145. Dextrality and Sinistrality in Plants^{*)}

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II. *Medicago litoralis* ROHDE

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M. litoralis is an annual of slender habit. Its small spiny pods contain on the average 6 small seeds. Judging from the meager sample, the original population must have been very uniform, in contrast with the highly variable *M. tuberculata*. No traits were found which could be used as markers in recognizing eventual self-pollination which may easily occur in the crossing experiments.

The work with this species was carried out in the same way as with *M. tuberculata*. Seeds of single pods were sown separately but in general the figures are given collectively per plant. The same designations will be used, i.e. for clockwise right, right-handed or R; for anti-clockwise left, left-handed or L. R-plants or rights are right-handed and L-plants or lefts are left-handed. The genotypes are denoted by the respective italicized letters (*RR*, *RL*, and *LL*).

It may be stated in advance that in the main outlines the situation was in agreement with the findings in *M. tuberculata*. 1. Right dominates over left. 2. Reciprocal crosses are identical. 3. Segregation is simple.

The experiments started on a wrong track due to an unexpected situation which seems to prevail in the wild population. Among 10 plants obtained from the original sample four (48a, b, c, and d) were rights and six (49a, b, c, d, e, and f) were lefts. 48b was a delicate plant which flowered sparingly and yielded only 6 seeds. 48a, c, and d were fairly vigorous and could be employed in crossing experiments. Among the lefts mainly 49c and d were used. Between those right- and left-handed plants reciprocal crosses were carried out and at the same time their selfed offspring were raised.

Table I. Offspring ($=F_2$) of No. 48
RL-plants used in the crossing
experiments

No.	Offspring No.	No. R- plants	No. L- plants	Sum
48a	105, 127	39	7	46
48c	128, 132	13	8	21
48d	213	4	3	7
Total		56	18	74

Table II. Offspring of 48b

No.	Genera- tion	No. R- plants	No. L- plants	Sum
48b	S_1	6	0	6
226	„	9	0	9
Total		15	0	15
306	S_2	33	0	33

Unexpectedly, all 3 rights (48a, c, and d) segregated in their offspring lefts (Table I), while the lefts bred true showing no trace of illegitimate pollination with *R*-pollen. Confronted with this inconsistency in the flowering and fruiting conditions of rights and lefts in the

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wild population, mutability of the rights was taken into consideration, an assumption which was supported by later observed sporadic appearance on the right-handed plants of irregular pods, i.e. pods in which the direction of coiling was changing, once or more often. This assumption was refuted in the course of the investigation, and the other alternative, illegitimate pollination, had to be accepted. Hence, the three original rights, 48a, c, d, have to be considered as *RL*-heterozygotes and their offspring as F_2 ; they will be denoted by No. 48 *RL* (Table I). Correspondingly, the constant, original lefts, 49a-f, will be designated by No. 49 *LL* (Table IV). Much later, two subsequent generations obtained from 48b showed that this was the only constant right-handed plant; owing to its sparse flowering and weak growth it was regrettably omitted from crossings (Table II). Thus, the investigation includes two series of the sequence F_1-F_3 , one obtained from the original rights and the other derived from our crossing experiments. Both will be briefly described, since the comparison is not without interest. Table III provides information on the F_3 -generation derived from 48a. Among 5 F_3 -lines obtained from R-plants 4 are segregating; the remaining, 105bf, could have been constant.

Table III. F_3 -offspring of 48a (*RL*-plant)

R-plant No.	Offspring No.	No. R-plants	No. L-plants	Sum
105bb	131, 133-134	21	9	30
„ ba	214-216	17	2	19
„ bc	217-219	12	4	16
„ bd	220-222	18	3	21
Total		68	18	86
105bf	223-224	9	0	9

Table IV. Offspring of the first L-plants used in crosses

L-plant No.	S_1 No.	No. R-plants	No. L-plants	Sum
49c	114, 129	0	24	24
49d	130	0	37	37
Total		0	61	61

The L-plants were constant and gave in the further generations only lefts.

Crosses. From the later established *RL* nature of the employed rights follows that the reciprocal crosses must have amounted to backcrosses. Table Va and b gives information for two *RL*-plants, 48a and 48c, respectively, crossed with *LL*-plants, and Table VI represents the reciprocal cross, *LL* $\times$ *RL*. Table VII comprises both backcrosses (Fig. 1).

It is evident from the tables that the reciprocal crosses were in fact test crosses. A preponderance of rights is noticeable, especially in the equation cross of Table Va, but the figures are small.¹⁾ All rights found in the above crosses

Fig. 1. *M. litoralis*. Reciprocal crosses between right-handed and left-handed plants. Upper row: Parental pods. Lower row: Filial generation equivalent to test cross $RL \times L$ or $L \times RL$

1) The question of competition between the R- and L-pollen grains must remain open until a much larger, now available material of the test cross $LL \times RL$ is examined.

