

舞草种子的蚂蚁传播

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摘要:舞草(*Codariocalyx motorius*)由于其小叶具有自身“摆动”的功能,从而具有较高的观赏价值。在长期的演化过程中,舞草与蚂蚁形成了互惠共生的关系:舞草种子生成了附生其上的能吸引蚂蚁的油质体,蚂蚁在搬运取食中,使舞草种子得以传播。舞草种子最重要的传播者是圆叶铺道蚁(*Tetramorium cyclotobium* Xu et Zheng)和布立毛蚁(*Paratrechina bourbonica* Forel)。另外长足光结蚁(*Anoplolepis gracilipes* Smith)和两种大头蚁(*Pheidole* sp. 1 和 sp. 2)也搬运其种子。野外试验表明,圆叶铺道蚁日搬运活动与气温呈显著正相关,即 $Y(\text{搬运种子数}) = -9.5058 + 0.045608X(\text{气温})$ ($r = 0.7196^{**}$, $n = 33$, $P < 0.01$),中午搬运效率达到高峰。布立毛蚁日搬运活动在上、下午各有一个高峰,上午的高峰出现时间不稳定,下午的高峰出现在 16:00~18:00。舞草种子上附生的油质体是吸引蚂蚁并产生搬运行为的主要物质。化学分析表明,油质体富含蚂蚁生长发育所必需的 10 种氨基酸和多种无机元素。样地采用陷阱诱捕蚂蚁的调查显示,5 种搬运者中,圆叶铺道蚁数量最大,分别占蚂蚁总量的 8.26% 和搬运蚂蚁总量的 48%。这说明圆叶铺道蚁在舞草种子的搬运中起着主要作用。

关键词:舞草; 种子; 蚂蚁; 搬运

Codariocalyx motorius seed removed by ants in Xishuangbanna

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Abstract: Many relationships between plants and insects have formed during a long evolution, and mutualism is one of these relationships and therefore is a trend of coordinating evolution between them. Many reports on seed dispersal by ants have been given out outside of China. At present, it is still attracting many researchers, and the focus is about removal rate of seed, that is RRS, as well as affecting factors. In China, reports on the topic are very few, and the study on mutualism between ants and *Codariocalyx motorius* (Houtt.) Ohashi is not reported oversea yet. The study has found out that *Codariocalyx motorius* is a myrmecochore and several species of ant remove seed of *Codariocalyx motorius* as well with phenomena of the mutualism between them.

The study was made in Xishuangbanna district, a tropic area, Yunnan Province of China. The geographical location of the spot is 21°41'N and 101°25'E, and the elevation is 600m above sea level. The annual mean temperature is 21.4 C and annual mean rainfall is 1557mm with relative humidity being 86%. The time of every year is divided into two periods; rain period (Jun. to Oct.) and dry period (Nov. to May).

Codariocalyx motorius (Houtt.) Ohashi is a small perennial shrub of Leguminosac. One of its values that attract people is of self-movement of its leaves obeyed to audio frequency around it. Its seed is average

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3. 18mm in length, 2. 58mm in width and 6. 985mg in weight. An opal elaiosome inter-grows on the hilum, and therefore attracts ants for removal.

Authors have found out five ant species that remove seeds of *Codariocalyx motorius*. They are respectively *Tetramorium cyclolobium* Xu et Zheng, *Paratrechina bourbonica* Forel, *Anoplolepis gracilipes* Smith and two *Pheidoles* (*P.* sp. 1 and *P.* sp. 2). In the test spot, by pitfall trapping way 436 ants are collected, among which there are 36 *Tetramorium cyclolobium*, making up of 8. 26% of the total, 8 *Paratrechina bourbonica* and 1. 83%, 23 *Anoplolepis gracilipes* and 5. 27%, and 8 *Pheidole* sp. 1 and 1. 83%. *Pheidole* sp. 2 is not found out in the trapper. The test result shows *Tetramorium cyclolobium* plays a greater role in removing seeds of *Codariocalyx motorius*.

The above 5 ants were observed for investigating their activity of removing the seeds of *Codariocalyx motorius*.

