

细叶百合的生物量和营养分配

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摘要 以栽培的2年生细叶百合(*Lilium pumilum*)为材料,于2000年的生长季从蕾期至种子成熟期进行6次取样,对其各器官生物量和氮、磷元素的配置进行了动态研究。结果表明,细叶百合虽然以种子繁殖为主,但在整个生长季用于生殖器官的生物量投资的比例并不大,大量干物质分配到地下器官鳞茎中(平均为60.17%);茎、叶的生物量分配比例仅次于鳞茎,雄蕊生物量分配比例明显高于雌蕊。在叶萌动及展叶初期植株全氮百分含量最高,从春季萌动至秋季果实成熟,叶中的氮呈逐渐递减的趋势;茎和生殖器官的全氮含量在蕾期最大,生殖器官与叶、鳞茎的全氮含量相关显著。磷在生殖器官的含量较高,这与磷在植物有性生殖过程中的重要作用相一致;生殖器官与茎的全磷含量相关显著。地下器官全氮、全磷随季节变化有增多的趋势,地上各器官全氮、全磷相关显著,随季节变化有明显减少的趋势。

关键词 细叶百合 生殖配置 生物量 营养元素

BIOMASS AND NUTRIENT ALLOCATION OF *LILIAM PUMILUM*

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Abstract In order to understand the relationship between biomass and nutrient allocation of *Lilium pumilum*, a widely spread perennial herb in China mainly used for medicinal purposes (bulbs are harvested) and as an ornamental, a study on the biomass of vegetative organs, reproductive organs and allocation of N and P in different developmental stages was carried out. The experimental material was obtained from the garden of Northeast Forestry University where *L. pumilum* had been seeded in a high bed of black soil in spring 1998 under conditions of full sunlight and received treatment of manual weeding, watering and no fertilization.

In 2000, samples were taken from May to November from blooming plants of *L. pumilum* at 6 different stages: bud stage (May 24th); middle period of bud spreading (June 11th); floral phase (June 26th); early fruit-set phase (July 26th); fructescence (August 29th); and seed maturation phase (October 3rd). Thirty individual plants together with their intact underground organs were carefully washed. Every plant was divided into bulb, stem, leaf, bud, flower and fruit (shell and seed), placed into envelopes, dried at 80 °C, and weighed. We determined the mean biomass of each organ at each growth period and then calculated the ratio of the mean biomass to total biomass. Also, two replicate samples of each tissue were analyzed for N and P content and the average percentweight of total-N and total-P was recorded.

The results showed that the percent mean biomass averaged across all developmental stages decreased in the following order: bulbs (60.17%); leaves (13.28%); stems (12.84%); reproductive organs (9.18%); and roots (5.78%). The large investment in the bulb might be a self-protective mechanism for a population of perennial bulbaceous plants as a means for maintaining their long term development. The bulb reached maximum biomass at the early bud stage, and seed maturation phase and the minimum at floral stage. If we want these results indicate that to harvest edible bulbs, the fruitlet should be removed at the post floral stage to increase bulb biomass at the post floral stage and thus improve the bulb harvest. Bulbs should be harvested at the period of maximum biomass, that is, at the bulb stage and seed maturation phase. Seasonal biomass dynamics of reproductive organs were negatively correlated with non-reproductive organs.

The results revealed that the mean percent total-N in tissues averaged across all development stages decreased in the following order: leaves (2.19%); reproductive organs (1.50%); bulbs (1.16%); roots (1.03%); and stems (0.99%). Total-N tissue concentrations reached their peak during leaf sprouting and early leaf spreading phase; this occurred when the N content of the reproductive organs were positively correlated with leaf N content and negatively correlated with that in the bulb. The mean total-P content decreased in

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the following order: reproductive organs (0.035 6%); bulbs (0.031 6%); stems (0.027 8%); roots (0.026 6%); and leaves (0.026 4%). The total-N content of the reproductive organs was positively correlated with that in the stem. This research also revealed that the content of total-N and total-P in aboveground organs tended to increase while organs underground tended to decrease with changing seasons.

