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人工恢复与自然恢复模式下苔草草丘生态特征比较

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摘 要 本研究以哈尔滨太阳岛草丘湿地为对象,对比了人工恢复与自然恢复下苔草草丘个体和种群的生态特征,并分析其与环境因子的关系.结果表明:苔草植株生长随时间呈现先增加后降低的变化趋势(5—8 月),初期(5—6 月)生长迅速,6 月达到峰值.人工恢复和自然恢复模式下,苔草草丘个体和种群特征差异显著:自然恢复下苔草叶面积、叶宽、单株鲜重、单株干重、丘墩高度、直径、丘顶面积、丘墩表面积、丘墩体积等苔草草丘个体特征均显著高于人工恢复,人工恢复下苔草草丘密度、盖度、生物量等种群特征显著高于自然恢复,物种多样性无显著差异.土壤含水量、水深、草丘密度、丘间距离是导致 2 种恢复模式下苔草草丘生长差异的主要因素,自然恢复区土壤含水量、水深、间距均显著高于人工恢复区,对草丘个体的形成和发育具有促进作用,人工恢复区高移栽密度是导致草丘密度、盖度、生物量高于自然恢复区的主要因素.建议未来开展苔草草丘湿地恢复和保护时,应参考自然恢复湿地中草丘的分布特点,适当调整丘间距离(54.22~117.89 cm)和种群密度(1.9~3.1 墩·m^{-2}),同时采取干旱区春季适当补水措施,保持适宜的土壤含水量和水深,促进苔草草丘的生长发育和快速恢复,维持其种群长期健康稳定.

关键词 苔草草丘; 恢复模式; 生态特征; 环境因子; 太阳岛湿地

Comparison of ecological characteristics of *Carex* tussock under natural and artificial recovery. QI Qing[1,2], LIU Xiao-wei[3], TONG Shou-zheng[1*], ZHANG Dong-jie[1,2], ZHANG Ming-ye[4], AN Yu[1], WANG Xue-hong[5] ([1]*Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun* 130102, *China*; [2]*University of Chinese Academy of Sciences, Beijing* 100049, *China*; [3]*School of Geographical Sciences, Northeast Normal University, Changchun* 130024, *China*; [4]*Yanbian University, Yanji* 133000, *Jilin, China*; [5]*Ludong University, Yantai* 264025, *Shandong, China*).

Abstract: We compared the ecological characteristics of tussock individuals and populations undergoing natural and artificial restoration in *Carex* tussock wetlands in the Sun Island in Harbin and identified the relationships between the growth of *Carex* tussock and environmental factors. Results showed that there were obvious seasonal dynamics in morphological characteristics of *C. appendiculata*. Tussocks grew rapidly from May to June, peaked in June, and then decreased steadily from July to August. There were significant differences in ecological characteristics of *Carex* tussocks between natural and artificial restorations. The morphological characteristics of individual tussock, including leaf area, leaf width, fresh weight per ramet, dry weight per ramet, and the hummock shape indicators (hummock height, diameter, volume and surface area) in natural restored area were significantly higher than those in artificial transplanting area. For the *Carex* tussock community, tussock density, coverage and biomass in natural restoration area were significantly lower than those in artificial transplanting area. Soil water content, water depth and hummock spacing in natural restoration area were significantly higher than those in artificial restoration area, which facilitated the formation and development of individual tussock. Higher transplanting density was the main fac-

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tor leading to higher density, coverage, and biomass in artificial restoration area. Our results suggested that the distribution characteristics of tussocks in natural restoration area should be taken into account in future restoration and protection works. Appropriate adjustment of the distance between hummock (54.22-117.89 cm) and population density (1.9-3.1 ind · m^{-2}), as well as proper water recharge measures in spring in arid areas to regulate soil water content and water depth, would be conducive to promoting the growth and rapid recovery of *Carex* tussock, which would maintain the long-term health and stability of tussock wetland.

Key words: *Carex* tussock; restoration method; ecological characteristics; environmental factor; Sun Island wetland.

湿地是水陆综合作用形成的自然综合体,具有涵养水源、均化洪水、净化环境、调节气候、提供生境等多种生态功能,是自然界生产力最高的生态系统之一[1].研究表明,湿地的退化和丧失已成为全球范围内无可争辩的事实,2009 年以来,全球湿地面积损失了至少 33%[2],中国天然湿地面积的减少率高达 9.3%[3].湿地保护和恢复已成为当前湿地生态研究的焦点之一[4].