Workers of *Tetramorium cyclolobium* look for food alone. When finding out food, it leads its fellows to move the food. Although being small, the worker of *Tetramorium cyclolobium* can alone remove one seed. During removing seeds, these ants often stop for searching out road and then go back to carry seed. The daily intensity of removing seeds for *Tetramorium cyclolobium* increases with rising of temperature, and generally reaches a peak at noon when daily temperature goes to the highest point. Total number of removed seeds for *Tetramorium cyclolobium* is highly positive relative to daily temperature, and the linear regression equation between them is:

$$Y = -9. 5038 + 0. 5608X \quad (Y: \text{Total number of removed seeds}; X: \text{temperature } ^\circ\text{C})$$

($r = 0. 7196^{**}$, $n = 33$, $P < 0. 01$)

The results from field tests show that *Paratrechina bourbonica* has two peaks of removing seed every day, one being from 10 am to 12 am, with not good stability, and another being from 4 pm to 6 pm with good stability. When temperature exceeds 25 $^\circ\text{C}$ at noon, activity of removing seed reduces. Total number of removed seed by *Paratrechina bourbonica* is not significantly relative to daily temperature.

When there are enough food and there are no other ants coming to get food, *Tetramorium cyclolobium* and *Paratrechina bourbonica* do not directly move seeds. And therefore, these two species of ants may bite elaiosomes bit by bit and take them to their nest. It is very obvious for them to do so in order to save their energy. However, when they compete for food and their numbers are near equal, *Paratrechina bourbonica* will drive *Tetramorium cyclolobium* away. But *Tetramorium cyclolobium* will expel *Paratrechina bourbonica* too when its number is over the number of *Paratrechina bourbonica* and sees the latter to act alone.

Anoplolepis gracilipes looks for food by single too, but it is not seen that they queue for moving seeds together when they find out seeds. Its moving distance is longer and may covers 7~8m. *Anoplolepis gracilipes* still loots seeds from other species of ants that are moving seeds.

Pheidole sp. 2 moves one seed by single and will still transport the seed whose elaiosome is off. *Pheidole* sp. 1 also looks for food by single, but when seeds are found out, the fellows of *Pheidole* sp. 1 can come forward to move. Generally, one *Pheidole* sp. 1 moves one seed. And however, when the seed is moved near to the nest, other fellows can help for moving the seed into the nest. *Pheidole* sp. 1 is the smallest, the mean weight being 0. 000138g, and however the weight of one seed is 0. 00698g, being 50. 6 times of *Pheidole* sp. 1's weight.

Investigation of the nests shows that *Tetramorium cyclolobium* and *Paratrechina bourbonica* only eat elaiosome of *Codariocalyx motorius* and leave the complete seed in the nests. *Tetramorium cyclolobium* and *Paratrechina bourbonica* are the most important removers among these ants.

The experiments that elaiosomes attract ants give out the results that the 80%~90% of seeds retain-

ing elaiosome are removed away by ants within 30 minutes after seeds are laid out, and those seeds with no elaiosome are left, and all of seeds retaining elaiosome are moved within 60 minutes and therefore 10% ~ 20% of seeds without elaiosome are also removed. The observation also finds out that the ant, which removes seeds without elaiosome, is mainly *Pheidole* sp. 2 and others ants do not move those seeds retaining no elaiosome. Therefore, the activity that ants remove seeds of *Codariocalyx motorius* is mainly originated from fact that seed's elaiosome attracts ants.

According to analyzed results, the seed elaiosome contains 17.85% of protein, 13.1% of amino acids. There are 18 kinds of amino acids, 10 kinds of which are basic for ants, respectively being arginine, histidinol, leucine, isoleucine, lysine, methionine, alanine, threonine, tryptophan and valine. Contents of arginine and histidinol as well with aminoglutaric acid and proline make respectively up more than 10% of total amino acids.

Seed elaiosome also has 11 kinds of inorganic elements, 8 kinds of which are necessary for ants; respectively being calcium, phosphorus, iron, potassium, copper, manganese, magnesium, zinc.

