

松嫩平原碱化草甸旱地生境芦苇种群的芽流和芽库动态*

杨允菲** 魏春雁 张宝田 刘 宝

(东北师范大学草地研究所, 植被生态科学教育部重点实验室, 长春 130024)

【摘要】 在松嫩平原碱化草甸, 旱地生境芦苇种群的根茎分布在土层约 1 m 的不同深度, 一般可生活 6 个年度, 个别根茎可存活 7~9 年, 乃至更长的时间. 通过芦苇根茎芽调查, 创建了植物种群的芽流模型. 提出了采用当年 1 龄级根茎芽的输入率与其它龄级休眠芽库存率之和估计芦苇种群芽库贮量动态的方法. 结果表明, 随着生长季的进程, 芦苇种群芽库输入率呈不断增加趋势, 而萌发输出率呈不断减少的趋势, 死亡输出率则大体保持相同的较低水平. 至休眠前期的 9 月底, 芽库输入率已为输出率的 2.04 倍. 在松嫩平原碱化草甸旱地生境, 芦苇种群各龄级根茎的休眠芽有一个稳定的萌发输出过程. 定量分析结果表明, 芦苇种群不同龄级根茎的休眠芽每年都有 11% 的比率萌发形成 1 龄级新根茎. 1 龄级根茎顶端翌年发育为分蘖株后, 可为直接相连接的老龄级根茎就近输送养分, 从而实现老龄级根茎芽的活力.

关键词 芦苇 根茎 龄级 芽库 芽流模型 碱化草甸 旱地生境

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Dynamics of bud flow and bud bank of *Phragmites communis* population in dry land habitat of alkalized meadow in the Songnen Plains of China. YANG Yunfei, WEI Chunyan, ZHANG Baotian, LIU Bao (Key Laboratory for Vegetation Ecology, Ministry of Education, Institute of Grassland Science, Northeast Normal University, Changchun 130024, China). -*Chin. J. Appl. Ecol.*, 2005, 16(5): 854~858.

In the dry land habitat of alkalized meadow in Songnen Plains, the rhizomes of *Phragmites communis* population are distributed in different depths of one meter soil layer, which usually live for 6 years and a few for 7~9 years or even longer. Based on the investigation of their buds, a "bud flow" model of the population was established, and the method for estimating the dynamics of its bud bank storage, i. e., adding the input rate of 1st year age-class rhizome buds to the storage rate of other age-classes dormant buds in the bank, was put forward. The results showed that the input rate of the bud bank increased with plant growth seasons while the burgeoned output rate exhibited a decreasing trend, whereas the output rate of the dead remained at a low level on the whole. By the end of September in the early dormant period, the input rate of the bud bank was as 2.04 times as its output rate, and the dormant buds of each age-class manifested a steady burgeoned output. Quantitative analysis indicated that the burgeoned output rate of dormant buds increased by 11% each year. In another word, 11% of different age-classes dormant buds would germinate and form one-year class new rhizomes. The top of one-year class new rhizomes would develop to ramets in the next year, which would transport nutrients to nearby old-age rhizomes, and thus, maintain the vitality of old-age class rhizomes.

Key words *Phragmites communis*, Rhizome, Age class, Bud bank, Bud flow model, Dry land habitat, Alkalized meadow.

1 引 言

芦苇 (*Phragmites communis*) 是一种根茎型无性系禾本科植物, 具有广泛的生态适应性, 是世界广布种^[3], 天然种群主要依靠营养繁殖补充更新^[26]. 在沼泽地、河漫滩和浅水湖边, 芦苇依靠营养繁殖经常形成单优种群落. 但在旱地生境, 芦苇多以伴生种分布. 在松嫩平原盐生草甸, 不同盐生群落斑块均有芦苇分布. 其中, 在微地形低洼处以及表土完全丧失的碱斑上也可形成单优种群落. 芦苇分株生长和生

产的生态可塑性较大, 因生境条件的差异, 这种可塑性则蕴涵着重要的生长与分配策略^[25]. 旱地生境的芦苇是优良的饲草, 营养生长阶段蛋白质含量在禾草中居于上等. 生长在重度盐碱化草甸碱斑上的芦苇, 强大的地下根茎和根系系统起到促进碱斑土壤通透性的作用, 具有较大的饲用价值和生态价值^[26].

