Table 10. Percentage occurrence of satellites

Chromosome	Sample E	Sample M
D	44	35
E	50	49
F	69	70
G	70	69

5. Reproductive behaviour

5.1. *Seed setting*

Plants from populations M, BO, CA, E, WO and PAR were submitted to selfings and crosses in order to gain insight into their breeding behaviour and to check on the possible sterility barriers. Five plants each from the populations E and M were left in the garden for an open pollination.

Forced crosses and both free as well as forced selfings were carried out in the greenhouse and climatic chamber. Selfed flowers were isolated with aseptic gauze bags. Cross-populations were performed by brushing reciprocally two flower heads each 24 hrs at noon over the whole or pratically the whole period (up to maximal 5 days) of flowering. The flower heads were subsequently isolated. A practical problem with some influence on the seed setting percentage was raised by the fact that two flower heads, which one decided to cross, did not always open and wither on the same day. As a result, the achenes in the centre of the delayed flower head were sometimes not pollinized by the partner flower head giving rise to a centered spot of empty seeds.

The flowering period in the garden ranged from two up to eight days, varying between three and six days for most of the plants. The shorter flowering periods coincided with sunny weather, whereas cool, cloudy or rainy days coincided with the longer periods. Most flower heads with a seed setting higher than 50 % flowered on either sunny, or lightly clouded, periodically sunny days, whereas heads with lower seed output flowered on cloudy, cool or rainy days. Apart from diminutive *Staphylinidae*, the predominant insect-visitors were syrphid flies. The shortest seed ripening period with the garden plants was 21 days. It corresponded to the average duration of the ripening period in the greenhouse. The seed output from open pollinations was generally lower than that resulting from the forced crosses. Average seed setting of 4 individuals each from populations E and M amounted to 38 and 50, respectively. The average values were taken from the average values per individual.

In general, free-selfed flower heads did not develop and their distinct shrinking began about nine days after the opening of the flower head, the processus being completed in about 15 days.

Most of the ripened fruit heads developing after cross-pollination (30 against 39, 77 %) opened in the period of 18 - 22 days after the first day of flowering.All fruit heads except one opened in the period of 16 - 24 days.

The average seed setting of forced crosses was of 52.8 % for 30 E-heads and of 54.9 % for 28 M-heads. The average seed setting of free selfings was nil for 21 E-heads and of 2.0 % for 31 M-heads; the relatively high value for sample M is due to a self-compatible individual with seed output of 30 %, obtained from free selfings. Average seed setting in forced selfings between various heads of the same individual was of 5.8 % for 28 E-heads and 18.9 % for 26 M-heads. The relatively high seed setting percentages of forced selfings result from the behaviour of three E- and four M-individuals with a nil seed setting in free selfings and average seed settings of 19.2 % and 29.6 %, respectively, in forced selfings. The highest seed setting observed in forced selfings, with an average value of 89 % (!, 4 heads), occurred in an apparently self-compatible M-individual.

Seed setting percentages of the intrapopulation crosses in population samples BOP, CA, WO and PAR range from nil (7 heads) to 91 % over a total of 30 heads. In these populations the average seed setting resulting from free selfings (28 heads) was of 0.8 %, whereas the average seed setting

Table 11. Seed output and development of seedlings.
A = Selfings; B = Intrapopulational crosses; C = Interpopulational crosses.