Key words: *Codariocalyx motorius*; seed dispersal; ants

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植物与昆虫在长期的演化过程中形成了许多复杂的相互关系,互惠共生是其中的一种,并且是植物与昆虫协同演化的趋势。互惠共生指两个种群的相互作用对各自种群的增长都有促进作用^[1]。这种现象在自然群落,特别是在热带生境中普遍存在,并对维持生态系统的平衡起着重要作用^[2]。蚂蚁与植物的互惠共生关系表现为前者依赖后者获得营养,能量和适宜的栖境,而后者则在免遭其它害虫为害,传播其种子和偶尔为其传粉等方面获得收益^[3]。蚂蚁作为植物种子的传播者和授粉者在生态和进化上具有重要意义^[4],近十几年有关的研究主要集中在这两个方面^[2]。蚂蚁搬运传播种子的现象比较普遍,至少在 83 科植物上被发现^[5]。通常人们把依靠蚁类携带散布种子的植物称为蚁运植物。这类植物的种子常附生有富含蛋白质、脂肪和油类等蚁类嗜食成分的种阜,它能作为诱饵吸引蚁类并借以完成自身的散播^[11-12],而带有油质体的植物种子特别能吸引蚂蚁^[13]。

蚂蚁传播植物种子的研究国外开展得较多,且目前仍是一个活跃的研究领域^[7,8,11]。研究的内容主要集中在蚂蚁传播种子的效率(Removal Rate of Seed 简称 RRS)及其影响因子上^[12,14-17]。目前国内鲜见这方面的报道,而有关舞草种子与蚂蚁互惠共生现象的研究在国外亦未见报道。

本文观察了几种蚂蚁对舞草种子的搬运传播行为,并就搬运种子的效率、种子油质体化学成分及对蚂蚁的引诱作用等进行了初步研究。

1 材料与方 法

1.1 样地 研究地点位于西双版纳勐腊县勐仑镇热带植物园,地处于北纬 21°41',东经 101°25',年均温 21.4℃,年降雨量 1557.0mm,相对湿度 86%,有雨季、旱季之分,雨季在每年的 6~10 月份,其余月份为旱季。试验样地选择在植物园苗圃地进行,内有几十种引种植物,其中舞草是 1999 年 4 月从思茅勐连引进栽培的。

舞草 [*Codariocalyx motorius* (Houtt.) Ohashi] 属多年生豆科小灌木,树高约 1 m,初生真叶为一对生小叶,此后为互生单叶,8 叶龄后多为互生三出复叶,中出大叶长椭圆形或披针形,侧出小叶为倒披针形,大叶的长度和宽度分别为小叶长和宽的 5~7 倍和 4~5 倍^[18]。舞草种子于每年 10~12 月份成熟。荚果镰形或直,长 2.5~4cm,阔约 5mm,腹缝线直,背缝线稍缢缩,成熟时沿背缝线开裂,裂口朝下,种子掉落地上。每个荚果可产 5~9 粒种子。种子深褐色,表面具蜡质,种脐处附生乳白色的油质体,易与种子剥离。种子长平均 3.18 mm,宽 2.58 mm,千粒重 6.985g,油质体约占种子总重量的 3.6%。

1.2 方 法

1.2.1 蚂蚁搬运舞草种子行为的观察 将新鲜成熟的舞草种子随机放在样地里,观察记录蚂蚁搬运情

况,当蚂蚁将其搬运 15cm 以上距离后,分种采集部分蚂蚁装于盛有 75%乙醇的小瓶中,带回室内鉴定。

1.2.2 主要蚂蚁种类日搬运活动及搬运种子效率比较 将新鲜成熟的种子 15 粒随机放在舞草植株茎秆周围 10 cm 的土壤中,放置环境与种子掉入土壤的自然状态一致。从 8:00~19:00,每小时记录一次温度和各种蚂蚁搬运的种子数,并随时补充种子,连续观察记录 3d。

1.2.3 种子油质体对蚂蚁的吸引作用 将 10 粒除去油质体的种子与 10 粒未除去油质体的种子放在地上,间隔环状排列,在 30min 和 60min 时,分别观察记录种子被蚂蚁移动的数量,重复 3 次。

