养分供应对 3 种舞花姜属植物繁殖方式的影响

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摘 要 该研究选用的 3 种舞花姜属植物中, 毛舞花姜(*Globba barthei*)和双翅舞花姜(*G. schomburgkii*)自然条件下开花不结实, 以珠芽进行繁殖; 异果舞花姜(*G. racemosa*)则同时以种子和珠芽进行繁殖。在人工栽培条件下, 高养分处理显著增加毛舞花姜的珠芽干重((1.11 ± 0.10) g vs. (3.08 ± 0.69) g, $p = 0.0107$)、珠芽数量((30.58 ± 2.92) vs. (74.74 ± 9.73), $p = 0.0004$)、珠芽大小((10.5 ± 1.48) mg vs. (53.50 ± 11.42) mg, $p = 0.0015$)、植株营养体重((3.99 ± 0.23) g vs. (9.67 ± 1.17) g, $p = 0.0002$)和双翅舞花姜的珠芽数量((51.74 ± 3.64) vs. (108.71 ± 21.52), $p = 0.0181$)。不同养分条件下两种舞花姜的开花数量无显著差异。人工去除珠芽、花对两种舞花姜植株当年生花和珠芽的数量无显著影响($p < 0.05$)。自然条件下异果舞花姜不同居群间珠芽大小、珠芽数、珠芽重、果实重、种子数和营养体重等均存在极显著差异($p < 0.001$)。异果舞花姜各居群植株珠芽数和营养体重($r = 0.901$, $p < 0.05$)、珠芽重和珠芽大小($r = 0.849$, $p < 0.05$)呈显著正相关; 果实重和种子数($r = 0.998$, $p < 0.05$)呈显著正相关。土壤因子主成分分析表明前 3 个主成分提供的信息量分别为 50.575%、18.204% 和 11.883%, 其中第一主成分中的全氮(0.959)、速效氮(0.885)和有机质(0.821)负荷量最大, 第二主成分中土壤速效磷(0.824)负荷量最大。植株营养体重和土壤速效磷极显著正相关($r = 0.906$, $p < 0.01$), 珠芽大小与全氮($r = 0.798$)、速效氮($r = 0.780$)和有机质($r = 0.821$)均呈显著正相关($p < 0.05$)。果实重和种子数与土壤因子相关性不显著($p < 0.05$)。3 种舞花姜的无性繁殖器官更易受到养分供应的影响, 有性繁殖器官对养分供应变化响应不显著, 有性和无性繁殖之间似不存在补偿关系。

关键词 舞花姜属 有性繁殖 无性繁殖 营养生长 土壤因子

THE EFFECT OF NUTRIENT SUPPLY ON SEXUAL AND ASEXUAL REPRODUCTION OF THREE SPECIES OF *GLOBBA*

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Abstract Among the three *Globba* species in this study, *Globba barthei* and *G. schomburgkii* propagated only by bulbils and with no seed set while *G. racemosa* propagated by both seeds and bulbils under natural conditions. The aim of this study was to understand the effect of nutrition supply on the relative levels of sexual and asexual reproduction of these three species in both natural and artificial conditions and to determine whether there is compensatory mechanism that enhances sexual reproduction when asexual reproduction is constrained and vice versa.

For *G. barthei* and *G. schomburgkii*, young seedlings propagated by bulbils were planted in flowerpots (30 cm in diameter) and placed under a rain and insect proof greenhouse in XTBG. The soil medium in the flowerpots was composed of forest soil (2), coarse sand (2), peat (2) and scattered brick (1). Treatments in the experiment included: 1) high-level fertilizer supply consisted of 150 ml per pot of a 5% mixed fertilizer (N:P:K = 15:15:15) once every two weeks; 2) high-level fertilizer supply (same as treatment (1)) plus removal of flowers buds everyday; 3) high-level fertilizer supply (same as treatment (1)) plus removal of bulbils once a week; 4) low-level fertilizer supply (only water supplied) 5) low-level fertilizer plus removal of flower buds everyday; 6) low-level fertilizer plus removal of bulbils once a week. The results showed that 1) high-level fertilizer supply significantly increased bulbil dry weight ((1.11 ± 0.10) g vs. (3.08 ± 0.69) g, $p = 0.0107$), bulbil number ((30.58 ± 2.92) vs. (74.74 ± 9.73), $p = 0.0004$), bulbil size ((10.5 ± 1.48)