湿地恢复与重建的方法包括自然恢复、人工辅助恢复及人工恢复[5].自然恢复以减弱或移除导致湿地退化的干扰因子为主要措施,由自然演替主导湿地恢复;人工辅助恢复是通过改善生态系统结构和理化环境促进生态系统恢复;人工恢复通常借助工程措施直接调控或重建生态系统[6].由于湿地类型及退化原因存在差异,各地区在湿地恢复与重建中采取的恢复方法及技术体系也不同[7],恢复效果存在差别.周远刚等[8]对比了不同恢复方式对湿地植被的影响,发现人工恢复能够有效促进植被生长,自然恢复则更有助于物种多样性的维持,对植被生长发育的促进作用却不明显.有研究发现,自然恢复和人工恢复均可提高植被高度[9-10].张冬杰等[11]针对臌囊苔草(*Carex schmidtii*)草丘湿地群落物种多样性的研究表明,人工辅助恢复可快速恢复湿地物种种群,有效促进湿地植物群落稳定.苔草草丘湿地是一种典型的湿地类型,广泛分布于温带沼泽湿地、河流洪泛湿地及山区沟谷湿地中[12-15].草丘湿地具有多种生态功能,丘墩的凸起增加了微地貌的异质性,改变了局部地表水热条件[16-18],对于湿地微生境营造和物种多样性形成及维持等具有重要作用[12].研究表明,草丘地上部分碳库高于其他草本系统,苔草分蘖根形成的密丛型生态结构(草丘),促进了难分解物质的累积,对草本泥炭的形成起关键作用[19],在应对全球变暖和减缓 CO_2 浓度升高方面具有巨大的潜力[14].因此开展不同恢复方式下苔草草丘生态特征研究对于草丘湿地保护与恢复具有重要意义.

受地表水位下降、农田排水、农业开垦、经济活动等影响,近年来东北地区苔草草丘湿地受到不同程度的破坏[20-22],草丘大面积死亡[23],土壤理化性质发生改变[24],草丘湿地的固碳功能和生物栖息功能显著下降[25-27],退化草丘湿地亟需得到恢复.目前,对于苔草草丘的研究主要集中在自然苔草草丘的结构、空间分布、物种多样性等方面[14,28-30],针对退化苔草草丘恢复的研究尚不多见.本研究以哈尔滨太阳岛景区自然恢复和人工恢复的灰脉苔草(*Carex appendiculata*)草丘为对象,通过比较 2 种恢复模式下苔草草丘个体及种群的生态特征和环境条件差异,解析草丘生态特征差异的主要原因,明确影响苔草草丘生长发育的环境因子,为苔草草丘湿地的保护和恢复提供基础数据,为受损苔草草丘湿地恢复方式的选择和改进提供参考.

1 研究地区与研究方法

1.1 研究区概况

研究区位于黑龙江省哈尔滨市太阳岛风景区,地处松花江沿岸.该区属于温带大陆性季风气候,年均温 5.24 ℃,年降水量 569.1 mm,主要集中在 6—9 月,植物群落以灰脉苔草群落、芦苇(*Phragmites australis*)群落、香蒲(*Typha orientalis*)群落为主,伴生有小叶章(*Deyeuxia angustifolia*)、桃叶蓼(*Polygonum persicaria*)、泽芹(*Sium suave*)等,7—8 月植被覆盖可达 80%以上.主要的土壤类型为黑土、沼泽土和草甸土[30].研究区曾有大面积苔草草丘发育,21 世纪初受人类活动影响,该区域水文条件发生明显变化,导致苔草草丘严重退化和大面积死亡.为了保护和恢复苔草草丘湿地,中国科学院东北地理与农业生态研究所湿地恢复研究团队研发了草丘原位分根(分株)取苗和干湿交替的根茎克隆恢复技术[31],于 2008 年开展小区试验,成功恢复苔草草丘湿地 120 m^2,证实了根茎克隆繁殖结合水位调控可实现

