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Original article

The ant *Lasius flavus* alters the viable seed bank in pastures

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Abstract

The creation of small-scale vegetation mosaics by mound building is an important aspect of ant activity in grasslands. The consequences of this process for the composition of the viable soil seed bank are poorly understood. In this study we quantified the impact of the yellow ant *Lasius flavus* on both aboveground vegetation and seed bank of a low-intensity pasture located in the Vogelsberg area (Hesse, Germany). A few species of the mound vegetation (mainly therophytes) were restricted to the mounds, but most species also occurred in the surrounding area. The seed bank of ant mounds differed from that of the pasture soil between the mounds, with the abundance of germinating seeds being twice as high in the mounds. This was mainly due to the very large number of seeds originating from winter annuals and *Thymus pulegioides*. Seed abundance of most other species was lower in the mounds. Our results showed that this is partly due to dispersule weight limiting dispersal of seeds from the surrounding vegetation onto the mounds.

Keywords: Formicidae; *Lasius flavus*; Soil seed bank; Grassland vegetation; Ecosystem engineering

1. Introduction

Mound building by ants impacts the grassland vegetation by changing physico-chemical soil conditions, with ants biting leaves and roots, and covering plants with soil, altering belowground herbivory and creating micro-topographical heterogeneity [1,2,4,8–10,13,17]. Thereby, ants have beneficial effects on some plant species like winter annuals by providing gaps in the otherwise dense vegetation cover whereas others like rosette perennials suffer from covering with soil. This leads to small-scale vegetation mosaics that may even persist for several decades after abandonment of the mounds [17]. The vegetation on top of *Lasius flavus* mounds in grasslands, for example, resembles that of sand dunes of similar base status [8]. The vegetation on the mounds generally is a sub-sample of the species occurring in the space between the mounds (interspace), with permanently open gaps on the mounds potentially increasing overall plant diversity by competitive release from tall grasses [15,17]. Although aboveground vegetation of ant mounds has been studied extensively, the effects on the soil seed bank are still poorly understood [7]. Studies of the seed bank are important because the regeneration by seeds is important for the maintenance of plant populations in perennial grasslands and ants might provide suitable microsites for successful seedling establishment [3].

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We have studied the impact of the yellow ant *L. flavus* (F. 1781) on the aboveground vegetation and the viable soil seed bank of a low-intensity pasture where *L. flavus* builds persistent soil mounds. This species predominantly lives belowground, feeding on root aphids and their honeydew [17]. It is not known for dispersing seeds. The aim of the study was to compare the seeds contained in *L. flavus* mounds to those in the surrounding interspace soil. Moreover, we wanted to relate potential differences to plant traits (life form, dispersule weight). Due to differences in the vegetation cover between ant mounds and grassland [2,4,10,17], we expected a differentiation of the seed bank to occur. This differentiation should be caused by (i) limited invasion potential of certain seeds onto the mounds projecting above the surface, (ii) lesser vegetation cover on the mounds, (iii) increased seedling mortality on the mounds, (iii) soil heaping of the ants leading to burying of heavy seeds and carrying of small seeds to the mound tops, and (iv) flowering and fruiting on ant mounds of plant species that withstand or avoid burial by ant-heaped soil.

2. Materials and methods

2.1. Field studies

The study site is located in the Lower Vogelsberg region of Eastern Hesse, Germany. It is a species rich, productive pasture of the alliance *Cynosurion* that has been grazed by sheep at low-intensity for around 20 years. Elevation of the site is 240 m a.s.l., mean annual temperature is 8.4 °C, mean annual precipitation is 954 mm, and mean soil pH is 6.5. Dominating soil types are cambisols (FAO classification) above tertiary basalt with loess. All field studies were conducted on a 546-m^2 plot. Though this bears the risk of bias due to pseudoreplication, we are quite confident that our results apply to a wide range of similar ecosystems. Generalizations are nevertheless only possible with great caution. Aboveground vegetation was studied at the end of May 1997. Species richness and cover of the individual species were surveyed on 28 mature nest mounds of *L. flavus* and in 28 randomly selected sub-plots (50 cm × 50 cm) in the interspaces. Soil samples for seed bank analyses were taken in November 1996 with a soil corer (diameter: 5 cm) from seven mounds dominated by grasses (grass ant mounds), seven mounds dominated by herbs (herb ant mounds) and seven sub-plots in the interspace (pasture soil). Three soil cores per sample were taken to a depth of 12 cm and were mixed for further analyses. The height of the mounds ranged from 18 to 30 cm.