	Cross	Seed setting %	Age of seeds (months)	Germination %	Number of seeds	Seedling viability %	Number of seedlings %	Fertility %
A	E 10 (4 heads)	32	8	100	42	88	31	28
	M 11 (4 heads)	89	8	24	42	100	8	21
B	M20xM14	81	8	77	26	100	14	60
	scar.			70	10			
	M24xM29	56	8	85	26	89	18	39
	scar.			70	10			
	M29xM24	64	8	70	10	44	9	24
	scar.			100	10			
	E22xE4	59	3	100	26	100	17	56
	scar.			90	10			
	E25xE10	67	3	95	21	100	16	65
	scar.			100	10			
	E26xE15	62	3	100	21	90	10	53
	scar.			90	10			
	E13xE14	55	3	100	21	94	18	50
	E14xE13	49		100	21	100	18	
	BOP5xBOP6	26		71	21	100	14	18
	BOP6xBOP5	36		47	17	100	9	
	CA2xCA4	53	3	90	21	100	18	49
	CA4xCA2	80		57	21	100	12	
	PAR7xPAR8	62		76	21	100	14	44
	PAR8xPAR7	79		48	21	100	11	
C	M7xE13	91	8	96	26	100	18	89
	scar.			100	10			
	M11xE18	96	8	69	26	75	12	57
	scar.			90	10			
	E19xM19	58	8	100	25	100	13	58
	scar.			100	10			
	E14xBOP5	62	3	90	21	100	17	41
	BOP5xE14*	25		100	21	100	17	
	CA3xE3	16	3	100	21	94	18	15
	M9xBOP6	67	3	85	20	94	16	25
	BOP6xM9*	24		29	17	100	5	
	M4xCA4	94	3	86	21	100	17	62
	CA4xM4	79		57	21	100	12	
	BOP5xCA5	78	3	57	21	100	12	39
	CA5xBOP5	36		81	21	100	17	
	Mean fertility (%) in intrapopulation crosses (14 cross combinations of which 8 reciprocal)							46
	Mean fertility (%) in interpopulation crosses (12 cross combinations of which 8 reciprocal)							48

* = very small seeds
scar. = scarificated seeds

in forced selfings (30 heads) was of 2.2 %. The residual percentage in free selfings mainly resulted from a self-compatible individual with a seed setting of 20 %. This individual produced as well 32 % of seeds in the forced selfings which represent the highest percentage obtained in these experiments.

The highest seed setting of the interpopulation crosses (26 heads) was of 94 %, the average value percentage amounting to 48 %.

It can be concluded that the investigated population samples are mainly outcrossing and panmixous. The more intensively investigated populations E and M show a comparable reproductive behaviour. The results of the present experiments agree with the data of ROUSI (1973), who found no seed setting after free selfings and concluded that autonomous apomixis might be ruled out. The major part of this material was self-incompatible. The average seed setting upon crossing was relatively low, which ROUSI mainly contributed to incompatible cross combinations.

5.2. *Seed germination*

Three- and eight-month-old seeds from various experiments were water-soaked over 12 hrs and transferred onto wet blotting paper in Petri-dishes. The Petri-dishes were left in the dark at room temperature (+/- 20 ^{o}C).

First germinations occurred in about four days after soaking of the seeds; most seeds germinated within 10 days after water soak-up. In general, germination was good (table 11), seeds which were scarificated by partial dissection of the seed coat, behaving similarly to the unscarificated ones. The age of the seeds did not seem to have any noticeable effect on germination.

Over-all germination percentages of the interpopulation crosses were somewhat higher than those of the intrapopulation crosses (85 vs. 81 %, table 11). Only one interpopulation cross showed a relatively low germination (29 %). Seeds from this cross were markedly small. The reciprocal cross combination had a higher seed setting (67 %), a normal seed size and germination. The germination percentages of the two investigated selfings differed strikingly (table 11). The individual M 11 appeared to be more self-incompatible than could be expected on account of seed setting percentages, the average of two reciprocal selfings being 89 % (4 heads).On the contrary, the other self-compatible individual, viz. E 10, in which seed setting was considerably lower (32 %), showed a germination percentage of 100 %.

5.3. *Development of seedlings*

To check on seedling viability, up to 18 germinated seeds per strain were planted in soil and grown in a climatic chamber (dry temperature at day: 17^{o}C, at night 10^{o}C; day length 16 hrs.; 13'000 Lux., relative air humidity 70 %).

Seedling viability, defined as the percentage of germinated seeds which developed further, was very high in nearly all crosses, its average being 95 % (table 11).

Up to 10 seedlings that germinated within a four-day-interval, were potted separately and grown in the climatic chamber. The rate of development was expressed by the duration of the period from germination, +/- two days, until the stage of five leaves was reached. The offspring of various grassland populations obtained from both intra- and interpopulational crosses showed the shorter duration of development (42 days or less) than the offspring of *L. hyoseroides* (43 days or more). Exceptionally slow development was observed in the seedlings originating from a cross between M 29 and M 24 as well as the selfing M 11. All seedlings from selfing M 11 had wrinkled leaves,which did not unfold entirely. It seems plausible, that the relatively slow development of *L. hyoseroides* might be related to its longer leaves: the average length of the longest leaf per seedling in the five-leaf-stage was between 37 and 58 mm for 4 M-strains, between 75 and 108 mm for 6 E-strains and between 41 and 70 mm for 6 E x M-strains. The *L. hyoseroides* sample PAR 670 mm) corresponded roughly to the sample E, whereas the grassland strains from samples BOP and CA again had shorter leaves of 60 and 49 mm, respectively.

