系数最大,这与枯落物对种子的捕获以及种子萌发形成地表植物群落有较大关系[38, 58]。所有河流湿地的研究结果都小于 70%,相似性系数明显小于其他 3 种湿地类型。这可能是由于河岸系统的一些物理过程影响了种子库的组成,如水文状况、水力传播以及矿物质和有机沉积物的侵蚀与沉积等[72]。各湿地类型中二者的相似性系数范围都比较大,尤其是近海与海岸湿地(图 1),因此,目前还不能就种子库与地上植被的物种组成的差异性和相似性得出统一的结论,但湿地中二者的相似性系数多集中在 40%—60%,占总数据量的 54%。

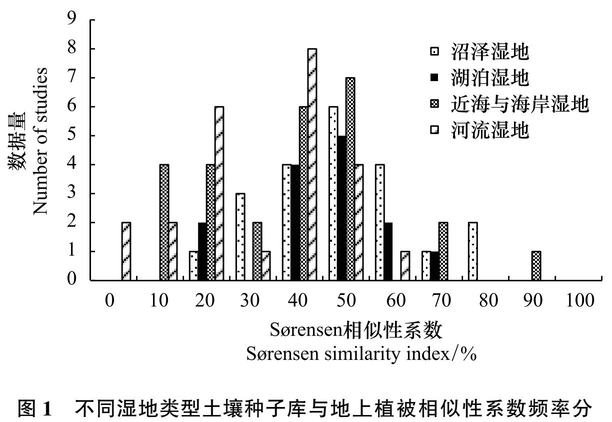

图 1　不同湿地类型土壤种子库与地上植被相似性系数频率分布图

Fig.1　Frequency distributions of the Sørensen′s similarity values for each wetland type reviewed

表 1 不同湿地类型、植被类型和气候带的湿地土壤种子库与地上植被的 Sørensen 系数

Table 1 Sørensen's similarity index between soil seed bank and vegetation in different wetland types, vegetation types and climate zones

类型 Types		数据量 Number of studies	Sørensen 相似性系数/% Sørensen similarity index
湿地类型 Wetland types	沼泽湿地 Marshy wetland	21	53.7±3.4 a
	湖泊湿地 Lacustrine wetland	14	50.7±3.8 ab
	近海与海岸湿地 Coastal wetland	26	43.9±4.1 ab
	河流湿地 Riverine wetland	24	35.8±3.4 b
植被类型 Vegetation types	草本群落 Herbaceous community	62	48.7±2.3 a
	灌木群落 Shrub community	6	36.7±5.0 ab
	乔木群落 Forested community	17	35.1±4.5 b
气候带 Climatic zones	热带 Tropical zone	5	54.7±2.3 a
	亚热带 Subtropical zone	33	37.3±3.4 b
	温带 Temperate zone	42	49.4±2.8 a
	寒带 Frigid zone	5	51.5±1.4 a

不同小写字母表示差异显著($P<0.05$)

2.2 不同植被类型的比较

不同湿地植被类型中土壤种子库与地上植被的相似性系数存在显著差异($F=4.597$, $P=0.013$)。草本群落显著大于乔木群落,相似性系数分别为(48.7±2.3)%和(35.1±4.5)%(表 1),而草本群落与灌木群落、灌木群落与乔木群落中相似性的差异不显著。Hopfensperger 的研究表明草地生态系统的相似性系数大于森林生态系统[71],本文统计结果与此相类似。一般而言,草本植物易于形成土壤种子库,但不同生活型草本的土壤种子库大小不同,在多年生草本占优势的地域,土壤种子库很小。由于木本植物种子形体大、容易被捕食等原因,一般木本植物在土壤中积累的种子很少[71,73],所以木本植物对土壤种子库的贡献很小,通常只形成短暂土壤种子库。