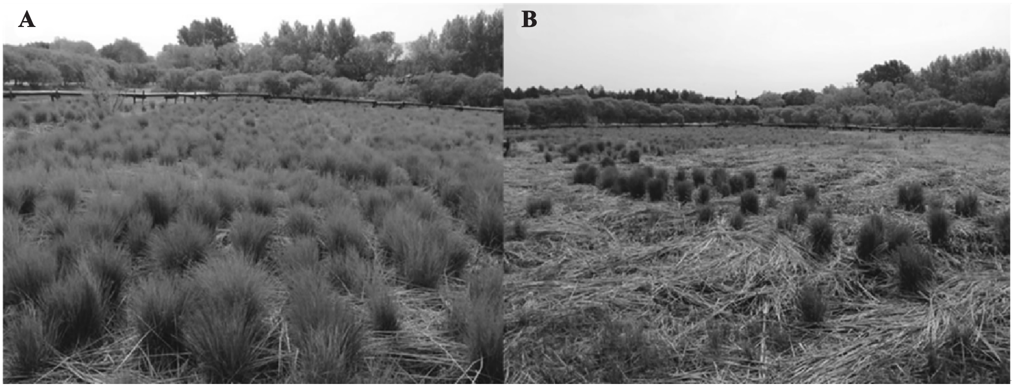

图 1　2018 年 5 月人工恢复(A)与自然恢复(B)苔草草丘景观

Fig.1　Artificially (A) and naturally (B) restored *Carex* tussock landscapes in May, 2018.

苔草草丘的快速恢复[32].基于上述技术,研究团队于 2009 年开展了大面积草丘恢复工作,到 2010 年成功恢复苔草草丘 1500 m^2.经过 8 年的自然繁衍,该区目前已形成相对独立的自然生态系统,并且在人工恢复区域外围,自然衍生了草丘群落,形成了人工与自然恢复并存的草丘景观(图 1).

1.2　样地选择

如图 2 所示,根据草丘形成方式将研究区划分为 2 个类型:1) 人工恢复区:该区域苔草草丘于 2009—2010 年通过人工移栽形成,由 26 个形状规则的 5 m×10 m 的长方形格田和 2 个不规则格田构成,总面积约 1500 m^2;2) 自然恢复区:位于人工移栽区外围东西两侧地势低洼处,通过自然恢复形成,边缘异质性较高.2010 年该区仅残留个别退化严重的苔草草丘,经过 8 年的自然恢复,苔草草丘面积达到 700 m^2.

1.3　样品采集和测量

2018 年 5—8 月开展野外调查、测量、样品采集.

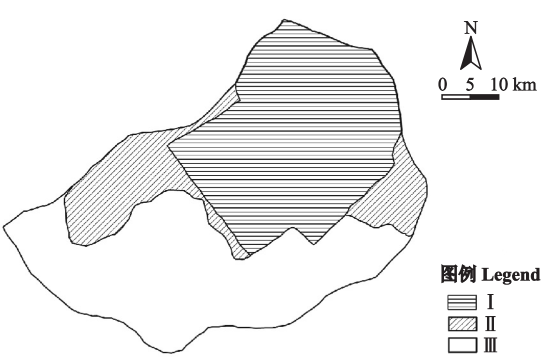

图 2　人工恢复与自然恢复的苔草草丘空间分布

Fig.2　Distribution of *Carex* tussock for natural recovery and artificial recovery.

Ⅰ:人工恢复苔草群落 Artificially restored *Carex* community; Ⅱ:自然恢复苔草群落 Naturally restored *Carex* community; Ⅲ:芦苇-香蒲群落 *Phragmites australis-Typha orientalis* community.

采用网格布点法,基于恢复区面积,在人工恢复区布设 17 个采样点,自然恢复区布设 7 个采样点.由于草丘形态的独特性,传统样方设计会导致较大的调查误差,故本研究设置 3 m×3 m 的样方,共测量草丘 120 个,利用卷尺测量每个样方内苔草草丘的株高、墩高、直径、冠幅及丘间距离、水深,调查苔草草丘种群盖度、密度及群落物种组成.每个样方中选取 3 株长势良好的苔草植株,用叶面积仪测量上数第 2 片叶的叶面积、叶宽,称量单株鲜重后于 65 ℃下烘干称单株干重.采集表层土壤样品,利用土壤水分仪测定土壤体积含水量、电导率,用烘干法测量土壤质量含水量[33],土壤容重由土壤质量含水量除以体积含水量求得.采用苔草植株生长特征(株高、冠幅、叶面积、叶宽、单株鲜重、单株干重)和丘墩形态特征(墩高、直径、丘顶面积、丘墩表面积、丘墩体积)表征苔草草丘个体生长,采用草丘密度、盖度、生物量表征苔草草丘种群生态特征.