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mg vs. (53.50 ± 11.42) mg, $p = 0.0015$) and vegetative organ dry weight ((3.99 ± 0.23) g vs. (9.67 ± 1.17) g, $p = 0.0002$) of *G. barthei* and the bulbil number ((51.74 ± 3.64) vs. (108.71 ± 21.52) , $p = 0.0181$) of *G. schomburgkii*; 2) different levels of fertilizer supply did not significantly affect the flower number of the two species ($p > 0.05$); 3) removing bulbils or flowers had no significant effect on the number of flowers or the bulbils in the current year ($p > 0.05$).

For *G. racemosa*, we collected 30 individuals from six native populations throughout Yunnan Province and measured the biomass and size of sexual and asexual organs of each individual. Meanwhile, we collected three soil samples from each of the six populations and analyzed the physical and chemical characteristics of the soil samples. The bulbil size, bulbil number, bulbil dry weight, fruit dry weight, seed number and vegetative organ dry weight among the six populations varied significantly ($p < 0.001$). Bulbil number was positively correlated to vegetative organ dry weight ($r = 0.901$, $p < 0.05$), bulbil dry weight was positively correlated to bulbil size ($r = 0.849$, $p < 0.05$). Fruit dry weight was positively correlated to seed number ($r = 0.998$, $p < 0.05$). A principal component analysis on soil factors of the six populations indicated that the three principal factors could explain 50.58%, 18.20% and 11.88% of the total variation. Total nitrogen, available nitrogen and soil organic matter were the main factors of the first principal component, and the loading values were 0.959, 0.885 and 0.821, respectively. Available phosphorous was the main factor for the second factor with a loading value of 0.824. Vegetative organ dry weight had a significant positive relationship with available phosphorous ($r = 0.906$, $p < 0.01$), bulbil size was positively related to total nitrogen ($r = 0.798$, $p < 0.05$), available nitrogen ($r = 0.780$, $p < 0.05$) and soil organic matter ($r = 0.821$, $p < 0.05$). Fruit dry weight and seed number were not significantly correlated to any soil factors.

As a whole, the asexual organs of the three *Globba* plants were more sensitive to different levels of nutrient supply whereas the sexual organs did not show any significant response. Compensatory mechanisms between sexual and asexual reproduction were not detected in these three species.

Key words *Globba*, Sexual reproduction, Asexual reproduction, Vegetative growth, Soil factors

自然界大多数植物往往保留有性和无性两种繁殖方式,不同的繁殖方式可能对其扩散、居群遗传结构以及物种的适应能力产生不同的影响。有性繁殖通过基因的重组,提高居群的遗传多样性和可塑性,从而增加对外界环境的适应能力(Grant, 1981);有性繁殖产生的种子也往往更适合于长距离传播,有利于植物占据新的生境(Husband & Barrett, 1996)。无性繁殖则可能作为一种相对“低耗”的繁殖策略,有利于在特定的、相对稳定的条件下迅速扩大有利基因型(Grant, 1981);尤其在种苗建成受到阻碍时,更有利于维持当地居群的稳定(Pitelka *et al.*, 1985; Angevine & Handel, 1986; Eriksson, 1988, 1989; Nault & Gagnon, 1993)。由于植物有性无性繁殖后代具有不同的生态和遗传特征,植物对有性无性繁殖的资源分配往往会影响到植物的适合度(Sato, 2002),植物可能在特定条件下形成最优的繁殖策略(Biere, 1995; Margaret & James, 2000)。

植物采用不同繁殖方式的机理及其进化意义一直是研究的热点。有研究表明,植物繁殖方式受环境的影响。植物的有性无性繁殖能力可以对不同的环境条件做出反应(Holler & Abrahamson, 1977; Piquot *et al.*, 1998);在供肥条件好的情况下植物可能更多采用无性繁殖,在供肥条件差时采用有性繁