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** 通讯联系人.

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由于芦苇的广布性及其较高的经济和生态价值,自 20 世纪 60 年代以来,国内外学者已开展了广泛的研究,从器官的形态结构^[9]、个体的生物生态学特性^[4,6,10-13]、生理生化特征^[5,7,8,20,23,24,31-33]、种群发展^[14]、根茎的年龄结构^[26]、种间竞争^[2]、分布格局^[11]、群落调节^[15,16],到芦苇湿地的生态效应^[17]、栽培管理^[21,22]等都已有多报道.但对芦苇不同生活年限根茎的繁殖力及其芽库的定量研究,迄今尚无系统报道.

本文根据实地调查,在其它植物种群芽库研究的基础上^[19,27,30],不仅分析了松嫩平原盐生草甸旱地生境的芦苇种群的芽库,还扩展了芽流分析.

2 研究地区与研究方法

2.1 研究地区概况

本研究是在松嫩平原南部的吉林省长岭种马场内东北师范大学草地生态研究站进行(44°38'N, 123°41'E). 该区属于温带半湿润、半干旱气候^[18,19,27]. 样地设在羊草草甸,角碱蓬(*Suaeda corniculata*)、翅碱蓬(*S. hetroptera*)、碱地肤(*Kochia sievieriana*)、虎尾草(*Chloris virgata*)、星星草(*Puccinellia tenuiflora*)、朝鲜碱茅(*P. chinampoensis*)、碱蒿(*Artemisia anethifolia*)等单优势种或混生种的盐生群落镶嵌于羊草(*Leymus chinensis*)群落中,土壤为碱化草甸土. 在地势较低洼地段,全年无积水或 7~8 月份雨季积水时间甚短,经常形成羊草+芦苇群落,微地形中心也可形成几十至几百平方米不等的单优势芦苇群落斑块,芦苇分蘖株的高度在(53.4±13.77)cm 之间,盖度在 90% 以上^[25]. 样地多年来一直作割草场,每年 8 月上旬割草制备冬贮干草.

2.2 研究方法

分别于 2000 年 7 月 20 日、8 月 12 日和 9 月 29 日,在芦苇种群的营养生长旺盛期、生殖生长初期和停止生长休眠前期,在单优势芦苇群落作 3 次挖取根茎取样. 为了保证地上分蘖株和挖取全体根茎的自然联系,先挖一个 1 m 宽、至芦苇根茎分布最底层约 1 m 深的剖面,再向一侧跟踪性挖取根

茎,每次至少挖取 1 m³ 的所有根茎,有些跟踪至最老根茎的死亡点. 回室内按根茎的生活年限划分龄级,其识别方法是,当年形成的根茎为 1 龄级根茎,形成当年分蘖株的上一年度形成的根茎为 2 龄级根茎,与上一年度枯株茬直接相连的根茎为 3 龄级根茎,以此类推^[26,28-30]. 结合芦苇根茎随着年龄的增加色泽变深,以及不同年份形成的根茎直径大小有一定差异等特征,逐条根茎判断龄级. 按各龄级根茎节间芽的现时状态,分别记数休眠芽、已萌芽和死亡芽的数量. 休眠芽按有明显的芽凸计数,已萌芽按形成根茎剪下点计数,死亡芽按既未形成根茎,又失去生活力的芽眼计数.

2.3 数据处理

按当年形成的 1 龄级根茎节间芽的数量及其占全体芽的比率作为芽流的输入量及输入率,将 2 龄级以上各龄级根茎节间休眠芽的数量及其占全体芽的比率作为芽库贮存量或贮存率;将 2 龄级以上各龄级根茎节间已经萌发形成根茎的芽数量及其占全体芽的比率,以及 2 龄级以上各龄级根茎节间已经死亡的芽数量及其占全体芽的比率共同作为芽流的输出量或输出率. 逐龄级计算休眠芽、已萌芽和死亡芽的相对比率. 分别对休眠芽比率和已萌芽比率与龄级之间作相关性统计分析.