Key words *Lilium pumilum*, Reproductive allocation, Biomass, Nutrient element

生物量和营养分配是生态学中的热门领域之一,尤其在草本植物的生物量、能量及营养元素(C、N、P、K等)配置方面的研究成果更加突出,木本植物的能量分配也有少量报道(Douglas, 1971; Abrahamson, 1982; Delph, 1990; Jonasson, 1995; 钟章成, 1995; 苏智先等, 1998; 王海洋等, 1999; 王仁忠等, 1999; 汪仁忠, 2000; 刘广全等, 2001; 杨持等, 2002),但对多年生球根类植物的生物量和营养分配的研究还未见报道。细叶百合(*Lilium pumilum*)为百合科百合属植物,广泛分布于我国的东北、华北和西北地区。其花色鲜红、抗性极强,是著名的多年生球根类观赏植物。同时,细叶百合的鳞茎又是清心安神、滋阴润肺的中药材。该研究以细叶百合为材料,对其生物量及氮、磷元素在各器官中的分配进行动态追踪,揭示细叶百合的营养器官及生殖器官生物量和营养配置规律,为多年生球根类植物生态学研究及资源植物开发管理提供基础资料。

1 材料和方法

1) 实验材料采集地点为东北林业大学花圃,其地理坐标是45°41'N, 126°37'E,海拔高度171.7 m。年平均气温3.6℃,平均相对湿度67%,平均降水量462.9 mm。平均日照时数2 745.7 h,全年无霜期136 d。实验地土壤为黑土。实验材料高床种植,人工锄草、灌溉,不施肥。从2000年5月开始,在实验地内挖取2年生细叶百合的开花植株,大约每个月取材1次,依次为现蕾初期(5月24日)、花蕾伸长期(6月11日)、花期(6月26日)、座果初期(7月26日)、果实充分膨大期(8月29日)及种子成熟期(10月3日),共取样6次。每次随机选取开花植株30株,挖大土坨,植株连同地下部分一起带回实验室。水浸洗去地下部土后,将植株按根、鳞茎、茎、叶、蕾、花、果(果壳和种子)等器官分开,放入纸袋,80℃恒温烘干至恒重后,用万分之一天平称重,计算各生长期不同器官的平均生物量及各器官平均生物量占总生物量的比例。

2) 将烘干后的各器官样品用研钵研成细末,供氮、磷测试时用。全氮的测定方法采用硫酸-高氯酸

消煮、凯氏定氮法;全磷的测定方法采用硫酸-高氯酸消煮、钼锑抗比色法。数据单位为被测样品中含全氮或全磷的质量百分比。

2 结果与分析

2.1 生物量的分配

细叶百合是多年生球根类植物,生物量生殖分配规律有其自身特点(表1)。细叶百合虽然以种子繁殖为主,但在整个生长季用于生殖器官的生物量投资的比例并不大,大量干物质分配到地下器官鳞茎中(平均为60.17%)。鳞茎是植物体的一个巨大能量贮藏库和调节器,在植物一生中起着绝对重要的作用。叶、茎的生物量分配比例也较大,这对植物扩大光合面积,增加有机物的合成以及茎的支撑作用是十分必要的。生殖器官生物量从现蕾初期至花蕾伸长期增加350倍,生殖器官的生物量在生长季内的迅猛增加,是植物在有限时间内,完成其有性生殖过程的一种适应。雄蕊生物量分配比例明显高于雌蕊,其机制可能是提高雄性适合度,以提供足够的花粉来保障生殖成功,或是因为花粉生产需要高代谢消耗,这种消耗较产生种子或雌性生殖器官更大(钟章成, 1995)。种子成熟期果壳的生物量分配占整个果实的较大比例,如此高比例的投资可能是保证种子成熟,并以有性过程来沿续种群必须付出的代价。