殖(Piquot *et al.*, 1998)。植物通过有性、无性互换可能作为一种保险机制,以便对环境条件作出适当反应(Holler & Abrahamson, 1977)。另一重要Eriksson假说则认为植物同时维持有性、无性繁殖是资源分配投资权衡(Trade-off)的进化结果(Eckert, 1999)。自然环境下植物有性和无性繁殖的资源分配也可能存在此消彼长的权衡关系(Cheplic, 1995)。亦有研究表明有性无性繁殖投资权衡是基于遗传基础上,不会对当代的资源供应做出响应(Ronsheim & Bever, 2000)。植物有性无性繁殖如何对环境作出反应尚待更多的研究。

姜科舞花姜属(*Globba*)植物具有多样的繁殖系统。毛舞花姜(*G. barthei*)、异果舞花姜(*G. racemosa*)和双翅舞花姜(*G. schomburgkii*)在云南南部和西南部的原生林和林缘都有分布。在自然条件下毛舞花姜和双翅舞花姜花期为7~10月,花正常开放但高度不育,未见结果实,以花序下部苞片内或叶腋生成的珠芽进行无性繁殖。毛舞花姜珠芽为球形或梭形,直径约为0.2~1 cm,每株产珠芽 16.46 ± 3.56 个;双翅舞花姜珠芽为圆球状,直径约为0.2 cm,每株产珠芽 14.25 ± 3.63 个(刘志秋等, 2004)。异果舞花姜花期5~9月、果期9~11月,花能育同时有较多珠芽生成,珠芽为梭形,直径约为1~1.5 cm,果

实和珠芽常在同一花序上混合排列。我们以 3 种舞花姜为研究对象,试图回答以下的问题:1)人工和自然条件下不同养分对舞花姜属植物有性和无性繁殖器官有何影响?2)舞花姜属植物的有性和无性繁殖之间是否存在互相补偿机制,即无性(或有性)繁殖的阻断或减弱能否促进有性(或无性)繁殖能力的增强?

1 材料和方法

1.1 毛舞花姜和双翅舞花姜

于 2001 年 10 月从野外居群中收取毛舞花姜和双翅舞花姜的珠芽若干,翌年 3 月 7 日将珠芽放置苗床上催芽,5 月 9 日移苗至口径 60 cm 的花盆中,所用土壤介质由森林土(2)、粗沙(2)、泥炭(2)、碎砖(1)配制而成。试验植株放置在中国科学院西双版纳热带植物园的防雨防虫大棚中,该大棚上部有塑料薄膜顶防雨,并有 50% 的遮荫网,四周为 40 目的防虫网。正常供水(3~4 d 1 次,每次每盆 30 ml),去除杂草。

共设置 6 种处理:1)高肥:每两周施肥 1 次,用复合肥(丹麦产狮马牌,N:P:K=15:15:15)配成 5% 水溶液,每次每盆 150 ml,5 月 22 日第一次施肥,9 月 24 日结束;2)高肥去花:同 1)的高肥条件下在花期每天去除花序上的花蕾(通常花蕾直径<0.2 cm);3)高肥去珠芽:同 1)的高肥条件下每周 1 次去除植株花序上幼小珠芽(通常珠芽直径<0.1 cm);4)低肥:等量水溶液;5)低肥去花:同 4)的条件下在花期每天去除花序上未开的花朵;6)低肥去珠芽:同 4)的条件下每周 1 次去除植株花序上幼小珠芽。每个处理 10 盆,每盆 5 株(考虑到同盆的 5 株之间会有相互影响,结果统计时取 5 株平均值),单株做好标志,放置于防虫大棚中。

记录每一植株上花数、花期,于 10 月 4 日采集

完全部植株,记录每株上的珠芽数量、珠芽的鲜重和干重以及地上部营养体的鲜重和干重。

1.2 异果舞花姜

于 2003 年 10 月在云南省 6 个野外居群(表 1)开展调查。调查每个居群生长相对一致的 30 株植株,每株做好标记,测量株高,记录叶片数、果实数、种子数和珠芽数,采回的这 30 株标本的根、茎、叶、果实和珠芽均在 80℃烘箱中烘 72 h 至恒重,称量并记录各部分的干重。其中,繁殖体重=珠芽重+果实重,营养体重=茎重+叶重。