1.2.4 样地蚂蚁调查 采用陷阱诱捕法。将口径为 7.5cm 的一次性塑料杯埋入地下,杯口与地面齐平,杯四周用泥土填平,杯中盛 1/3 的 3%乙醛溶液(防止蚂蚁逃跑和腐烂)。样地共设 16 个陷阱,按对角线放射状排列,陷阱间相隔 2m。放置 48h 后,将诱集到的蚂蚁移入盛有 75%乙醇的小瓶内分别标记保存,带回室内进行种类鉴定和数量统计。

1.2.5 种子油质体营养成分分析 种子采自思茅地区景谷县野外舞草大片生长地,室内人工取其油质体分析。蛋白质采用凯氏定量法;氨基酸采用盐酸水解法,用 HITACHI 835 50 测量;色氨酸采用比色法;无机元素采用 ICP-AES 法。

2 结果与分析

2.1 搬运舞草种子的蚂蚁种类及其搬运行为

本试验共观察到 5 种蚂蚁搬运舞草种子,它们是圆叶铺道蚁(*Tetramorium cyclolobium* Xu et Zheng)、布立毛蚁(*Paratrechina bourbonica* Forel)、长足光结蚁(*Anoplolepis gracilipes* Smith)和两种大头蚁(*Pec-dole*, sp. 1 和 sp. 2)。圆叶铺道蚁工蚁单独搜寻食物,当发现食物后便召集同伴列队前去搬运。尽管该蚁体小,但通常是一个蚂蚁搬运一粒种子,少数是 2 只蚂蚁合搬一粒。它们搬运的速度较慢,搬运 1m 的距离约需 30min。在搬运过程中,常将种子放下,四处探路,然后再回头将种子搬走。早晚均可见到活动,放在样地各处的种子,很快便被该蚁搬走。布立毛蚁在上午和下午各有一个活动高峰,工蚁也是单独搜寻食物,发现食物后列队搬运,通常一只蚂蚁搬运一粒种子。它们搬运的速度较快,并且选择最近的路线到达蚁巢。有时该蚁会将种子搬运到途中的洞穴里,将油质体分离后再快速运回。在食物多又没有其它蚁群竞争时,圆叶铺道蚁和布立毛蚁可不直接搬运种子,而是将种子上的油质体一点一点咬下搬走,显然这可以节省能量。但是通常在寻找和搬运途中都存在着种间竞争。在争夺种子资源时,如果圆叶铺道蚁的数量与布立毛蚁相差不多,一般布立毛蚁会将圆叶铺道蚁赶走;而当圆叶铺道蚁的数量多而布立毛蚁只是单个活动时,则后者会被前者赶离种子。长足光结蚁也是单个寻找食物,发现食物后不见列队搬运的现象,它搬运的距离较远,可达 7~8 m,搬运的速度也最快,搬运时种子不离身,会上树。通常它会在其它几种蚂蚁搬运途中将搬运者吓跑,然后将种子搬走。大头蚁 sp. 2 在搬运种子时一般也是一头蚂蚁搬运一粒种子,它在只剩下没有油质体的种子时也会把种子搬走。大头蚁 sp. 1 也是单个搜寻食物,当发现种子时有同伴前来搬运,一般一只蚂蚁搬运一粒种子,当快搬运到蚁巢时,许多头蚂蚁会合力搬运一粒种子。为了腾出空间贮存种子,该蚁会将蚁巢里面原先储放的昆虫肢体如翅、足等清理出来。大头蚁 sp. 1 个体最小,据测定每头平均重 0.000138g,而一粒舞草种子平均重 0.006985g,种子的重量是该蚂蚁的 50.6 倍。跟踪蚁巢调查显示,圆叶铺道蚁和布立毛蚁只取食种子油质体而留下完好无损的种子。