Table V. Crosses $RL \times LL$ a) $48a \times 49c$ and $49d$

Sowing date	Cross	Exp. No.	No. seeds	Germination	No. plants	No. R-plants	No. L-plants
March 1955	$48a \times 49$	106	5	5	5	4	1
" "	" $\times$ "	107	2	2	2	2	0
" "	" $\times$ "	108	3	3	3	2	1
" "	" $\times$ "	113	4	4	3	2	1
		106-113	14	14	13	10	3
March 1956	$48a \times 49$	255	7	7	5	2	3
" "	" $\times$ "	256	5	5	5	2	3
" "	" $\times$ "	257	5	5	5	3	2
" "	" $\times$ "	258	3	3	3	2	1
		255-258	20	20	18	9	9
Total	$48a \times 49$		34	34	31	19	12

b) $48c \times 49c$ and $49d$

Sowing date	Cross	Exp. No.	No. seeds	Germination	No. plants	No. R-plants	No. L-plants
March 1955	$48c \times 49$	109	5	5	5	2	3
" "	" $\times$ "	110	4	4	4	3	1
" "	" $\times$ "	111	5	5	5	3	2
" "	" $\times$ "	112	2	2	2	1	1
	$48c \times 49$	109-112	16	16	16	9	7
March 1956	" $\times$ "	254	4	4	4	2	2
	$48c \times 49$		20	20	20	11	9
Total	$RL \times LL$		54	54	51	30	21

Table VI. Cross $LL \times RL$ $49c \times 48a$ and $48c$

Sowing date	Cross	Exp. No.	No. seeds	Germination	No. plants	No. R-plants	No. L-plants
March 1955	$49c \times 48$	117	4	4	3	1	2
" "	" $\times$ "	118	5	5	5	4	1
" "	" $\times$ "	119	4	4	2	1	1
" "	" $\times$ "	122	6	6	6	3	3
	$49c \times 48$	117-122	19	19	16	9	7
March 1956	$49c \times 48$	259	8	8	8	4	4
" "	" $\times$ "	260	7	7	7	5	2
" "	" $\times$ "	261	7	7	7	3	4
	$49c \times 48$	259-261	22	22	22	12	10
Total	$LL \times RL$		41	41	38	21	17

Table VII. Crosses $RL \times LL$ and reciprocal added together

Crosses	No. seeds	Germination	No. plants	No. R-plants	No. L-plants
$RL \times LL$	54	54	51	30	21
$LL \times RL$	41	41	38	21	17
Total	95	95	89	51	38

Table VIII. Subsequent generation ($=F_2$) from R-plants of cross $RL \times LL$

Sowing date	R-plant No.	Exp. No.	No. seeds	Germination	No. plants	No. R-plants	No. L-plants
Sept. 1955	109a	138-140	16	16	16	13	3
" "	109c	141-142	10	10	10	7	3
" "	111a	157a-d	21	21	19	14	5
March 1956	106b	268-269	38	35	32	20	12
" "	108a	270	34	34	33	30	3
" "	112b	271-272	33	33	32	22	10
" "	113a	273	31	31	28	21	7
Total			183	180	170	127	43

were expected to be heterozygotes RL and to produce only segregating offspring equivalent to F_2 . Progenies of 11 such plants were examined, 7 from cross $RL \times LL$ (Table VIII) and 4 from the reciprocal cross (Table IX).

Table IX. Subsequent generation ($=F_2$) from R-plants of cross $LL \times RL$

Sowing date	R-plant No.	Exp. No.	No. seeds	Germination	No. plants	No. R-plants	No. L-plants
Sept. 1955	118b	171-174	23	23	22	20	2
" "	" c	175-180	51	51	50	41	9
" "	" e	185-188	20	20	20	16	4
" "	" d ¹⁾	181-184	25	24	23	20	3
March 1956	" "	275	37	37	35	25	10
Total		171-184 and 275	156	155	150	122	28

1) The figures obtained for the same No. 118d in 1955 and 1956 show how variable is the ratio of rights and lefts.

Table X. Subsequent generation ($=F_2$) from R-plants of both reciprocal crosses, $RL \times LL$ and $LL \times RL$

	No. seeds	Germination	No. plants	No. R-plants	No. L-plants
R $\times$ L	183	180	170	127	43
L $\times$ R	156	155	150	122	28
Total	339	335	320	249	71

All 11 offspring segregated in monohybrid fashion, according to the total figures. Here again we see, like in *M. tuberculata*, a notable deficit of lefts when the mother of the cross was LL (49c or d).