丘顶面积、丘墩表面积、丘墩体积由以下公式[28]计算:

$$S_{top}=\pi\left(\frac{D}{2}\right)^2$$

$$S_{sur}=S_{top}+\pi DH_t$$

$$V=\left(4/3\pi H_t\left(\frac{D}{2}\right)^2\right)/2$$

式中:S_{top}为丘顶面积;S_{sur}为丘墩表面积;V 为丘墩体积;D 为丘墩直径;H_t为丘墩高度.

物种丰富度指数(P):

$$P=S$$

Shannon 多样性指数(H):

$$H=-\sum_{i=1}^{S}P_i\ln P_i$$

Pielou 均匀度指数(E):

$E=H/\ln S$

式中：S 为样方内物种数；P_i 为样方内物种的重要值. 其中，P_i =（相对高度+相对盖度）/2；相对高度 = 某物种的平均高度/所有物种的平均高度之和；相对盖度 = 某物种的盖度/所有物种的盖度之和.

1.4 数据处理

采用 Excel 2010 软件进行数据统计分析，利用 SPSS 23 软件进行独立样本 t 检验和单因素方差分析（one-way ANOVA）（$\alpha=0.05$）. 利用 Canoco 5 软件进行冗余分析，利用 Origin 9.0 和 ArcGIS 10.2 作图. 图表中数据为平均值±标准差.

2 结果与分析

2.1 苔草草丘个体生长特征

2.1.1 苔草植株生长特征　如图 3 所示，在 5—8 月的生长过程中，苔草叶面积、叶宽、单株鲜重、单株干重表现为自然恢复>人工恢复，并在 6 月表现出显著差异. 苔草株高和冠幅长势基本一致，自然恢复≈人工恢复. 此外，苔草植株生长随时间呈现出明显的先升高后降低的季节动态，5—6 月生长迅速，6 月苔草叶面积、叶宽、株高、冠幅、单株鲜重、单株干重均达到最大值，随后逐渐下降或基本稳定.

2.1.2 丘墩形态特征　自然恢复和人工恢复的苔草草丘的丘墩形态差异显著，自然恢复区丘墩高度、直径、丘顶面积、丘墩表面积、丘墩体积分别比人工恢复区高 12.8%、10.8%、24.7%、28.0% 和 48.7%（图 4）.

2.2 苔草草丘种群生态特征

人工恢复和自然恢复苔草草丘种群生态特征差异显著，苔草草丘盖度、密度、生物量表现为人工恢复>自然恢复（图 5）. 人工恢复区草丘密度是自然恢复区的 1.9 倍，生物量是自然恢复区的 1.8 倍. 草丘平均盖度最大值为 86.7%，出现在人工恢复区，平均盖度最小值为 37.0%，出现在自然恢复区，2 种恢复方式下草丘盖度在 5—8 月均有明显的先增加后降低的变化趋势，并在 6 月达到峰值，随后缓慢降低或基本不变.

2.3 苔草草丘群落物种组成及多样性特征

由表 1 可知，自然恢复和人工恢复苔草草丘群落物种组成分别为 13 和 22 种，其中共有种 9 种，分别为灰脉苔草、香蒲、小叶章、刺蓼（*Polygonum senticosum*）、芦苇、浮萍（*Lemna minor*）、桃叶蓼、稗草（*Echinochloa crusgalli*）及青绿苔草（*Carex breviculmis*）. 人工恢复区物种组成更丰富，但 2 种恢复方式下物种丰富度指数、多样性指数、均匀度指数均未表现出显著差异.

2.4 苔草草丘生态特征与环境因子的关系

对不同恢复方式下苔草草丘生态特征与环境因子进行冗余分析（RDA），如图 6 所示，前 2 轴的解释率为 55.4%，其中第 1 轴解释率 32.4%，第 2 轴解释率 23.0%. 单株鲜重、单株干重、叶宽与土壤容重、土壤含水量、水深、电导率、间距呈正相关，与草丘密