3 结果与分析

3.1 芽库和芽流的季节动态

把全部休眠芽的数量视为芽库,把芽库输入与输出的流通量或比率视为芽流. 不同生育期芦苇种群的芽库及其芽流如图 1. 由图 1 可以看出,随着生长季的进程,输入率呈不断增加,而休眠库存率和萌发输出率呈不断减少的趋势,死亡输出率则大体保持相同的较低水平. 在芦苇种群营养生长旺盛期的 7 月中旬,输出率是输入率的 3.28 倍,而在生殖生长初期的 8 月中旬和休眠前期的 9 月底,输入率分别是输出率的 1.13 倍和 2.04 倍. 由此反映出至生长季末期,芦苇种群对芽库的补充量已经远远多于其萌发输出和死亡输出量.

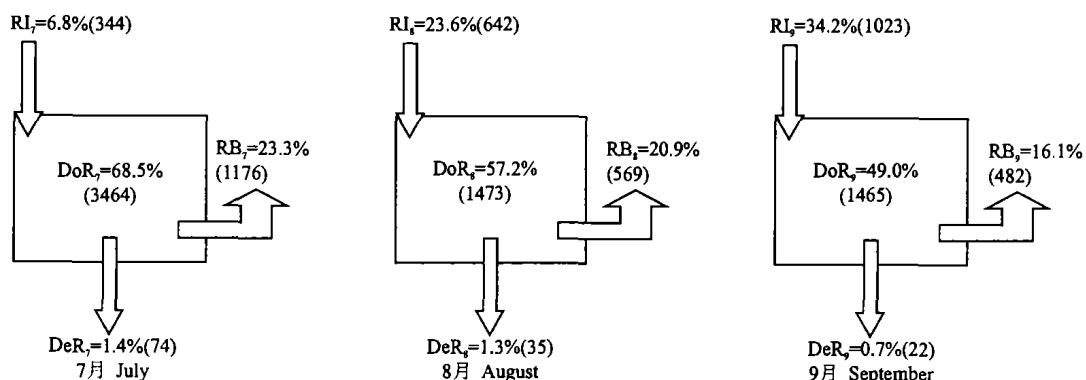


图 1 芦苇种群根茎芽库和芽流的季节动态

Fig. 1 Seasonal dynamic of bud banks and bud flow for rhizomes in *Phragmites communis* population.

RI: 输入率 Ratio of input; RB: 已萌输出率 Ratio of bourgeoned output; DeR: 死亡输出率 Ratio of death output; DoR: 休眠库存率 Ratio of dormancy storage; 括号中的数字为芽的观测数据 Numerals are observed data of the buds in parenthesis.

3.2 不同龄级根茎芽库及输出的季节动态

芦苇种群芽库不同龄级根茎的休眠芽、已萌芽及死亡芽的相对数量统计结果见表1。由表1可以看出,3个生育期的休眠芽比率和已萌芽比率有着明显的逆向变化,呈随着龄级的增加,休眠芽比率依

表1 芦苇种群芽库不同龄级根茎芽的库存及其输出比率

Table 1 Ratios both storage and output of bud banks in the rhizome of different age classes in *Phragmites communis* population (%)