根、鳞茎、茎、叶与生殖器官的相关系数分别为: $R^2 = 0.5867$, $R^2 = 0.3785$, $R^2 = 0.3423$, $R^2 = 0.0002$ ($p > 0.05$),相关均不显著。这在某种程度上反映出,各营养器官与生殖器官之间的生物量分配存在着更为复杂的关系。

2.2 细叶百合全氮的分配

细叶百合各器官全氮含量的季节动态见表2。从表2中可以看出,各器官氮素含量的差异与其结构及功能有关。叶是植物的光合器官,是新陈代谢最旺盛的部位,因此,在整个生长季保持着较高的氮素含量。从春季萌动至秋季果实成熟,叶中的氮呈逐渐递减的趋势,这反映出生命活动的周期变化。茎和生殖器官的全氮含量在蕾期最高,然后降低,这

表 1 细叶百合各器官生物量分配季节动态(%)
Table 1 Seasonal dynamics of biomass allocation for *Lilium pumilum*

日/月 Day/ month	根 Root	鳞茎 Bulb	茎 Stem	叶 Leaf	蕾 Bud	花 Flower	果 Fruit
24/5	7.7(2.25)	72.6(9.63)	6.0(3.01)	13.5(2.89)	0.0(0.01)	-	-
11/6	8.1(3.17)	52.3(6.48)	18.1(4.47)	21.4(3.72)	7.5(1.06)	-	-
26/6	5.3(1.92)	41.7(5.14)	21.8(3.75)	18.1(4.38)	-	12.9(2.06)	-
						8.6(2.51) (PR)	
						2.9(0.32) (St)	
						1.3(0.06) (P)	
26/7	4.0(1.54)	51.0(5.99)	16.0(2.95)	13.3(3.69)	-	-	15.5(3.91)
29/8	5.0(2.76)	70.3(5.48)	7.9(2.02)	7.1(2.73)	-	-	9.5(2.65)
3/10	4.3(3.01)	72.9(7.66)	7.0(2.05)	6.0(2.79)	-	-	9.5(2.88)
							3.0(0.17) (SC)
							6.5(2.08) (S)

括号中的数字为标准差 The figures are standard deviation in brackets PR 瓣及花托 Petal and receptacle St 雄蕊 Stamen P 雌蕊 Pistil SC :果壳 Seed capsule S 种子 Seed

表 2 细叶百合各器官全氮含量季节动态(%)
Table 2 Seasonal dynamics for total N content in different organs of *Lilium pumilum*

日/月 Day/ month	根 Root	鳞茎 Bulb	茎 Stem	叶 Leaf	蕾 Bud	花 Flower	果 Fruit
24/5	1.1(0.06)	0.8(0.05)	2.4(0.13)	4.0(0.08)	1.8(0.06)	-	-
11/6	0.8(0.07)	1.1(0.08)	0.9(0.06)	2.8(0.15)	1.8(0.03)	-	-
26/6	0.7(0.03)	1.1(0.11)	0.8(0.02)	2.1(0.07)	-	1.6(0.03)	-
26/6	0.7(0.07)	1.1(0.06)	0.8(0.10)	2.1(0.13)	-	1.6(0.05)	-
26/7	1.1(0.04)	1.2(0.16)	0.9(0.07)	1.9(0.04)	-	-	1.4(0.06)
29/8	0.8(0.09)	1.2(0.05)	0.5(0.05)	1.4(0.06)	-	-	1.0(0.11)
3/10	1.5(0.12)	1.4(0.07)	0.2(0.05)	0.7(0.04)	-	-	1.1(0.05)
							0.1(0.07) (SC)
							1.5(0.04) (S)