2.2. Laboratory methods

Soil samples were air dried, and cleaned of ants, vegetation, roots and rhizome fragments. The seed bank was analyzed with the seedlings emergence method [14]. Soil samples were transferred in a 2 cm thick layer to 18 cm × 28 cm Styrofoam basins and exposed in a greenhouse (day length 12 h, mean daily temperature 21 °C). The basins were watered regularly. Seedlings emerging from germinating seeds were identified to the species level and removed once or twice every week. The study was continued for 23 weeks until germination declined and no further species could be recorded. The seedling emergence method is 'not designed to provide a complete assessment of the seed flora present' [16] but it can come close to this ideal. Although some viable seeds may have remained in the soil samples beyond the experiment, the application of the seedling emergence method should have resulted in complete germination of seeds of most species within this time period.

2.3. Statistical methods

We calculated species richness (S_v) of the aboveground vegetation as well as the frequency [%] and the mean cover [%] of the individual species for both interspace and ant mounds. The soil seed bank was characterized by counting the number of seedlings emerging (N_s), the species richness (S_s) and the frequency of their occurrence in interspace as well as in grass and herb ant mounds. Following Grime et al. [5] and Klotz et al. [12], each species was assorted to one of three life forms (chamaephyte/hemicryptophyte/therophyte) and to one of five classes of dispersule weight (DW; $1 \leq 0.20$ mg, $2 = 0.21–0.50$ mg, $3 = 0.51–1.00$ mg, $4 = 1.01–2.00$ mg, $5 = 2.01–10.00$ mg). Differences in S_v, S_s and N_s for all species and for the life forms and dispersule weight classes were analyzed by means of one-way ANOVAs. Homogeneity of variances was tested with the Levine's test. If necessary, data were log-transformed prior to analyses. Differences between means were tested with Tukey's HSD test at the $P < 0.05$ level only in cases where ANOVAs showed significant results. All statistical analyses were done using the STATISTICA 6.0 program package (StatSoft, Inc., Tulsa, CA).

3. Results

Total and mean species richness of the aboveground vegetation was higher in the interspace than on *L. flavus* mounds (Tables 1 and 2). Seventeen species were confined to the interspace, whereas seven species exclusively occurred on mounds. The richness of hemicryptophytes and of chamaephytes was significantly higher in the interspace, whereas that of therophytes was significantly higher on ant mounds (Table 2). Interspace and mounds did not differ in the richness of species with small dispersules (weight class 1), while the number of species with heavier dispersules was significantly higher in the interspace (Table 2).

Cumulative seed bank richness of the two types of ant mounds ($S_s = 47$) was higher than the seed bank richness of the interspace soil (Table 1). The significantly lower means of S_s for both types of ant mounds revealed by the ANOVA thus reflects the strong variability between mound types (Table 3). However, S_s was generally lower than S_v, with 18 species of the aboveground vegetation not occurring in the seed bank samples and nine species germinating from the seed bank not being found in the aboveground vegetation (Table 1). In contrast, the number of seedlings (N_s) was higher in the mound soil than in the interspace soil (Tables 3 and 1). As for the aboveground vegetation, richness and abundance of hemicryptophytes was significantly higher in the interspace soil (Table 3). S_s of chamaephytes was higher in the interspace soil than in the grass ant mounds but equally high in herb ant mounds. Significant effects on chamaephyte seedlings may result from the very high seed density in herb ant mounds when compared to grass ant mounds. S_s of therophytes was not significantly different between the samples, but N_s of therophyte seedlings was higher in ant mounds than in interspace soil. S_s and N_s of species belonging to dispersule weight classes 3 and 4 were significantly higher in interspace soil. S_s of the other weight classes did not differ between the treatments. In contrast, the number of seedlings emerging from weight class 1 was four to five times higher in ant mound soil than in interspace soil (Table 3).