取样时间 Sampling time		龄级 Age class (yr.)						平均 Mean
		1	2	3	4	5	6	
2000.7.20	休眠 Dormancy	99.3	89.1	76.0	66.3	68.6	26.5	76.8
	已萌 Bourgeoned	0.7	10.9	20.3	32.4	31.4	70.4	21.9
	死亡 Death	0	0	3.7	1.3	0	3.1	1.3
	合计 Total	100	100	100	100	100	100	100
2000.8.12	休眠 Dormancy	92.9	89.4	66.1	57.6	45.1	25.0	76.1
	已萌 Bourgeoned	7.1	9.1	31.2	39.9	53.8	75.0	22.4
	死亡 Death	0	1.6	2.7	2.6	1.2	0	1.5
	合计 Total	100	100	100	100	100	100	100
2000.9.29	休眠 Dormancy	86.2	84.4	75.6	64.1	59.2	50.0	78.4
	已萌 Bourgeoned	12.1	14.8	22.9	35.3	39.3	48.2	20.3
	死亡 Death	1.7	0.8	1.6	0.6	1.5	1.8	1.3
	合计 Total	100	100	100	100	100	100	100
平均 Mean	休眠 Dormancy	92.8	87.6	72.6	62.7	57.6	33.8	77.1
	已萌 Bourgeoned	6.6	11.6	24.8	35.9	41.5	64.5	21.5
	死亡 Death	0.6	0.8	2.6	1.4	0.9	1.7	1.4
	合计 Total	100	100	100	100	100	100	100

表2 芦苇种群根茎休眠芽(y_d)与已萌芽(y_b)比率与龄级(x)之间的拟合方程及其显著性检验

Table 2 Simulated equations and significance tests on relationship between ratios both dormancy buds (y_d) and bourgeoned buds (y_b) and age class (x) in the rhizome of *Phragmites communis* population ($n = 6$)

取样时间 Sampling time	休眠芽比率 Ratios of dormancy buds (%)			已萌芽比率 Ratios of bourgeoned buds (%)		
	方程 Equation	r	P	方程 Equation	r	P
2000.7.20	$y_{d7} = 114.49 - 12.434x$	-0.9251	0.008	$y_{b7} = -14.53 + 12.060x$	0.9328	0.007
2000.8.12	$y_{d8} = 110.77 - 13.740x$	-0.9867	0.000	$y_{b8} = -12.21 + 13.780x$	0.9838	0.000
2000.9.29	$y_{d9} = 96.73 - 7.660x$	-0.9877	0.000	$y_{b9} = 2.13 + 7.611x$	0.9880	0.000
平均 Mean	$y_{dm} = 107.33 - 11.278x$	-0.9786	0.001	$y_{bm} = -8.21 + 11.151x$	0.9797	0.001

4 讨论

在松嫩平原盐碱化草甸的旱地生境,芦苇种群的根茎一般均由6个龄级组成。根茎的龄级按生活年限划分^[29],表明旱地生境芦苇种群的根茎一般可生活6个年度。笔者对不同旱地生境芦苇种群根茎累积长度的年龄结构研究结果表明,在羊草+芦苇群落,经过排洪一整年的地表积水(水淹),群落演替为单一优势种的芦苇群落,经过两整年的自然渗透和蒸发,群落进入旱生化演替的初期,芦苇种群的根茎仅由4个龄级组成,其中最高的4龄级仅占10%^[26]。其他3个旱地生境均由6个龄级组成,并以2、3龄级的比率较大,4龄级均开始减小,5龄级已明显减少,在年龄谱中占7.7%~11.1%,至6龄级仅占2.2%~4.4%^[26],反映出芦苇根茎的寿命与生境条件有关,水淹生境的比旱地生境的短。而在旱地生境,芦苇根茎从第4年开始有一定数量死亡,

次降低,已萌芽比率依次增高;各龄级的死亡比率均甚低,其变化也没有规律性。由此反映出芦苇根茎芽的绝大多数是与根茎共存亡的,各龄级的根茎芽均有一个累积萌发输出过程。

经进一步统计分析,3个生育期的休眠芽比率和已萌芽比率与龄级之间均有极显著的直线相关关系,其拟合的方程参数 a 值均具有季节性变化规律,即随着生长季的进程,休眠芽比率的 a 值依次减小,已萌芽比率的 a 值依次增大(表2)。由此反映出在生长季后期,部分1龄级根茎休眠芽相继萌发输出。 b 值虽然没有季节性变化规律,但休眠芽比率和已萌芽比率随着龄级增加,各月份 b 的绝对值均大体相同,反映出休眠芽比率的减少与已萌芽比率增加具有高度的同步性。如果以3次调查平均值的方程 b 值作为衡量2龄级以上根茎芽动态指标,则每增加1个龄级,休眠芽比率将减少约11%,而已萌芽比率将增加约11%。由此进一步反映出在松嫩平原盐碱化草甸的旱地生境,芦苇种群各龄级根茎芽的有序及定量输出过程。