2.3 不同气候带的比较

对不同气候带湿地土壤种子库与地上植被的相似性系数进行 Welch 检验,组间均值差异达到极显著水平($P=0.004$)。由表 1 可以看出,亚热带气候条件下湿地土壤种子库与地上植被的相似性系数较低,与其他气候带差异较大,而热带和寒带地区的相似性系数相对较高。目前湿地土壤种子库的研究主要集中在温带和亚热带地区,热带和寒带地区研究比较少,其中土壤种子库与地上植被关系的研究还有待加强。掌握各气候带湿地种子库与地上植被关系的规律性,有利于探究不同地带中的湿地植物群落特性,进而指导相应地带中的湿地保护与管理。由于有些分类组内样本量较小,本文统计结果是否具有稳定性,还需要更多湿地种子库的研究进行补充。

3 湿地种子库与地上植被相似性关系的时空变化特征

3.1 时间变化

种子库与地上植被的相似性会随时间变化,不仅体现在季节动态上,而且有年际变化。二者相似性的季节变化一般对应于淹水等环境条件的变化,以及种子库组成的季节变化和植物的季节性枯荣[14, 74]。

大量研究表明湿地土壤种子库与地上植被的相似性随植物群落演替过程的发展呈下降趋势[22,40,57,75]。这可能是因为演替早期的物种通常产生大量、个体小、寿命长的种子,演替后期的物种一般产生少量、个体大、寿命短的种子,导致演替早期的物种在整个演替系列期的种子库中占优势,而在后期的地上植被中并不常见[22,40-41,48]。另外,土壤条件,特别是土壤水分空间格局的改变[76],以及演替阶段所反映的干扰状况的差异,也可能对演替过程中湿地土壤种子库与地上植被的相似性产生影响。通常干扰频率高、距离扰动时间短的生境中,地上植被与种子库的相似性高[57,77]。根据两者关系在演替过程中呈现的规律,可以反推湿地的演替阶段:Blood 等[27]研究发现 Bonita 沼泽中种子库和地上植被的相似性系数处于中等水平,据此推断该森林湿地处于中期演替阶段。但也有一些研究结果与上述结论不一致。Ma 等[78]对青藏高原高寒湿地土壤种

子库的研究发现,随着湿地向成熟草甸演替,两者的相似性反而增大,认为是由于后期演替阶段的环境条件更适宜种子萌发和幼苗存活,种子库对植被的贡献较大导致的。

短时间尺度内种子库与地上植被关系的年际变化并不明显,Leck[53]在一个新建的潮汐淡水湿地的研究发现,前 4a 种子库与植被的相似性系数变化范围在 11%—53%之间,但是年际间没有特定的变化模式,而且地点和位置间也没有特定变化模式。

目前,关于长时间序列内种子库和地上植被关系变化的研究比较少,大多是以空间代替时间的方法来进行研究。为了更好地阐明演替过程中两者的关系,需要进行长期定位观测。

3.2　空间变化

在空间上由于微地貌的作用,湿地土壤种子库的组成会随海拔梯度及环境梯度的变化而呈现出空间异质性[79-81]。湿地种子库与地上植被的相似性在空间上随着环境梯度变化通常也呈现出一定的规律性。在海岸和河岸生态系统中,随着距水岸距离的增加,水分条件由湿到干,水文扰动频率由高到低,种子库与植被的相似性都呈降低趋势[29, 40]。这是因为洪水扰动及水力传播导致繁殖体广泛分布呈现均质化,而地上湿地植被由于水分条件限制生长在特定生境。Hopfensperger 等[19]在对潮汐淡水沼泽植被与种子库动态的研究中发现,1 年生植物群落种子库与植被的相似性随海拔升高而减小,而多年生植物群落的相似性随海拔升高而增大,并建议修复湿地时要考虑景观及空间结构要素使群落多样性最大化。但是 Lu 等[57]在对三峡库区消涨带种子库的研究中发现,种子库及地上植被的物种丰度随水位的变化有相似的趋势,都是水位越深,物种越少,而水位深度对种子库与地上植被的相似性没有影响。