The rank–abundance curve of seedlings from interspace soil was considerably different from those of the two ant mound types (Fig. 1). The flatter curve of the interspace seed bank suggests a comparatively more homogeneous dominance structure, while the steeper curves in ant mounds point to the dominance of a few species. The abundance of the remaining species was even lower in the mounds than in the interspace soil. Species with the highest seedling abundance in interspace soils were *Luzula campestris agg.*, *Holcus lanatus*, *Erophila verna*, *Saxifraga granulata* and *Cerastium holosteoides*. Dominating species in grass ant mounds were *E. verna*, *Arabidopsis thaliana*, *Myosotis* spec., *Festuca ovina* and *Agrostis capillaris*, dominating species in herb ant mounds were *Thymus pulegioides*, *E. verna*, *Myosotis* spec., *A. thaliana* and *Veronica arvensis* (Table 1).

4. Discussion

Our study shows that the plant community of *L. flavus* mounds mainly is a sub-sample of the surrounding grassland vegetation. This is consistent with the results of other authors [2,8–10,13,15,17]. In contrast, mounds of *Camponotus punctulatus* in Argentine pastures promote the invasion of herb weeds into the vegetation [4].

In our study, a few species, most of them therophytes, were restricted to the ant mounds. Among them were winter annuals for which the ant mounds constitute regeneration niches by providing gaps in the close grassland vegetation [6]. The drought tolerant winter annuals can grow, produce seeds and germinate again in the next year [17]. Species avoiding the mounds either cannot grow up through heaped soil (like rosette perennials) or prefer more humid soils. In addition, species with larger seeds were less frequent on mounds. This indicates that the projection of the mound above the grassland surface limits seed dispersal [17]. We observed a distinct differentiation between ant mounds dominated by graminacious (mostly *F. ovina*) and those dominated by herbaceous vegetation (mostly *T. pulegioides*). The herb ant mounds are probably generated by a single *Thymus*-plant that out competed all other species by rapidly growing up through the mounds after being covered with soil [17].

The interspace seed bank was significantly different from that of the two ant mound types. This particularly holds for the distributions of species abundances, while total richness and the richness of hemicryptophytes and chamaephytes as well as that of most dispersule weight classes mirror the richness of the aboveground vegetation. Since therophytes growing on mounds shed their small seeds also into the interspace soil, the comparatively high species number of this functional group on ant mounds was less pronounced in the seed bank. The

Table 1
Frequency and cover of plant species of aboveground vegetation of the pasture and *L. flavus* mounds and frequency and number of seedlings emerging from the seed bank of pasture, grass and herb ant mound soil. S.D. = standard deviation of the mean