同时采集所研究居群内的土壤样品。采用对角线混合取样法(间隔大于 1 m,取样深度为 0~20 cm),每个居群采集 3 个样品,采样点距离大于 5 m。土壤样品送中国科学院西双版纳热带植物园生物地球化学实验室分析,测定土样的有机质、pH 值、速效氮、速效磷、速效钾、全氮量、全磷量和全钾量。pH 值用电位测定法(土:水=1:2.5)测定;有机质含量测定采用硫酸、重铬酸钾氧化-容量法测定;土壤全氮采用 H₂SO₄-HClO₄ 消解,凯氏定氮法测定;全磷和全钾含量测定采用 HClO₄-HF 消解,ICP-AES 测定;有效氮用碱解扩散法测定;有效磷用 0.06 N NH₄F-0.05N HCl 浸提,钼锑抗比色法测定;速效钾用 1 mol·L⁻¹中性 CH₃COONH₄ 浸提,ICP-AES 测定。

1.3 数据分析

采用方差分析(ANOVA)方法分析各种处理对毛舞花姜和双翅舞花姜的有性无性繁殖以及营养体生长生物量分配影响差异的显著性和不同居群之间异果舞花姜有性无性繁殖和营养生长特征差异显著性。采用主成分分析(PCA)方法分析异果舞花姜不同居群中的环境因子数据,提取典型特征,探究土壤的表征主要因子,用 Pearson 相关分析研究植物体各部分器官与土壤主要因子的相关性。所有的数据分析均在 SPSS 11.0 环境下进行。

表 1 异果舞花姜野外 6 个居群的地理位置、海拔及居群所处生态环境
Table 1 Location, altitude and ecological condition of the six populations of *Globba racemosa*

居群 Population	经纬度 Latitude and longitude	海拔(m) Altitude	居群大小(hm ²) Population size	土壤水分状况 Soil water supply	受干扰程度 Degree of disturbance	土壤类别 Soil group
1	22°53' N, 99°48' E	1 700	5~10	丰富 Rich	中 Slight	红壤 Red earths
2	24°05' N, 99°44' E	1 873	5~10	少 Little	强 Intense	黄棕壤 Yellow brown earths
3	24°04' N, 97°48' E	1 136	10~20	丰富 Rich	少 Little	黄壤 Yellow earths
4	24°25' N, 97°50' E	1 456	10~20	极丰富 Very rich	少 Little	红壤 Red earths
5	24°35' N, 97°40' E	1 352	10~20	少 Little	强 Intense	黄红壤 Yellow red earths
6	24°56' N, 102°29' E	2 100	10~20	极少 Very little	中 Slight	黄棕壤 Yellow brown earths

2 实验结果

2.1 不同养分供应下毛舞花姜和双翅舞花姜有性无性繁殖特征变化

在人工栽培条件下,高养分处理显著增加毛舞花姜的珠芽干重((1.11 ± 0.10) g vs. (3.08 ± 0.69) g, $p = 0.0107$) (图 1A)、珠芽数量((30.58 ± 2.92) vs. (74.74 ± 9.73), $p = 0.0004$) (图 1B)、珠芽大小((10.5 ± 1.48) mg vs. (53.50 ± 11.42) mg, $p = 0.0015$) (图 1C)、植株营养体重((3.99 ± 0.23) g vs. (9.67 ± 1.17) g, $p = 0.0002$) (图 1E)和双翅舞花姜的珠芽数量((51.74 ± 3.64) vs. (108.71 ± 21.52), $p = 0.0181$) (图 1B);不同养分条件下两种舞花姜的开花数量无显著差异($p > 0.05$) (图 1D)。