2.2 主要蚂蚁种类日搬运活动及搬运种子效率比较

搬运舞草种子的蚂蚁主要是圆叶铺道蚁和布立毛蚁两种。这两种蚂蚁日搬运活动见图 1,搬运种子效率见图 2。

从图 1 看出,布立毛蚁日搬运有两个高峰,一个高峰出现在上午的 10:00~12:00,另一个在下午的 4:00~6:00,中午气温超过 25℃,活动减少。上午高峰出现的早晚受当日日出时间和温度的影响较大,17 日日出较早,温度较高,高峰出现的时间为 10:30;18 日日出稍后,且温度低于 17 日,高峰出现的时间为 11:00;而 19 日日出在 12:05,因此,上午搬运活动很少,未出现高峰。下午搬运高峰比较稳定,3d 观察都在 16:00~18:00。圆叶铺道蚁日搬运活动随温度升高而加强,一般在中午温度最高时达到高峰,搬运种子量与日气温呈正相关,即 $Y = -9.5038 + 0.5608X$, (Y :搬运种子数, X :气温 $^{\circ}\text{C}$; $r = 0.7196^{**}$, $n = 33$, $P < 0.01$)。布

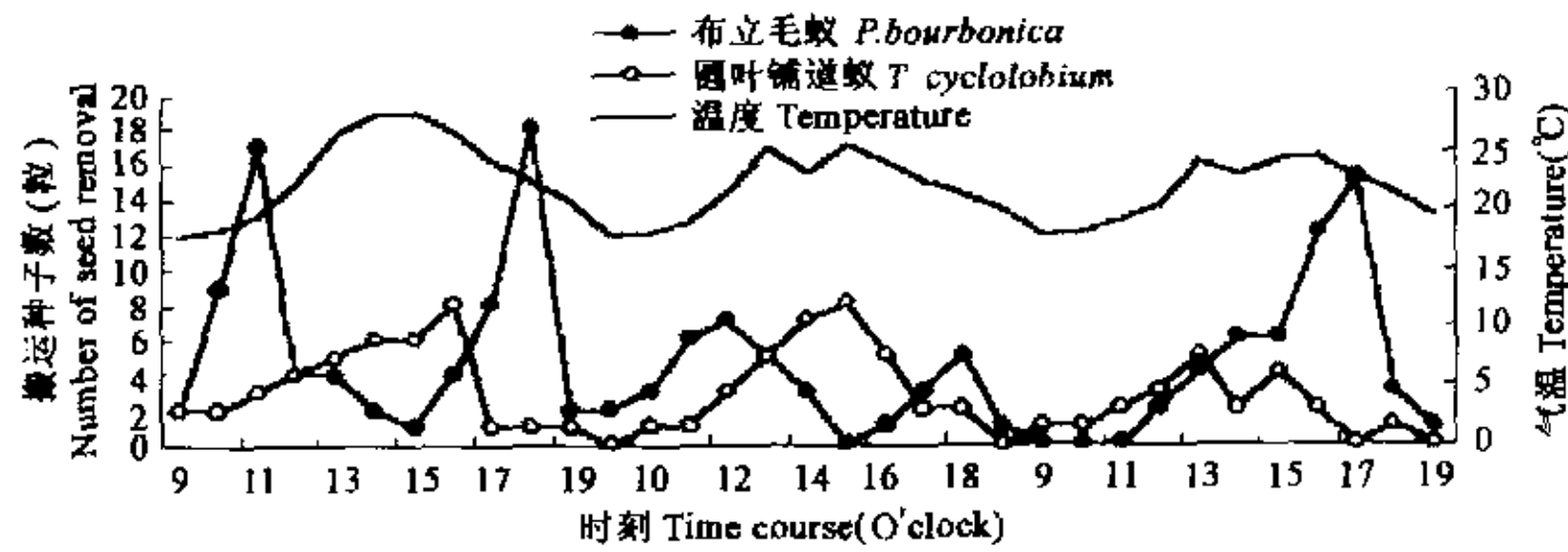


图1 圆叶铺道蚁、布立毛蚁搬运种子量和气温日变化

Fig. 1 Daily changes in cumulative numbers of seed removal and air temperature for *P. bourbonica* and *T. cyclolobium*