	Above-ground vegetation						Viable soil seed bank					
	Pasture (*N* = 28)			Ant mound (*N* = 28)			Pasture (*N* = 7)		Grass ant mound (*N* = 7)		Herb ant mound (*N* = 7)	
Number of species	55			44			42		34		35	
Number of seedlings							546		1232		1075	
	Frequency (%)	Mean cover (%)	S.D.	Frequency (%)	Mean cover (%)	S.D.	Frequency (%)	Number of seedlings	Frequency (%)	Number of seedlings	Frequency (%)	Number of seedlings
L. campestris agg.	78.6	1.6	1.5	35.7	0.6	1.2	85.7	53	21.4	7	21.4	7
H. lanatus	71.4	2.1	1.8	39.3	0.7	1.4	78.6	52	14.3	4	50.0	16
Plantago lanceolata	64.3	1.3	1.4	10.7	0.1	0.2	78.6	29	14.3	3		
S. granulate	7.1	0.1	0.2	21.4	0.1	0.3	78.6	46	50.0	16	64.3	12
Cirsium spec.	3.6	0.0	0.1	3.6	0.0	0.1	64.3	20	21.4	3	7.1	1
Achillea millefolium	89.3	3.3	1.9	46.4	0.7	1.1	57.1	14	28.6	5	14.3	2
Trifolium repens	78.6	7.6	10.0	35.7	0.3	0.5	57.1	11	7.1	1	14.3	2
Pimpinella saxifraga	85.7	1.9	1.5	14.3	0.2	0.7	50.0	14	14.3	6	28.6	4
Veronica chamaedrys	64.3	1.5	1.6	53.6	1.7	2.6	35.7	24	7.1	2	71.4	25
C. holosteoides	32.1	0.5	0.9	46.4	1.1	1.6	64.3	44	28.6	12	35.7	21
F. ovina	57.1	2.1	2.5	96.4	21.9	18.9	50.0	23	78.6	88	57.1	18
V. arvensis	7.1	0.1	0.3	60.7	1.5	1.5	21.4	12	71.4	58	85.7	68
T. pulegioides	25.0	0.5	1.3	60.7	21.8	28.6	50.0	11	28.6	11	100.0	346
Poa pratensis	46.4	1.4	2.3	25.0	0.7	2.0	21.4	7	42.9	20	42.9	14
Campanula rotundifolia	53.6	0.7	1.0	14.3	0.1	0.3	50.0	13	21.4	4	14.3	4
Daucus carota	21.4	0.4	0.9	7.1	0.1	0.7	35.7	10	28.6	5	21.4	4
Lotus corniculatus	67.9	3.6	3.4	42.9	1.5	4.0	28.6	5	7.1	1		
Vicia tetrasperma	35.7	0.5	0.9	21.4	0.2	0.3	28.6	9	28.6	5	7.1	2
Helictotrichon pubescens	96.4	6.0	4.6	21.4	0.4	1.0	7.1	1	7.1	1		
Agropyron repens	64.3	1.8	1.9	7.1	0.1	0.2	7.1	1	7.1	1		
Trisetum flavescens	82.1	2.0	1.6	28.6	0.3	0.8			14.3	2	42.9	10
Carex caryophyllea	17.9	2.3	7.5	3.6	0.0	0.2	7.1	1	14.3	11		
Galium mollugo	21.4	1.1	2.8	21.4	1.6	4.3			7.1	2		
Leucanthemum vulgare	39.3	0.3	0.5	0.0	0.0	0.0	14.3	3			14.3	2
Rumex acetosa	46.4	0.3	0.3	10.7	0.1	0.2	7.1	3			14.3	2
Vicia hirsute	21.4	0.1	0.3	50.0	0.4	0.5	14.3	5			14.3	2
Dactylis glomerata	25.0	0.4	0.9	7.1	0.4	1.9	14.3	2				
Hypericum perforatum	3.6	0.0	0.1				21.4	4			7.1	1
Centaurea jacea	78.6	1.4	1.5				42.9	8			21.4	3
Plantago media	7.1	0.2	1.0				28.6	4				
Viola spec.	10.7	0.2	0.7				21.4	5				
Silaum silaus	10.7	0.2	0.7				7.1	1				
Mentha arvensis	3.6	0.0	0.2				7.1	5				
Myosotis spec.				60.7	1.1	1.3	64.3	31	114.3	117	157.1	119
E. verna				57.1	1.6	1.6	64.3	48	100.0	443	100.0	224
A. capillaries				14.3	2.1	9.5	14.3	2	78.6	75	35.7	32

(continued)

Table 1 *(continued)*

	Above-ground vegetation						Viable soil seed bank					
	Pasture ($N = 28$)			Ant mound ($N = 28$)			Pasture ($N = 7$)		Grass ant mound ($N = 7$)		Herb ant mound ($N = 7$)	
Number of species	55			44			42		34		35	
Number of seedlings							546		1232		1075	
	Frequency (%)	Mean cover (%)	S.D.	Frequency (%)	Mean cover (%)	S.D.	Frequency (%)	Number of seedlings	Frequency (%)	Number of seedlings	Frequency (%)	Number of seedlings
Arenaria serpyllifolia agg.				21.4	0.4	0.9	7.1	1	21.4	15	21.4	22
A. thaliana				25.0	0.7	1.4	28.6	5	71.4	297	35.7	69
Dianthus deltoides				17.9	1.8	5.4	14.3	7			21.4	34
Juncus bufonius				3.6	0.5	2.8	7.1	1	28.6	5		
Trifolium dubium	10.7	0.1	0.2	17.9	0.4	1.3					7.1	1
Anthoxanthum odoratum	21.4	0.4	0.9	7.1	0.1	0.2					7.1	1
Briza media	50.0	1.2	1.6	17.9	0.3	0.8						
Trifolium pratense	42.9	2.2	4.3	14.3	0.1	0.3						
Galium verum	39.3	1.0	1.6	42.9	4.1	8.1						
Arrhenaterum elatius	39.3	1.0	1.7	21.4	1.2	3.1						
Origanum vulgare	32.1	0.9	1.6	7.1	0.1	0.2						
Leontodon hispidus	17.9	0.3	1.0	3.6	0.0	0.1						
Lathyrus spec.	14.3	0.3	0.8	28.6	0.8	2.9						
Festuca rubra	14.3	1.0	3.1	25.0	1.6	3.6						
Cynosurus cristatus	14.3	0.1	0.3	3.6	0.0	0.1						
Prunus spinosa juv.	32.1	0.8	2.1									
Agrimonia eupatoria	25.0	0.1	0.3									
Lychnis floscuculi	21.4	0.2	0.3									
Stellaria graminea	14.3	0.2	0.7									
Colchicum autumnale	3.6	0.0	0.1									
Sanguisorba officinalis	3.6	0.0	0.2									
Fragaria spec.	3.6	0.0	0.2									
Potentilla verna	3.6	0.2	0.9									
Rosa spec. juv.	3.6	0.0	0.1									
Bellis perennis	3.6	0.0	0.2						7.1	1		
Ranunculus bulbosus	14.3	0.1	0.2								7.1	1
Clinopodium vulgare							14.3	2	28.6	7		
Stellaria media							21.4	7			7.1	3
Brachypodium pinnatum							7.1	1				
Oxalis spec.							7.1	1			7.1	1
Chenopodium album											7.1	1
Epilobium ciliatum									7.1	1		
Epilobium montanum									14.3	2		
Epilobium tetragonum											7.1	1
Leontodon autumnalis									7.1	1		