人工去除珠芽、花对两种舞花姜植株当年生花(图 2A、B)和珠芽的数量(图 2C、D)无显著影响(p

> 0.05),仅仅在低肥条件下人工去除珠芽减少双翅舞花姜的花数($p = 0.041$) (图 2B)。

2.2 不同居群异果舞花姜的繁殖及营养生长特征差异

从图 3 可以看出,野外 6 个不同居群中,异果舞花姜的珠芽大小、珠芽数、珠芽重、果实重、种子数和营养体重均存在极显著差异($p < 0.001$)。居群 4 和居群 1 的果实重和种子数显著高于其它居群($p < 0.05$)。居群 4 和居群 3 的珠芽数显著高于其它居群($p < 0.05$),居群 6 的珠芽大小显著高于所有其它居群($p < 0.05$)。居群 3 的营养体重显著高于其它居群($p < 0.05$)。

2.3 异果舞花姜野外居群不同土壤因子的贡献率和主分量值

主成分分析的结果表明,前 3 个主成分提供的信息量分别为 50.575%、18.204% 和 11.883% (表

图 1 不同肥力下毛舞花姜和双翅舞花姜繁殖和营养生长特征比较(t-test)

Fig.1 Comparison of reproductive traits and plant characteristics of *Globba barthei* and *G. schomburgkii* under different fertilizer-level (t-test)
1. 毛舞花姜 *Globba barthei* 2. 双翅舞花姜 *Globba schomburgkii* 数据点为平均值 ± 标准误 (n = 10) Bars are means ± SE (n = 10) 珠芽大小是每个珠芽的重量,其余参数是指整个植株的总和 Bulbil size mean the weight of a single bulbil, and the other parameters were the sum of each individual plant * : $p < 0.05$ ** : $p < 0.01$ *** : $p < 0.001$ ns : $p > 0.05$

图2 不同肥力下去除花(珠芽)对毛舞花姜和双翅舞花姜珠芽数(花数)的影响(*t*-test)
Fig.2 The effect of removing bulbils (flowers) to the number of flowers(bulbils) of *Globba barthei* and *G. schomburgkii* under different fertilizer-supply (*t*-test)
数据点为平均值 ± 标准误 (*n* = 10) Bars are means ± SE (*n* = 10) 1. 低肥 Low fertilizer 2. 高肥 High fertilizer * : *p* < 0.05 ns: *p* > 0.05

表2 不同土壤因子的贡献率和主分量值 Table 2 The ratio of contribution and main weight value of different soil factors			
土壤因子 Soil factors	主分量 1 Compent 1	主分量 2 Compent 2	主分量 3 Compent 3
pH值 pH value	0.594	0.319	0.649
有机质 Organic matter	0.821 *	0.331	- 0.303
速效氮 Available nitrogen	0.885 *	0.140	- 0.336
速效磷 Available phosphorous	- 0.223	0.824 *	0.305
速效钾 Available potassium	0.726	0.005	0.104
全氮 Total nitrogen	0.959 *	0.094	- 0.201
全磷 Total phosphorous	0.742	- 0.265	0.280
全钾 Total potassium	- 0.436	0.6847	- 0.319
各分量贡献率 Rate of variance (%)	50.575	18.204	11.883
累计贡献率 Cumulative rate (%)	50.575	68.779	80.662

* : 负荷量 > 0.800 Loading value > 0.800

2) ,其中第一主成分中的土壤全氮(0.959)、土壤速效氮(0.885)和土壤有机质(0.821) 的负荷量最大;第二主成分中土壤速效磷(0.824)负荷量最大(表2)。

2.4 土壤主成分因子和异果舞花姜繁殖分配之间的相关性

不同居群异果舞花姜珠芽大小与土壤全氮(*r* = 0.798)、速效氮(*r* = 0.780)和有机质(*r* = 0.821)均

显著正相关(*p* < 0.05)。营养体重与土壤速效磷呈显著正相关(*r* = 0.906, *p* < 0.05),繁殖体重/营养体重与土壤速效磷呈极显著负相关(*r* = - 0.893, *p* < 0.05)(表3)。不同居群的果实重和种子数和居群所在土壤因子相关不显著(表3)。

由表4可知,异果舞花姜植株有性繁殖能力(果实重、种子数)和无性繁殖能力(珠芽数、珠芽大小)之间相关不显著。每株的果实重分别与种子数(*r* =

图 3 不同居群中异果舞花姜的繁殖和营养生长特征比较(ANOVA)