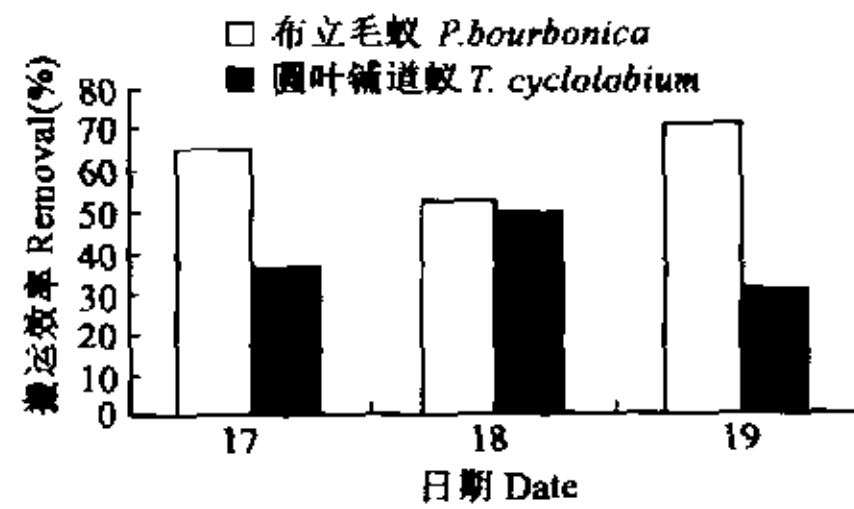


图2 圆叶铺道蚁、布立毛蚁搬运种子效率比较

Fig. 2 Removal rates of seeds by *P. bourbonica* and *T. cyclolobium*

所有带油质体的种子均被搬走,而且有10%~20%的无油质体的种子也被搬走。据观察,无油质体的种子主要是由大头蚁 sp. 2 搬走的,没有发现其它几种蚂蚁搬运无油质体种子的现象。由此可见,舞草种子主要以其油质体吸引蚂蚁搬运。

2.4 搬运舞草种子的蚂蚁在样地内所占的比重

用陷阱诱捕法在样地内共获蚂蚁 436 头,其中圆叶铺道蚁 36 头,占样地内蚂蚁总量的 8.26%;布立毛蚁 8 头,占 1.83%;长足光结蚁 23 头,占 5.27%;大头蚁 sp. 1 有 8 头,占 1.83%;样地陷阱内未发现大头蚁 sp. 2。由此也可看出,圆叶铺道蚁在舞草种子的搬运传播中起着主要作用。

2.5 种子油质体营养成分

种子油质体含蛋白质 17.85%、氨基酸总量 13.1%,氨基酸种类及含量见表 1,无机元素种类及含量见表 2。

舞草种子油质体含有的氨基酸种类较多,在已测定的 18 种中,以谷氨酸、脯氨酸、组氨酸、精氨酸含量较高,均占总量的 10%以上;而蛋氨酸、缬氨酸

立毛蚁搬运量与日气温相关性不显著。

图 2 显示,布立毛蚁的日搬运效率比圆叶铺道蚁高,这是由于布立毛蚁个体较大,搬运的速度比圆叶铺道蚁快,在竞争中处于优势所致。

2.3 种子油质体对蚂蚁的吸引作用

舞草种子放置后 30min,即有 80%~90%的带油质体的种子被搬走,留下所有无油质体的种子;60min 后,

表 1 舞草种子油质体氨基酸种类及含量

Table 1 The components and contents of amino

氨基酸种类 A A	acids of the elaiosome	
	占种子油质 体的百分比 Percentage in the elaiosome	占氨基酸总量的 百分比 Percentage in the amino acids total contents
ASP 天门冬氨酸	0.90	6.91
THR 苏氨酸	0.30	2.29
SER 丝氨酸	0.31	2.35
GLU 谷氨酸	1.54	11.74
PRO 脯氨酸	1.64	12.50
GLY 甘氨酸	0.72	5.49
ALA 丙氨酸	0.24	1.83
CYS 胱氨酸	1.06	8.08
VAL 缬氨酸	0.10	0.76
MET 蛋氨酸	0.02	0.15
ILE 异亮氨酸	0.74	5.64
LEU 亮氨酸	0.71	5.41
TYR 酪氨酸	0.32	2.44
PHE 苯丙氨酸	0.48	3.66
LYS 赖氨酸	1.10	8.38
HIS 组氨酸	1.41	10.75
ARG 精氨酸	1.32	10.05
TRP 色氨酸	0.21	1.60
总量 Total contents	13.12	100