括号中的数字为标准差 The figures are standard deviation in brackets SC S 同表 1 See Table 1

与茎和花蕾光合作用的能力、时期相一致。根和鳞茎是行使吸收和贮存功能的地下器官,新陈代谢较地上器官弱,且变化较平稳,故氮素在整个生长季保持着较为平稳地增加。

对生殖器官与各非生殖器官全氮含量的相关性分析结果显示,生殖器官与根的相关系数 $R^2 = 0.116$ ($p > 0.05$),二者不相关。与茎的相关系数 $R^2 = 0.589$ ($p > 0.05$),二者亦不相关。生殖器官与鳞茎的相关系数 $R^2 = 0.674$ ($p < 0.05$),二者相关显著,即随着季节变化,生殖器官全氮含量在缓慢递减,而鳞茎全氮在平稳地增加。生殖器官与叶的相关系数 $R^2 = 0.816$ ($p < 0.05$),二者呈显著的正相关,生殖器官与叶在氮的积累、转移等代谢途径可能有着相似之处。

2.3 细叶百合全磷的分配

细叶百合各器官全磷含量的季节动态见表 3。磷在生殖器官的含量最高,现蕾初期为最大值,然后逐渐降低,这与磷在植物有性生殖过程中的重要作

用相一致。茎、叶的全磷含量从蕾初期至种子成熟期呈缓慢下降的趋势。鳞茎全磷含量的平均值仅次于生殖器官,在整个生长季呈小幅度波动变化,但呈升高趋势。根的全磷含量在整个生长季中波动明显。

生殖器官与根、鳞茎、叶的全磷含量相关系数分别为 $R^2 = 0.0017$, $R^2 = 0.3965$, $R^2 = 0.4493$ ($p > 0.05$) 相关均不显著。生殖器官与茎的相关系数 $R^2 = 0.8642$ ($p < 0.05$),二者呈显著的正相关。

2.4 各器官全氮与全磷季节动态的相关性分析

根、鳞茎全氮与全磷含量季节动态的相关系数分别为: $R^2 = 0.0176$ ($p > 0.05$), $R^2 = 0.2836$ ($p > 0.05$) 均不相关。茎的全氮与全磷的相关系数 $R^2 = 0.8281$ ($p < 0.05$),二者呈显著的正相关。叶的全氮与全磷含量的相关系数 $R^2 = 0.8277$ ($p < 0.05$),二者呈显著的正相关。生殖器官全氮与全磷含量的相关系数 $R^2 = 0.8869$ ($p < 0.01$),二者呈极显著的正相关。可见,茎、叶及生殖器官均随着全氮

表 3 细叶百合各器官全磷含量季节动态(%)
Table 3 Seasonal dynamics for total P content in different organs of *Lilium pumilum*

日/月 Day/ month	根 Root	鳞茎 Bulb	茎 Stem	叶 Leaf	蕾 Bud	花 Flower	果 Fruit
24/5	0.026 K(0.000 8)	0.028 X(0.001 0)	0.043 A(0.001 2)	0.035 Y(0.000 9)	0.042 Z(0.000 5)	-	-
11/6	0.025 K(0.001 1)	0.028 Y(0.000 7)	0.038 X(0.001 0)	0.034 Z(0.000 6)	0.040 I(0.001 4)	-	-
26/6	0.033 A(0.001 3)	0.029 Y(0.001 5)	0.030 Z(0.000 7)	0.026 X(0.000 17)	-	0.039 Y(0.001 1)	-
26/7	0.011 Y(0.000 6)	0.025 A(0.001 2)	0.025 Z(0.001 6)	0.027 K(0.001 1)	-	-	0.032 Z(0.000 8)
29/8	0.031 X(0.001 2)	0.038 Y(0.000 7)	0.017 X(0.000 5)	0.022 Y(0.001 3)	-	-	0.028 A(0.001 2)
3/10	0.031 A(0.000 7)	0.038 A(0.001 6)	0.016 Y(0.000 6)	0.011 X(0.000 8)	-	-	0.031 K(0.001 0)
							0.028 A(0.001 4) X(S)
							0.032 Z(0.001 0) X(S)