Table 2
Mean species richness [0.25 m^{-2}] (S_v) of all plants and of life form types and dispersule weight classes of the aboveground vegetation in pasture and on ant mounds

S_v	Pasture ($N = 28$)	Ant mound ($N = 28$)	P
All plants	18.5 ± 3.0	11.8 ± 3.6	****
Hemicryptophytes	14.3 ± 2.8	6.3 ± 2.7	****
Therophytes	0.4 ± 0.6	3.0 ± 1.6	****
Chamaephytes	3.2 ± 1.0	2.5 ± 1.1	*
Dispersule weight 1	3.9 ± 1.5	4.6 ± 1.8	n.s.
Dispersule weight 2	4.1 ± 1.6	3.3 ± 1.1	*
Dispersule weight 3	3.0 ± 1.2	1.3 ± 1.1	****
Dispersule weight 4	4.6 ± 1.3	1.1 ± 1.1	****
Dispersule weight 5	2.1 ± 1.0	1.0 ± 0.9	****

* = $P < 0.05$, **** = $P < 0.0001$, n.s. = non-significant.

abundance of therophyte seedlings was nevertheless significantly higher in the mound soil, because most of the seeds were still released into the immediate surrounding of the plants. Environmental conditions provided by ant mounds increase the chances for short lived therophyte species to permanently establish themselves in grasslands by stimulating flowering, fruiting and building up of a seed bank [7,17]. The significantly higher abundance of chamaephytes in herb ant mounds was due to the large number of *Thymus* seeds. In general, only a few species were responsible for the more than two times higher seedling abundance in mound soil, while more than half of the species occurring in the seed bank had a lower abundance in mounds than in interspace soil. This is in accordance with the findings of King [7] and Dostal [3] for acidic grasslands in South Wales and Slovakia.

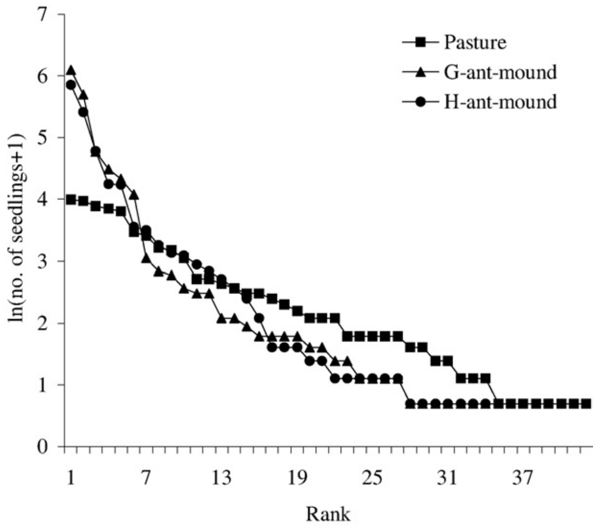

Fig. 1. Rank–abundance curve of the seedlings emerging from the interspace pasture soil and from grass (G ant mound) and herb dominated (H ant mound) ant mound soil.