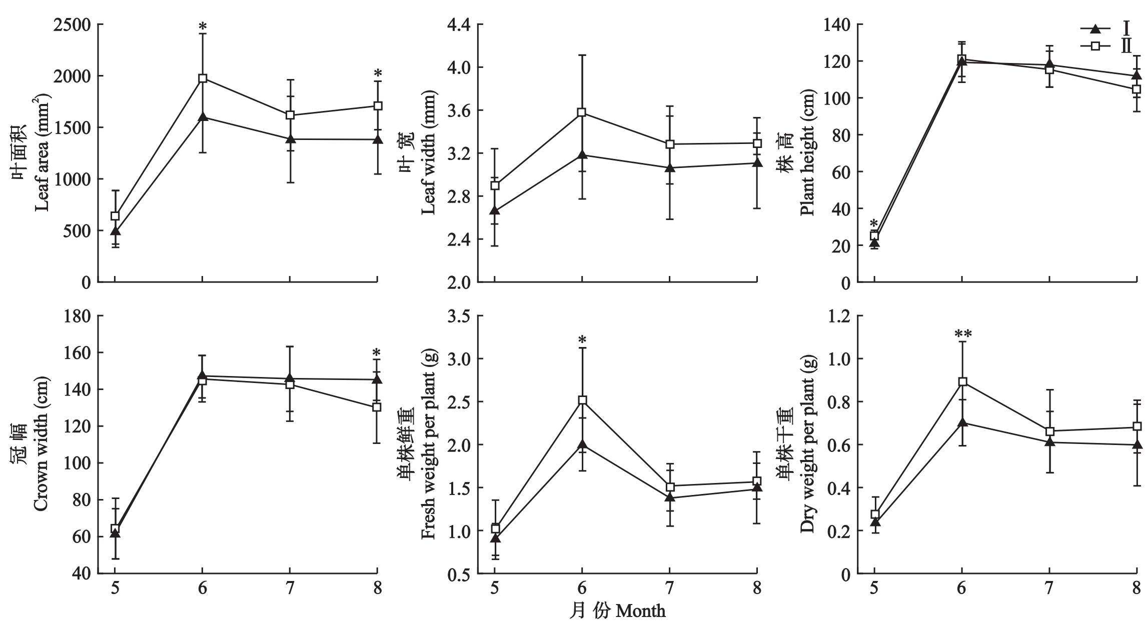

图 3 人工恢复与自然恢复苔草植株 5—8 月生长动态特征

Fig.3 Dynamic features of *Carex* with artificial restoration and natural restoration from May to August in 2018.

Ⅰ：人工恢复 Artificial restoration；Ⅱ：自然恢复 Natural restoration. 下同 The same below. * P<0.05；* * P<0.01.

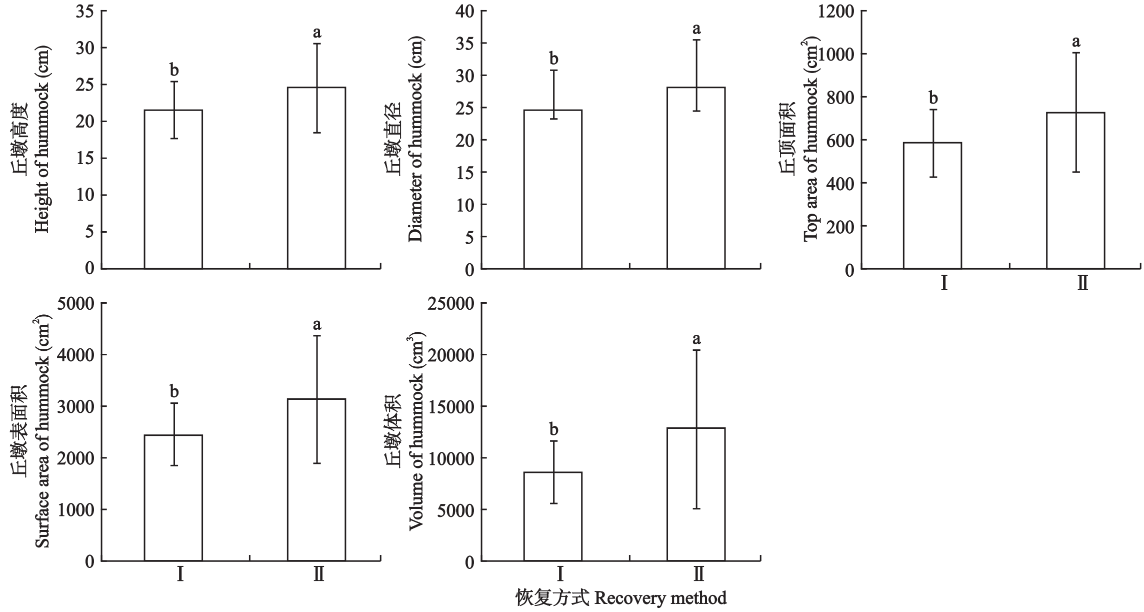

图 4　人工恢复与自然恢复苔草草丘丘墩形态特征

Fig.4　Morphological characteristics of hummock in artificial restoration and natural restoration *Carex* tussock wetland.