括号中的数字为标准差 The figures are standard deviation in brackets SC, S 同表 1 See Table 1

含量的季节性(从春到秋)减少,全磷也随之显著减少。这说明常量元素氮、磷不同时期在地上各器官中的积累规律的一致性,这种一致性在生殖器官中表现得更加突出。同时,细叶百合虽为多年生植物,但每年秋季其地上器官或结实,或枯萎,营养转移至地下,并以地下器官渡过漫长的寒冬(杨利平, 2000),因此,地上各器官氮、磷的季节性减少可以认为是物种长期演化过程中对自然的一种适应。

3 结论与讨论

生殖器官的生物量与鳞茎生物量的季节变化呈负相关,即在生殖器官形成初期所需的物质和能量很可能大部分由鳞茎提供,因为当时的叶还没有完全展开和发育完全,达不到足够的光合能力,不可能完全满足生殖器官干物质以几十倍至几千倍的增加。茎和叶所分配到的干物质次之,并且生殖器官的生物量与茎、叶的生物量呈正相关。茎、叶生物量比例的增大,增加了光合面积,提高了有机物的积累,从而保证有性生殖的物质需要。

植物体内的氮、磷在植物生长发育和形态构成中起着非常重要的作用,研究植物体内化学成分的含量及季节变化对揭示植物的营养需求有重要意义(刘广全等, 2001)。茎、叶及花蕾的氮、磷含量蕾期最高,然后逐渐降低,种子成熟期最低。这种现象被解释为,其形态在 5 月 24 日为建成初期,组织结构发育均不完善,细胞大多具有分裂能力,需要大量的蛋白质和核酸,因此对氮和磷的选择性吸收较多,浓度较高。随后由于光合作用产生的碳水化合物的增加,引起稀释效应,氮和磷的浓度开始下降(孙书存等, 2001)。特别是叶,作为重要的光合器官在 8 月 29 日至 10 月 3 日期间氮和磷的浓度下降速度极快,分别降至原来的 47.95% 和 51.98%。可以认为叶片在枯落前,其中的氮、磷养分发生了向其它器官的

转移(Schlesinger *et al.*, 1989)。何兴元等(1997)、徐福余等(1997)、王文卿等(2001)在不同种木本植物中均发现类似现象。细叶百合的地下器官根和鳞茎的氮、磷含量在整个生长季呈波动变化,波动变化的出现或者是各器官内、器官间营养转移的表现,或者是实验时间内(2000 年)遭遇罕见的干旱而造成植物代谢异常的结果。到种子成熟期,根和鳞茎的氮、磷含量基本达到最大值,这是根系吸收能力增强和同化器官内的营养输入的结果。秋季地下器官生物量和营养含量的增加对抵御寒冬及第二年春季向同化器官和生殖器官输出营养提供了保障。生殖器官在蕾初期的 5 月 24 日氮、磷含量最高,随着器官发育的完善及同化能力的增加,含量不断减少,到 8 月 29 日的果实充分膨大期(此时果仍为绿色)营养含量降至最低。在种子成熟期生殖器官(此时果已变为褐色)中的氮、磷含量又分别增加 0.02% 和 0.0027%,此时生殖器官养分的增加部分也可能来自同化器官的营养输出,这对种子的成熟和品质十分重要。

参 考 文 献

- Abrahamson, W. G. 1982. On the comparative allocation of biomass energy and nutrients in plant. *Ecology*, **63**: 982 ~ 991.
- Delph, L. F. 1990. Sex-differential resource allocation patterns in the subdioecious shrub *Liebe subalpina*. *Ecology*, **71**: 1342 ~ 1351.
- Douglas, D. A. 1971. The balance between vegetative and sexual reproduction of *Mimulus primuloides* at different altitudes in California. *Ecology*, **69**: 295 ~ 310.
- He, X. Y. (何兴元), C. G. Zhang (张成刚), S. H. Yang (杨思河), W. Chen (陈玮), Y. Zhang (张粤), H. C. Liu (刘惠昌) & D. Y. Su (苏道岩). 1997. Role of nitrogen-fixing trees in mixed forest. II. Seasonal variation patterns of N and contents in leaves of nitrogen-fixing trees. *Chinese Journal of Applied Ecology (应用生态学报)*, **8**: 235 ~ 239. (in Chinese with English abstract)
- Jonasson, S. 1995. Resource allocation in relation to leaf retention time of the wintergreen *Rhododendron lapponicum*. *Ecology*, **76**:

- 475 ~ 485.
- Liu, G. Q. (刘广全), S. D. Zhao (赵士洞), H. Wang (王浩), X. Y. Tu (土小宇) & L. Q. Gong (龚立群). 2001. Seasonal variation of growth and nutrient contents for photosynthetic organ of the sharp-tooth oak stands. *Acta Ecologica Sinica* (生态学报), **21**: 884 ~ 889. (in Chinese with English abstract)
- Schlesinger, W. H., E. H. Delucia & W. D. Billings. 1989. Nutrient-use efficiency of woody plants on contrasting soils in the western Great Basin Nevada. *Ecology*, **70**: 105 ~ 113.
- Su, Z. X. (苏智先), S. L. Zhang (张素兰) & Z. C. Zhong (钟章成). 1998. Advances in plant reproductive ecology. *Chinese Journal of Ecology* (生态学杂志), **17**(1): 39 ~ 46. (in Chinese with English abstract)
- Sun, S. C. (孙书存) & L. Z. Chen (陈灵芝). 2001. Leaf nutrient dynamics and resorption efficiency of *Quercus liaotungensis* in the Dongling mountain region. *Acta Phytocologica Sinica* (植物生态学报), **25**: 76 ~ 82. (in Chinese with English abstract)
- Wang, H. Y. (王海洋), J. K. Chen (陈家宽) & J. Zhou (周进). 1999. Influence of water level gradient on plant growth, reproduction and biomass allocation of wetland plant species. *Acta Phytocologica Sinica* (植物生态学报), **23**: 269 ~ 274. (in Chinese with English abstract)
- Wang, R. Z. (王仁忠). 2000. Energy allocation to growth and reproduction in *Leymus chinensis* population. *Chinese Journal of Applied Ecology* (应用生态学报), **11**: 591 ~ 594. (in Chinese with English abstract)
- Wang, R. Z. (王仁忠), Y. G. Zu (祖元刚) & S. Q. Nie (聂绍荃). 1999. Preliminary study on biomass reproductive allocation in *Leymus chinensis* population. *Chinese Journal of Applied Ecology* (应用生态学报), **10**: 553 ~ 555. (in Chinese with English abstract)
- Wang, W. Q. (王文卿) & P. Lin (林鹏). 2001. Comparative study on seasonal changes in element concentrations in leaves of *Kandelia candel* and *Rhizophora stylosa* at Jiulongjiang estuary. *Acta Ecologica Sinica* (生态学报), **21**: 1233 ~ 1238. (in Chinese with English abstract)
- Xu, F. Y. (徐福余), L. H. Wang (王力华), J. Z. Li (李境芝), S. M. Xu (许思明) & S. Y. Zhang (张颂云). 1997. Internal and external nutrient transfers in foliage of some north deciduous trees. I. Changes of nutrient concentration and contents. *Chinese Journal of Applied Ecology* (应用生态学报), **8**: 1 ~ 6. (in Chinese with English abstract)
- Yang, C. (杨持), Z. B. Jia (贾志斌), Y. Hong (洪洋) & X. H. Han (韩向红). 2002. A comparative study on reproductive allocation of mutual species moderate-temperate and warm-temperate steppe. *Acta Phytocologica Sinica* (植物生态学报), **26**: 39 ~ 43. (in Chinese with English abstract)
- Yang, L. P. (杨利平). 2000. Study on anther flowering and fertility of *Lilium concolor* var. *pulchellum* (Fisch.) Regel. *Bulletin of Botanical Research* (植物研究), **20**: 389 ~ 394. (in Chinese with English abstract)
- Zhong, Z. C. (钟章成). 1995. Reproductive strategies of plant populations. *Chinese Journal of Ecology* (生态学杂志), **14**(1): 37 ~ 42. (in Chinese with English abstract)

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