第5年大量死亡,至第6年仅有少量存活。但在本研究的一次跟踪性挖掘中,获得了比6龄级高出3个龄级的根茎样本,反映出在旱地生境,芦苇种群的个别根茎可存活7~9年,乃至更长的时间。对于芦苇根茎在旱地生境长寿性的生物生态学机制有待进一步研究。

植物的根茎既是重要的营养繁殖器官,也是重要的养分贮藏器官,禾本科植物根茎的每个节间都可以形成一个芽,每一个芽都有发育出一条根茎或一个分蘖株的潜在能力。而芽的萌发和生长过程都将发生营养物质的不同消耗。其中,在形成分蘖株上的消耗一般要比形成根茎上的消耗少。当分蘖株的叶片通过光合作用所生产的物质满足自身代谢消耗时,根茎开始不再为分蘖株提供营养物质,当分蘖株生长到一定时期以后,所生产的物质还将向根茎转移;但新根茎的整个生长过程都是由老根茎提供营养物质,使老根茎中的营养物质不断消耗。松嫩平原

碱化草甸旱地生境的芦苇根茎分布在土层约 1 m 的不同深度,除了靠近地表处的根茎芽可以直接形成分蘖株外,大部分芽均形成根茎。在土壤剖面可以看到,芦苇根茎大体有 3 个走向,一是向上生长,形成的根茎较短,顶芽形成分蘖株;二是横向生长形成较长的根茎;三是向下生长,但达到一定深度后又转为横向生长,形成的根茎也较长。因此,芦苇根茎每一个芽的萌发和生长都将消耗老根茎中的大量养分。对于芦苇根茎生长的方向性,以及不同方向新根茎对养分的消耗状况有待于进一步研究。

种子是有性繁殖的潜在种群,芽是营养繁殖的潜在种群。如同种子库的种子流一样,芽库也存在芽流,即芽的输入与输出。由于芦苇种群的各龄级根茎芽总是有部分可在一个生长季中同时萌发输出或死亡输出,所以已萌输出率和死亡输出率均为多年累积值。在松嫩平原盐碱化草甸的旱地生境,芦苇种群的当年根茎主要是在生长季后期不断形成的,一般新生根茎芽很少发生死亡和萌发输出,基本都补充到休眠芽库中。因此,即使采用当年形成芽的输入率与芽库多年累积的输出率相比,仍然可以较真实的反映出芽流的季节动态。对于芽库的实际贮量的季节动态,可以通过当年 1 龄级根茎芽的输入率与其它各龄级根茎休眠芽库存率之和来加以有效估计。

在松嫩平原碱化草甸旱地生境,芦苇种群各龄级根茎的休眠芽有一个稳定的萌发输出过程。如果用 3 次调查平均值的拟合方程 b 值作为衡量各龄级平均累积输出的增长率指标,则根茎休眠芽的萌发输出率,理论上每年以约 11% 的比率累积增加;或者说不同龄级根茎的休眠芽每年都有 11% 萌发形成 1 龄级新根茎。而 1 龄级根茎的顶端大多在翌年发育为分蘖株,这些分蘖株又可以为直接相连接的老龄级根茎源源不断地就近输送养分,籍以维持老龄级根茎及其芽的生活力。这正是不同旱地生境芦苇种群根茎干物质贮量均随着龄级的增加而增大^[26]的原因所在。

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作者简介 杨允非,女,1956年生,硕士,教授,生态学博士生导师。主要从事草地生态学、湿地生态学、恢复生态学和植物种群生态学研究,发表论文120余篇。Tel:0431-5098994; E-mail:yangyf@nenu.edu.cn

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