不同小写字母表示差异显著($P<0.05$) Different lowercase letters indicated significant difference at 0.05 level.下同 The same below.

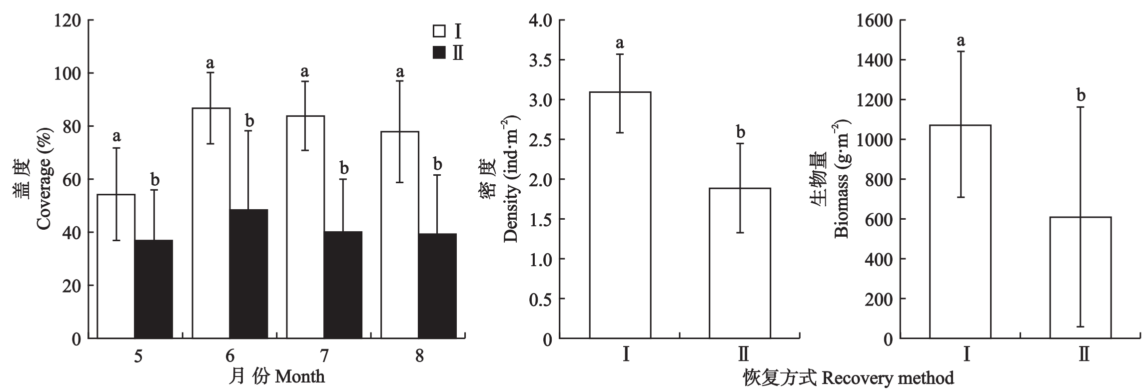

图 5　人工恢复与自然恢复苔草草丘种群生态特征

Fig.5　Ecological characteristics of *Carex* tussock populations with artificial restoration and natural restoration.

表 1　自然恢复区与人工恢复区苔草草丘群落物种组成及多样性特征

Table 1　Species composition and diversity characteristics of *Carex* tussock community in natural and artificial restoration areas

研究区 Study area	丰富度指数 Richness index	Shannon 多样性指数 Shannon diversity index	Pielou 均匀度指数 Pielou evenness index	物种组成 Species composition
自然恢复区 Natural recovery area	6.00±1.63	1.53±0.20	0.87±0.03	灰脉苔草 *Carex appendiculata*、香蒲 *Typha orientalis*、小叶章 *Deyeuxia angustifolia*、刺蓼 *Polygonum senticosum*、芦苇 *Phragmites australis*、浮萍 *Lemna minor*、桃叶蓼 *Polygonum persicaria*、稗草 *Echinochloa crusgalli*、青绿苔草 *Carex breviculmis*、菖蒲 *Acorus calamus*、慈菇 *Sagittaria trifolia*、泽泻 *Alisma plantagoaquatica*、东方蓼 *Polygonum orientale*
人工恢复区 Artificial recovery area	7.43±1.62	1.64±0.17	0.82±0.02	灰脉苔草 *Carex appendiculata*、香蒲 *Typha orientalis*、小叶章 *Deyeuxia angustifolia*、刺蓼 *Polygonum senticosum*、芦苇 *Phragmites australis*、浮萍 *Lemna minor*、桃叶蓼 *Polygonum persicaria*、稗草 *Echinochloa crusgalli*、青绿苔草 *Carex breviculmis*、打碗花 *Calystegia hederacea*、泽芹 *Sium suave*、大戟 *Euphorbia pekinensis*、泥胡菜 *Hemistepta lyrata*、繁缕 *Stellaria media*、毛水苏 *Stachys baicalensis*、灰绿藜 *Chenopodium glaucum*、柳蒿 *Artemisia integrifolia*、野大豆 *Glycine soja*、烟管蓟 *Cirsium pendulum*、葎草 *Humulus scandens*、地笋 *Lycopus lucidus*、苦荬菜 *Ixeris polycephala*

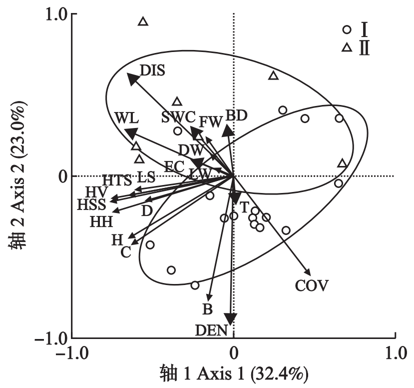

图 6 苔草生长状况与典型环境因子冗余分析

Fig.6 Bioplot of RDA for the relationships between selected environmental factors and growth status of *Carex* tussock.