Soil chemical and physical parameters are known to differ between *L. falvus* mounds and interspace soil [2]. However, in our study, like in the study of King [11], differences in soil properties were too small to significantly affect the distribution of plant species. Therefore soil parameters were not taken into consideration here.

In conclusion, the mound building activity of *L. flavus* not only creates small-scale heterogeneity of the aboveground vegetation but also increases the heterogeneity of the seed bank. Our results showed that

Table 3
Mean species richness (S_s) and number of seedlings (N_s) per sample unit of all plants and of life form types and dispersule weight classes of the seed bank in the interspace pasture soil and in grass (G ant mound) and herb dominated (H ant mound) ant mound soil

	Interspace ($N = 7$)	G ant mound ($N = 7$)	H ant mound ($N = 7$)	P
S_s seedlings	20.1 ± 4.6 ^{a}	13.9 ± 3.8 ^{b}	14.4 ± 4.7 ^{ab}	*
N_s seedlings	78.0 ± 35.6 ^{a}	176.0 ± 98.9 ^{b}	153.6 ± 60.4 ^{b}	*
S_s hemicryptophytes	13.1 ± 2.3 ^{a}	7.9 ± 3.2 ^{b}	7.3 ± 4.5 ^{b}	**
S_s therophytes	3.3 ± 1.5	4.4 ± 0.5	4.3 ± 0.8	n.s.
S_s chamaephytes	3.4 ± 1.1 ^{a}	1.6 ± 0.8 ^{b}	2.9 ± 1.3 ^{ab}	*
N_s hemicryptophytes	46.7 ± 17.9 ^{a}	38.0 ± 20.5 ^{ab}	24.3 ± 24.3 ^{b}	*
N_s therophytes	15.7 ± 15.0 ^{a}	133.6 ± 101.2 ^{b}	72.7 ± 28.0 ^{b}	****
N_s chamaephytes	14.9 ± 10.3 ^{a}	4.4 ± 2.6 ^{b}	56.6 ± 40.2 ^{c}	****
S_s dispersule weight 1	6.3 ± 2.5	6.1 ± 1.6	6.3 ± 1.4	n.s.
S_s dispersule weight 2	4.1 ± 1.3	3.4 ± 0.5	3.7 ± 1.9	n.s.
S_s dispersule weight 3	2.9 ± 0.7 ^{a}	1.0 ± 1.5 ^{b}	1.3 ± 1.1 ^{ab}	*
S_s dispersule weight 4	4.1 ± 0.9 ^{a}	1.1 ± 1.7 ^{b}	1.3 ± 1.0 ^{b}	****
S_s dispersule weight 5	1.4 ± 1.5	1.3 ± 0.8	1.0 ± 1.2	n.s.
N_s dispersule weight 1	26.4 ± 15.7 ^{a}	122.7 ± 85.5 ^{b}	118.0 ± 53.0 ^{b}	**
N_s dispersule weight 2	19.1 ± 19.6	34.0 ± 24.9	24.6 ± 10.3	n.s.
N_s dispersule weight 3	11.3 ± 4.8 ^{a}	2.0 ± 3.4 ^{b}	2.1 ± 2.1 ^{b}	****
N_s dispersule weight 4	11.3 ± 4.9 ^{a}	3. ± 5.8 ^{b}	1.4 ± 1.0 ^{b}	**
N_s dispersule weight 5	2.6 ± 4.2	11.4 ± 13.2	5.3 ± 7.5	n.s.

* = $P < 0.05$, ** = $P < 0.01$, **** = $P < 0.0001$, n.s. = non-significant.

this is partly due to dispersule weight limiting dispersal of seeds from the surrounding vegetation onto the mounds. Furthermore, the differentiation of the seed bank was enhanced by the occurrence of drought resistant species and gap specialists constricted to ant mounds, which shed their seeds predominantly on the mounds. Two additional reasons needing further investigations are the burial of heavier seeds to deeper soil layers, and the higher seedling mortality in ant mounds as shown by Dostal [3]. As a consequence, the abundance of most species is reduced in the mound seed bank. However, weak competitors, finding a regeneration niche on ant mounds, might be able to permanently establish themselves on grasslands by producing a large number of seeds, which they shed to both mounds and surrounding areas.

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