Fig.3 Comparison of reproductive traits and plant characteristics of *Globba racemosa* among six populations (ANOVA)
数据点为平均值 ± 标准误 (n = 30), 具有相同字母平均值没有显著差异 (p > 0.05) Bars are means ± SE (n = 30) The mean values indicated by the same letter are not significantly different (p > 0.05) 珠芽大小是每个珠芽的重量, 其余参数是指整个植株的总和 Bulbil size mean the weight of a single bulbil, and the other parameters were the sum of each individual plant

表 3 土壤主因子和异果舞花姜植株特征值之间的 Pearson 相关分析 r 值

	全氮 Total nitrogen	速效氮 Available nitrogen	速效磷 Available phosphorous	有机质 Soil organic matter
果实重 FMA	-0.377	-0.467	-0.153	-0.210
种子数 SNU	-0.398	-0.463	-0.114	-0.231
珠芽数 BNU	-0.417	-0.462	0.724	-0.092
珠芽重 BMA	0.403	0.392	0.777 *	0.604
珠芽大小 BSI	0.798 *	0.780 *	0.388	0.821 *
繁殖体重 RMA	-0.118	-0.218	0.366	0.190
营养体重 VMA	-0.402	-0.379	0.906 **	-0.057
果实重/珠芽重 FBM	-0.444	-0.599	-0.252	-0.270
果实重/营养体重 FVM	-0.422	-0.612	-0.319	-0.259
珠芽重/营养体重 BVM	0.672	0.740	-0.502	0.317
繁殖体重/营养体重 RVM	0.253	0.116	-0.893 **	0.053

FMA: Fruit mass SNU: Seed number BNU: Bulbil number BMA: Bulbil mass BSI: Bulbil size RMA: Reproductive mass VMA: Vegetative mass
FBM: Fruit mass/bulbil mass FVM: Fruit mass/vegetative mass BVM: Bulbil mass/vegetative mass RVM: Reproductive mass/vegetative mass *: p < 0.05
**: p < 0.01 n = 6 r_{0.05} = 0.754 r_{0.01} = 0.874

0.998)、果实重/珠芽重($r = 0.971$)和果实重/营养体重($r = 0.947$)三者均呈极显著正相关($p < 0.01$)。珠芽数和营养体重显著正相关($r = 0.901, p < 0.05$), 珠芽重和珠芽大小之间显著正相关($r = 0.849, p < 0.05$)。有性繁殖分配(果实重/营养体重)与果实重/珠芽重呈极显著正相关($r = 0.994, p < 0.01$)。

表 4 异果舞花姜有性无性繁殖特征和营养生长之间的 Pearson 相关分析 r 值
Table 4 r -value of Pearson Correlation among the sexual and asexual reproductive traits and plant vegetative characteristics of *Globba racemosa*

	FMA	SNU	BNU	BMA	VMA	FBM	RVM	FVM	BVM	BSI
种子数 SUN	0.998 **	I								
珠芽数 BNU	0.385	0.394								
珠芽重 BMA	-0.374	-0.367	0.526							
营养体重 VMA	0.145	0.170	0.901 *	0.629						
果实重/珠芽重 FBM	0.971 **	0.960 **	0.335	-0.469	0.105					
繁殖体重/营养体重 RVM	0.419	0.383	-0.484	-0.638	-0.792	0.434				
果实重/营养体重 FVM	0.947 **	0.930 **	0.307	-0.489	0.054	0.994 **	0.486			
珠芽重/营养体重 BVM	-0.589	-0.604	-0.768	-0.089	-0.794	-0.623	0.429	-0.581		
珠芽大小 BSI	-0.567	-0.572	0.047	0.849 *	0.126	-0.688	-0.287	-0.665	0.420	
繁殖体重 RMA	0.781	0.783	0.752	0.288	0.573	0.687	0.003	0.649	-0.668	-0.014

FMA, SNU, BNU, BMA, VMA, FBM, RVM, FVM, BVM, BSI; 同表 3 See Table 3 * : $p < 0.05$ ** : $p < 0.01$