The obtained data indicate that growth rate of seedlings is not im-

Table 12. Pollen size variation in parents and F_1-plants (values of pollen size in arbitrary units*; 50 - 80 grains measured in each sample).
A = Parents; B = Selfings; C = Intrapopulational crosses; D = Interpopulational crosses.

		3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5
A	E 10			3.7	40.7	48.1	7.4											
	E 13			1.9	23.1	71.2	3.8											
	E 14								76.5	23.5								
	E 19					3.8	1.9	11.5	67.3	15.4								
	M 4					1.9	3.8	21.2	69.2	3.8								
	M 7				1.9		3.8	11.3	75.5	7.5								
	M 9							11.7	68.5	20.4								
	M 11				29.4	54.9	13.7			2.0								
	M 19							9.6	65.4	23.1	1.9							
	BOP 5							2.0	82.4	15.7								
	CA 4							13.5	86.5									
B	E 10 S_1	1.4	4.1	6.8	8.2	12.3	41.1	12.3	5.5	1.4	4.1			1.4	1.4			
	E 10 S_2			3.8		1.9	37.7	23.1	9.6			3.8						
	M 11 S_1			3.0	13.4	3.0	9.0	14.9	40.3	1.5		1.5		1.5	3.0	3.0	6.0	
	M 11 S_2			2.5	8.8	1.3	11.3	25.0	27.5	6.3	2.5	3.8		10.0			1.3	
C	E 13 x E 14		1.9				35.2	50.0	73.0									
	E 25 x E 15			4.6	15.4	9.2	10.8	7.7	6.2	16.9	18.5	7.7		3.1				
	BOP6 x BOP5			3.6		5.4	53.6	30.4	7.1									
D	M 11 x E 18(1)			8.5	5.1	15.3	20.3	25.4	23.7	1.7								
	M 11 x E 18(2)			1.9	1.9	1.9	11.3	41.5	32.1	9.4								
	M 11 x E 18(3)			3.4	16.9	15.3	20.3	27.1	16.9									
	M 7 x E 13				5.1	3.4	42.4	40.7	6.8	1.7								
	M 19 x M 19			1.6	9.7	9.7	16.1	21.0	32.3	6.5								
	E 14 x BOP 5				4.0		14.0	50.0	30.0	2.0								
	BOP 5 x E 14				1.8	1.8	1.8	14.3	62.5	14.3	1.8			1.8				
	M 4 x CA 4			1.9	3.8	1.9	9.4	28.3	52.8	1.9								
	CA 4 x M 4			3.3	11.5	8.2	21.3	21.3	29.5	4.9								
	M 9 x BOP 6			4.3	5.7	5.7	8.6	7.1	38.6	25.7	4.3							

* 1,0 = 4,2 mm

peded by hybridizations. Checks performed on both seed germination and seedling development show that, in general, seed setting percentages can be used as a good measure for fertility.

6. Effect of hybridizations on pollen fertility

Pollen development was studied on three levels: a) intraindividual variation; b) variation between the individuals of a given strain and c) variation between strains. The results of measurements are presented in table 12.

a) The differences in the percentage of a well-developed pollen between two flower heads each per individual, determined for 25 individuals, ranged from 0 to 32 %, their average being 8.2 %.

b) Variation between the individuals of a strain. Percentages of well developed pollen were determined in each 4 - 6 individuals from 25 strains. The maximal difference between these percentages per strain ranged from 0 to 97 %, its average being 27 %; this wide range of variation within a given strain indicates that pollen development can be influenced by recombination factors. It should be added that the extent of variation was similar in hybrids between various populations as well as intrapopulation crosses.

c) Variation between various strains. Average percentages of well-developed pollen for the various hybridogenous strains, the strains from intrapopulation crosses and those from selfings ranged from 76 to 99 %, from 69 to more than 99 % and from 81 to 91 %, respectively. Apparently there is no decrease in percentage of well-developed pollen in both hybrids and offspring from selfings. Clumping and translucent pollen was observed only in a single hybrid cross.

Noticeable differences in the size variation of the well-developed pollen were observed in various individuals (tables 12, 13). It is interesting to note that wide variation ranges appeared to occur more frequently