WL: 水深 Water depth; DIS: 间距 Distance; EC: 电导率 Electrical conductivity; SWC: 土壤含水量 Soil water content; BD: 容重 Bulk density; DEN: 密度 Density; T: 温度 Temperature; FW: 单株鲜重 Fresh weight per plant; DW: 单株干重 Dry weight per plant; LW: 叶宽 Leaf width; LS: 叶面积 Leaf area; HTS: 丘顶面积 Hummock top area; HV: 丘墩体积 Hummock volume; HSS: 丘墩表面积 Hummock surface area; HH: 墩高 Hummock height; D: 直径 Diameter; H: 株高 Plant height; C: 冠幅 Crown width; B: 生物量 Biomass; COV: 盖度 Coverage.

度、温度呈负相关,其中间距、水深、土壤含水量、密度对单株鲜重、单株干重、叶宽影响较大.株高、冠幅、叶面积、墩高、直径、丘顶面积、丘墩面积、丘墩体积与水深、电导率呈正相关,其中水深对苔草草丘上述生态特征影响较大.生物量、盖度与草丘密度、温度呈正相关,与土壤容重、水深、间距、土壤含水量、电导率呈负相关,其中密度、间距、水深对草丘生物量、盖度影响较大.

由图 7 可以看出,2 种恢复方式下土壤含水量、水深、丘间距离、密度差异显著,电导率、容重、温度差异未达到显著水平.自然恢复区土壤含水量为(37.0±6.6)%、水深为(19.76±2.79) cm、草丘间距为(117.89±86.47) cm,均显著高于人工恢复区[分别为(28.9±4.0)%、(9.61±8.53) cm 、(54.22±25.13) cm],而自然恢复区草丘密度为(1.9±0.6)墩·m^{-2},显著低于人工恢复区的草丘密度,即(3.1±0.5)墩·m^{-2}.表明自然恢复区和人工恢复区土壤含水量、水深、丘间距离、密度差异是导致苔草草丘生态特征显著差异的主要因素.

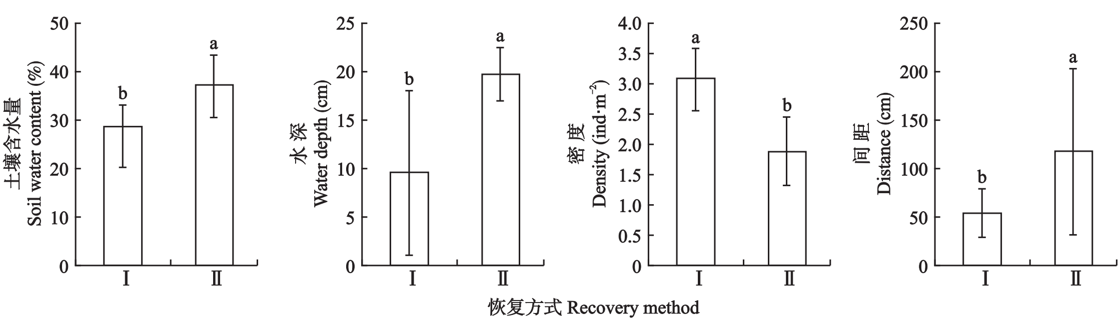

图 7 人工恢复与自然恢复苔草草丘湿地环境因子差异

Fig.7 Difference in *Carex* tussock wetland environmental factors between artificial restoration and natural restoration.