目前,大部分湿地土壤种子库的研究都局限在局域尺度上,仅在某一特定湿地内的不同植被类型之间或同一植被类型内开展,而在更大的尺度上两者的组成都会更加稳定。目前,景观尺度上湿地种子库的组成和变化开始得到关注[82-83],但种子库与植被关系的空间变化研究还较少。

4　湿地土壤种子库与地上植被关系的影响因素

Whipple[84]将土壤种子库与地上植被的关系分为 4 种情况:(1)有种子也有植株,(2)有种子而没有植株,(3)有植株但土壤中没有种子,(4)没有植株也没有种子。造成这种状况的原因多种多样,既有环境因子的影响,也有物种本身的生物学特征的差异。

4.1　种子传播

土壤种子库的物种组成主要受其地上植被的影响,但土壤中常含有一些地上植被不存在的物种,这可能是由于种子传播引起的[43]。湿地植物传播包括多种途径,如水流、风、动物等。水是湿地生态系统的重要组成部分和显著特征之一,水力传播是湿地繁殖体长距离传播的一种重要途径[42, 85-86]。此外,水禽、鱼类等动物在湿地种子传播中也起到积极作用[87]。繁殖体经过一定距离的传播进入土壤种子库,之后萌发成幼苗,并影响该区域的植被动态。种子传播是决定植物分布格局和种群遗传多样性的重要过程,对于维持和恢复破碎景观的生物多样性有重要意义[88-89]。

4.2　进化记忆

种子库的组成明显受到植被历史的影响。大多数种子散落到地表进入种子库后,要经历一个休眠阶段,由于物种种类和环境条件的差异,休眠时间可以从几天到很多年。一个植物群落的种子库通常会保存演替早期的物种,形成长久种子库,而这些物种在植被中可能已经消失,造成土壤种子库与地上植被的差异[22, 41],这也是演替后期两者相似性较低的原因之一。许多研究表明随着土壤深度的增加,植被与土壤种子库的相似性逐渐降低[41, 54,90]。Grandin 和 Rydin[41]研究了经过一百多年初级演替的种子库,通过对比不同时期调查的植物名录发现,当前植被与上层土壤种子库关系密切,而 12—15 cm 的土层中的物种在地上植被中已经消失。在受到扰动或遇到适宜的环境,土壤中埋藏的种子就会重新萌发。一个植物群落的种子库是对它过去状况的“进化记忆”[91],这种记忆效应有利于维持群落的稳定性,也是植被恢复的基础。

4.3　环境条件的适宜性

种子萌发是一个复杂的生理过程,取决于许多环境因素,比如光照、温度、水分等。湿地的水文状况,包括淹水深度、持续时间和淹水频率,以及冠层及枯落物对光照和温度的影响等都会影响种子库和

植被的动态[38, 92-93]。植株从种子到幼苗的转化是决定未来植被的重要过程,环境条件会影响种子萌发以及幼苗存活,进而影响土壤种子库与地上植被的关系。许多研究发现在土壤种子库中大量存在的物种,在地上植被中却很难发现其幼苗和成熟个体,这可能是由于种子萌发和幼苗生长受到限制引起的[33, 57,94-95]。特定环境中只有满足萌发和生长条件的种子才能转化为植被,因此,当环境条件满足多数物种萌发和建立的要求时,种子库和植被的相似性较高。反之,当生境条件仅满足少数物种的要求时,两者的相似性较低。只有结合不同时期和环境条件下的植被数据,才能准确理解种子库和植被之间的关系,例如在梁子湖湖岸沼泽湿地旱季和雨季对应的退水和淹水条件下,两者的相似性系数分别是66%、51%,结合两种条件下的植被与种子库,相似性系数达到81%[14]。