3 讨 论

3 种舞花姜属植物的无性繁殖和营养生长显著受养分供应的影响。在人工栽培条件下,高养分处理显著增加毛舞花姜的珠芽数量、珠芽大小和植株营养体重,也显著增加双翅舞花姜的珠芽数量(图 1)。自然条件下不同居群异果舞花姜的珠芽大小、珠芽数、珠芽重和营养体重差异均极显著 ($p < 0.001$),其中水分供应充足的居群 4 和居群 3 的珠芽数显著高于其它居群($p < 0.05$),海拔最高、最干旱的居群 6 的珠芽大小显著高于所有其它居群($p < 0.05$),居群 3 的营养体干重显著高于其它居群($p < 0.05$)。珠芽大小与土壤全氮、速效氮和有机质均显著正相关(表 3),珠芽重、营养体重和土壤速效磷极显著正相关(表 3)。可见,舞花姜属植物的无性繁殖和营养生长具有较大的表型可塑性,当土壤养分供应充足时,无性繁殖能力增强,这与 Wijesinghe 和 Whigham(1997)、Margaret 和 James(2000)研究结果相一致,但与 Reekie(1991)、Ronsheim 和 Bever(2000)的研究结论相反。

3 种舞花姜的有性繁殖对养分供应变化响应不显著。不同养分条件下毛舞花姜和双翅舞花姜的开花数量无显著差异。这与 Margaret 和 James(2000)对 *Allium vineale* 的研究结果相一致。但有研究发现有性繁殖随着氮的变化而变化(Jurik, 1985; Reekie & Bazzaz, 1987)。虽然自然条件下不同居群异果舞花姜果实重和种子数差异均极显著($p < 0.001$),但居群果实重和种子数与主要土壤因子之间无显著相关性。从 6 个野外居群分析看出,水分供应最充足、并且受人为干扰最少的居群 4,果实干重最重,种子数最多,其次水分供应充分位于背阴处、受人为干扰稍多的居群 1(图 3A、B)。水分和人为干扰程度也是影响舞花姜属植物的有性繁殖的重要因素,另外有

性繁殖的成功在很大程度上还受其它因子的影响,如传粉动物(Temeles *et al.*, 2000)和立地条件的光温环境等。控制异果舞花姜野外居群有性繁殖的关键因子尚待进一步研究。

我们的研究并没有发现舞花姜属植物的有性和无性繁殖之间存在补偿关系。无论在高肥还是低肥条件下,人工去除毛舞花姜和双翅舞花姜的珠芽、花对植株当年生花数量和珠芽的数量无显著影响。低肥条件下人工去除珠芽还可减少双翅舞花姜的花数($p = 0.0410$),这可能与在除去珠芽的时候部分损伤花序有关。自然条件下异果舞花姜植株有性繁殖能力(果实重、种子数)和无性繁殖能力(珠芽数、珠芽重、珠芽大小)之间相关不显著。我们的研究同 Douglas(1981)、Pitelka 等(1985)、Reekie(1991)及 Cain 和 Damman(1997)结论一致,没有发现有性无性互换,不支持有性、无性互换可能作为一种保险机制,来适应环境条件的假说(Holler & Abrahamson, 1977),也不支持自然环境下资源分配在植物有性和无性繁殖间存在的此消彼长的权衡关系假说(Reznick *et al.*, 2000; Worley & Harder, 1996; Prati & Schmid, 2000; Thompson & Eckert, 2004)。形成毛舞花姜和双翅舞花姜有性和无性繁殖之间不存在补偿关系也有可能是由于去花时间太晚,不能显著影响形成珠芽的数量,从而掩盖了花与珠芽之间的补偿关系。

毛舞花姜和双翅舞花姜无论在自然条件下还是人工栽培条件下均只开花不结实,与异果舞花姜差别显著,这种差异的形成可能主要是由遗传因素控制的。传粉媒介的观察、花粉分泌量的测定及繁育系统的检验表明,毛舞花姜和双翅舞花姜并不缺乏有效的传粉昆虫(刘志秋等,2004),造成毛舞花姜和双翅舞花姜不育的主要原因可能是花粉没有活力。舞花姜属植物染色体基数为 16,毛舞花姜和双翅舞

花姜的染色体均为 48(Takano & Okada, 2002), 为三倍体。染色体加倍引起的花粉败育可能是不能结实的主要原因。

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