3 讨　　论

影响苔草草丘生存发展的环境因素众多,水文、竞争、光照、火烧等对苔草草丘的生理生态特征具有较大影响[12,34-35].水文条件是湿地形成与发育的基础,是影响湿地植被生存发展的关键因素[36].Lawrence 等[28]通过控制水位波动频率和水位深度,发现长期处于高水位(+18 cm)和高、低水位(−18 cm)频繁波动条件下形成的苔草草丘丘墩周长、体积、叶长等均高于长期低水位和平水位(0 cm)条件下形成的苔草草丘.van Hulzen 等[37]发现,水位较低且波动频繁利于形成高大紧实的草丘,水位过深导致草丘结构松散,甚至死亡.张冬杰等[22]发现,干湿交替对苔草草丘的生长影响显著.在我国东北地区,苔草草丘湿地水深范围一般在 0~42 cm[38].本研究中,灰脉苔草草丘在 4 月下旬开始萌发,5—6 月生长最旺盛,在 6 月达到峰值,而研究区 5、6 月较干旱,无地表积水或仅在自然恢复区有 1~3 cm 的地表积水,测得土壤含水量较高的自然恢复区草丘丘墩体积、叶宽、叶面积、干物质积累均高于人工恢复区,表明在春季苔草萌发和快速生长阶段,增加土壤含水量利于苔草草丘的生长,这与 Yetka 等[39]关于苔草生长在春季达到顶峰且受水分影响较大的研究结果一致.因此,在苔草草丘湿地恢复过程中,应特别关注春季草丘湿地的水分状况,在干旱区域采取补水措施,适当提高土壤含水量和地表水深.

植物生长需要一定的生存空间以满足其对养分、水分及光照等环境资源的需求.密度和间距影响植物所占据空间资源的分配量,间距过小、密度过大可能导致植物种内竞争增大,影响植物的健康生长,或引起植物的自疏[40-42].van de Koppel 等[13]研究表明,丘墩间距一般维持在 60 cm 左右,以保证整个群体获得充足的物质和能量.在我国东北地区,苔草草丘丘墩间距一般在 70 cm 以上[38].本研究中,人工恢复区利用塔头分株移栽技术,在恢复最初,草丘间距设定为 40 cm,密度约为 9 墩·m^{-2},经过 8 年的自然演替后,人工恢复区草丘间距为(54.22±25.13) cm,密度为(3.1±0.5)墩·m^{-2},自然恢复区苔草草丘间距为(117.89±86.47) cm,密度为(1.9±0.6)墩·m^{-2},说明苔草草丘群落所需生存空间较大,恢复技术有待进一步提高.此外,自然恢复区间距大、密度小,形成的草丘个体长势优于人工恢复区,但种群盖度、生物量均较低.人工恢复区苔草草丘间距小、密度大,形成的草丘种群盖度、生物量高于自然恢复区,但草丘个体长势低于自然恢复区.因此,未来针对苔草草丘湿地的恢复过程中,应充分协调草丘个体长势和种群发展的关系,进一步改进恢复方式,将丘墩间距适当增大(不低于 54.22 cm),促进苔草草丘的形成和个体的生长发育.同时,应避免丘墩间距过大(不高于 117.89 cm)、密度过小,确保苔草草丘能够建群和维持种群健康持续发展.

有研究表明,不同恢复模式下湿地生态特征存在明显差异[43],自然恢复的湿地通常具备更完善的生态功能及更丰富的生物多样性[44],人工恢复模式在一定程度上可以加快植物群落的恢复进程,增强植物群落稳定性[45].湿地恢复一般需要很长时间[46-47],崇明东滩人工恢复 2 年的海三棱藨草(*Scirpus mariqueter*)与自然群落总体差异不大[48];南四湖人工恢复 4 年和自然恢复 6 年的湿地在植被覆盖、生产力、系统稳定性方面均无显著差异,表明人工恢复的湿地群落可以在较短时间内恢复湿地的大部分生态功能[49];三峡库区消落带经过 6 年的自然恢复和人工恢复,植物群落的生物量表现为人工恢复>自然恢复,说明人工恢复能快速重建消落带植物,促进群落生物量累积和恢复进程[45].在恢复工作开展 10 年的基础上,本研究中自然恢复区环境条件更适宜苔草草丘个体的生长,而人工恢复对于高盖度、高生产力的苔草草丘种群形成具有促进作用.目前,本研究中,2 种恢复方式下群落物种组成及多样性未表现出显著差异,但是生态系统是一个不断演化的动态系统,生物与环境的相互作用是长期的,不同的恢复年限和恢复阶段都可能导致湿地植被生态特征的差异,评价恢复湿地植被的健康程度及环境适应性应建立在较长的时间尺度上.因此,人工恢复和自然恢复对草丘湿地健康稳定和可持续发展的维持效果还需长期监测.

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