4.4 繁殖策略

种子库与地上植被相似性低的另一个原因是一些植物仅存在于地上植被中,而种子库中不存在或很少存在该物种的种子,这些物种主要依靠营养繁殖体进行繁殖,比如根状茎或块茎。例如在泥炭地和沼泽中占优势的芦苇(*Phragmites australis*),由于种子不具有活力,种子库中很难发现其种子[76,92]。Capers[96]对淡水潮汐湿地(freshwater tidal wetland)的研究发现沉水植物主要依靠营养繁殖体和营养生长来扩张新的生境,16 种沉水植物仅有 4 种出现在种子库中。中华水韭(*Isoetes sinensis*)、问荆(*Equisetum arvense*)等蕨类植物则不产生种子,通过孢子繁殖。已有研究表明,以 1 年生为主体的植被类型中,种子库与地上植被的相似性很高[19];以多年生为主体的植被类型中,二者的相似性较低[27, 56]。对大多数植物而言,存在营养繁殖和有性繁殖的均衡,并借以适应某些方式的干扰[97]。因此,干扰会通过植物的繁殖方式影响种子库与地上植被的相似性。Klimkowska[98]对沼泽湿地的研究结果显示,随着干扰强度的增加,植物种子产量增加,种子库与地上植被的相似性系数略有增大。除了以上几个影响因素,种子本身的生理、形态特征,人为干扰(火烧、耕作和放牧等)以及植物之间的化感作用等都会在不同程度上影响种子库和植被的动态[3, 99],进而影响土壤种子库和地上植被的关系。

5 土壤种子库在湿地保护与管理中的应用

土壤种子库是植被更新的物质基础,在湿地的保护和受损湿地的恢复与重建中的作用正日益受到重视。在湿地保护方面,土壤种子库与地上植被的相似性越高,植物群落在遭受破坏后恢复到原有水平的可能性越大。利用土壤种子库进行生态修复的前提之一是评估种子库的恢复潜力,检查一些在地上植被中消失的目标物种,在种子库中是否仍有存留。三江平原沼泽湿地开垦 10a 后,土壤种子库中保存有大量的湿地物种,优势物种小叶章和苔草依然存在,说明种子库具有很大的恢复潜力[100]。在湿地的保护和恢复实践中,可以通过种子库的原位萌发和异位移植等方法恢复湿地植被。日本利用湖泊沉积物中的种子库进行湖岸植被修复取得了较好的效果[15]。美国鱼类和野生动物保护协会在纽约北部对残存湿地土壤进行了移植实验,结果表明由于湿地土壤保留了较多湿地物种,种子库移植是一种有效的湿地植被修复技术[101]。利用种子库进行湿地植被恢复需要明确种子库移植的最佳时间、种子库萌发和建群的适宜生境条件以及非目标物种的去除方法等,以保证湿地恢复能达到预期效果。

6 研究展望

土壤种子库与地上植被存在相互转化的动态关系,共同推动植物群落的发展,因此全面掌握植物群落的结构和动态需要将二者结合。土壤种子库和地上植被不仅有物种组成上的差异,而且表现在生活型和种子及植物的丰度上。全面掌握湿地土壤种子库与地上植被的关系,在湿地保护和受损湿地的恢复与重建中具有重要作用。种子库与植被相似性低的湿地在退化或破坏后自我恢复的潜力相应较低,需要加强保护与管理。

目前土壤种子库与地上植被关系的研究还不系统,针对研究中存在的问题提出以下建议:(1)采取长期定位观测,减小短期调查中系统内部的波动,研究湿地土壤种子库、植被及其相互作用的动态,完善土壤种子库的理论体系。(2)改进土壤种子库的研究方法。一方面,要减少取样的随机误差,避免遗漏一些种子数量少的物种。另一方面,在物种鉴定上,大约 90%的研究都采用种子萌发法[102],但是在应用

萌发法时要考虑打破种子休眠和不同物种萌发所需要的条件,使尽可能多的种子萌发,以提高研究结果的精确性。(3)在掌握湿地土壤种子库和植被相似性规律的基础上,加强两者相互作用的机理研究,探究影响种子库和植被格局的主要因子。(4)探索在植物群落发展过程中土壤种子库和地上植被的相似性是否存在阈值来指示植物群落特征的变化,以利于湿地管理中的植被调控。(5)在全球气候变化与人为干扰加强的背景下,将二者关系的理论研究应用到湿地保护与管理的实践中,改变湿地严重退化的现状。

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