的含量较低,分别占总量的 0.15%、0.77%。种子油质体包含了昆虫营养上所必需的 10 种氨基酸,即:精氨酸、组氨酸、亮氨酸、异亮氨酸、赖氨酸、蛋氨酸、丙氨酸、苏氨酸、色氨酸、缬氨酸^[11]。

表 2 舞草种子油质体无机元素种类及含量

Table 2 The components and contents of inorganic elements of the elaiosome

元素种类 Elements	S	P	K	Ca	Mg	Cu	Zn	Fe	Mn	B	Mo
占种子油质 体的百分比 Percentage in the elaiosome	0.101	0.519	0.462	0.217	0.104	0.00137	0.00148	0.0391	0.0079	0.00097	0.0001

无机元素是蚂蚁外骨骼的主要成分,同时它们对维持各器官的正常生理功能具有重要作用。蚂蚁必需的无机元素有钙、磷、铁、钾、铜、锰、镁、锌、碘等。从表 2 看出,舞草种子油质体中除碘外含有其它 8 种蚂蚁必需的无机元素^[11]。

3 讨论

圆叶铺道蚁和布立毛蚁为舞草种子的主要传播者。圆叶铺道蚁数量较多,占样地搬运舞草种子蚂蚁数量的 48%,且分布均匀;布立毛蚁尽管数量较少,但搬运速度快,搬运效率高。另据调查,圆叶铺道蚁还搬运热带雨林的键物种——聚果榕的种子。

通常一种植物的种子都不仅由一种蚂蚁搬运,因此在做不同蚂蚁搬运效率比较时,仅仅在上、下午各观察 30min 或 1h,以此来比较分析月间或季节间搬运效率的差异,就显得观察时间过短,且无法排除蚂蚁季节性活动差异所造成的影响。此外,国外还采用另一种试验方法,即将植物种子放置地上,采取措施只让蚂蚁进入,48h 或更长时间后统计被移走的种子数,得出月间或季节间搬运效率的差异^[16,19]。此方法虽较省时、省力,但无法统计不同蚂蚁种的搬运情况。本试验采用连续时间段观察,尽管比较费时、费力,但可以掌握搬运者一天各自的搬运率及其与日温变化的关系。通过各个季节的观察则可以掌握不同蚂蚁种群的活动规律并可比较其季节间种子搬运率的差异。

舞草种子成熟后,果夹自然裂开,种子仅能落到近植株的地上。成熟种子上附生的油质体能吸引蚂蚁搬运取食,而种子外壳较硬,蚂蚁等小昆虫无法取食,从而使舞草种子得以传播,种群得以繁衍。舞草种子成熟季节在每年的 10~12 月份,风和雨量都较少,因此,蚂蚁是其种子的主要传播者。

种子油质体是植物长期适应环境而形成的。植物在生长过程中,要耗费一定的能量和营养才能生成这些能吸引蚂蚁的物质,使其种子得以传播,从而繁衍其种群。在澳大利亚的某些干燥地区,约有 24 科,87 属,约 1500 种植物的种子演化生成了这种油质体^[11]。油质体所占种子重量的比例变化较大,Stanislav 曾对 *Asarum europaeum*, *Viola hirta*, *V. mirabilis*, *V. matutina* 及 *Chelidonium majus* 几种植物的种子油质体与种子的比例作过分析^[14]。舞草种子平均重 6.985mg/粒,油质体重 0.248mg/粒,油质体占种子总量的 3.55%,与上述 5 种植物相比,油质体所占种子总量的比例最小,这表明舞草植物为了种子的传播所付出的代价最小。

种子油质体富含蚂蚁生长发育所必需的氨基酸和无机元素。由于样品有限,其它蚂蚁生长所需的营养成分,如脂肪、碳水化合物、维生素等有待进一步分析。

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