Table XI. Offspring of segregated L-plants of the crosses $RL \times LL$ and $LL \times RL$

Sowing date	L-plant No.	S_1 No.	No. seeds	Germination	No. plants	No. R-plants	No. L-plants
March 1955	109b	138-140	28	28	27	0	27
" "	109d	147-152	41	41	37	0	37
" "	109e	153-156	21	21	20	0	20
" "	111b	158-160	31	31	29	0	29
" "	111e	161-164	11	11	11	0	11
" "	118a	167-170	28	28	27	0	27
Total			160	160	151	0	151

Table XII. F_3 -generation from F_2 -rights of cross $LL \times RL$

Sowing date	F_2 R-plant No.	F_3 -offspr. No.	No. seeds	Germination	No. plants	No. R-plants	No. L-plants
March 1956	173b, 2	282 ¹⁾	29	29	27	19	8
" "	175c, 1	284	31	31	25	19	6
" "	175c, 2	286 ²⁾	29	29	24	24	0
" "	176, 3	287	39	39	28	26	2
" "	176, 5	288 ³⁾	32	32	27	27	0
" "	178b	289	40	39	34	26	8
" "	178e	293 ⁴⁾	43	34	32	24	8
" "	179, 1	294 ⁵⁾	34	34	29	29	0
" "	171b	301	11	11	8	6	2
" "	172c, 2	303	13	13	12	10	2
" "	173a	304-305 ⁶⁾	15	15	13	9	1
							Inter-RL!
							3

All segregating strains added: 130R: 37L

1) Tendency to irregularities. 2) Tendency to irregularities. 3) Tendency to irregularities, 1 left pod. 4) Strong tendency to irregularities. 5) 1 plant had irregular pods. 6) Comp. footnote 2 on p. 631.

This finding appears to be inconsistent with the figures given in Tables Va, b, and VI but the figures of those tables are too small to allow a comparison. The figures included in Tables VIII and IX are large enough to support the significance of our observation made in both species, considering that here too germination was excellent and relatively only a few plants died before flowering. Table X comprises the results for all 11 offspring.

All *LL*-plants hitherto investigated were constant (Table XI).

From *R*-plants of the segregating ($=F_2$ -) offspring the following generation, equivalent to F_3 , was raised (Tables XII and XIII).

Table XIII. F_3 -generation from F_2 -rights of cross $RL \times LL$

Sowing date	F_2 R-plant No.	F_3 -offspr. No.	No. seeds	Germination	No. plants	No. R-plants	No. L-plants
March 1956	139, 5	276	37	37	34	34	0
" "	141c, 2	277 ¹⁾	28	28	24	24	0
" "	142b, 2	280-281	33	33	32	32	0
" "	142a, 1	278 ²⁾	26	26	24	19	4
							Inter-RL! 1

1) Irregular pods on 1 plant.

2) Strong tendency to irregularities

15 F_3 lines were obtained, 11 derived from the backcross $LL \times RL$ ²⁾ and 4 from the reciprocal. This experiment was conducted in the very hot summer of 1956 and neither germination nor number of surviving plants were as good as in the previous experiments. Among the 11 lines of Table XII 3 were true breeding *RR* and the remaining segregated with a preponderance of rights in the total numbers. Line 304-305 was of special interest; the parental plant had several irregular pods and one left-handed pod (whose offspring are described on p. 632). Among 13 surviving plants 3 produced often left-handed pods among a majority of right-handed ones. Such plants have been termed as inter-R/L. In Table XIII the four remaining offspring, from the reciprocal cross $RL \times LL$, are listed. Only one line is segregating, the three others are constant *RR*. The high frequency of constant *RR*-lines is unexpected. It could be only partly explained by the assumption that self-pollination had occurred in the original *RL*-plants instead of cross-pollination. Among the segregating No. 278 one inter-R/L was found.

The constant No. 276 (Table XIII) was the first *RR*-strain recognized as such. It was at once employed in crosses with several *LL*-strains. This was taking place in the middle of the exceedingly hot summer of 1956, a period during which the plants do not set well. The cross with plants of No. 276 as pollen contributors was especially difficult. At closer inspection it was found that the anthers rarely opened. They contained only ca. 37% good pollen grains, while the left-handed plants had at the same time ca. 70% good grains and their anthers were usually shedding pollen. Should a comparable situation exist in the wild population, this would explain why the *RR*-

2) Emphasis was laid upon the derivatives from this direction of the cross, since all rights here obtained had beyond doubt the genotype *RL*.

plants must have been frequently spontaneously cross-pollinated in contrast with the *LL*-plants which were breeding true owing to self-pollination.

Appearance of irregular pods. Sometimes on the right-handed plants pods could be observed in which the direction of coiling changed once or several times (Fig. 2). Very seldom even entirely left-handed pods occurred. The frequency of the irregularities was increasing toward the end of the flowering period. This tendency seemed to be particularly pronounced in the *RL*-plants but irregular pods occurred also in *RR*-plants (Tables XII and XIII). A count taken in 1955 showed that among 1258 pods from various right-handed plants 38 were in various degrees irregular and 4 were left-handed. The recessive type showed very few irregularities; among 1517 pods only 4 were distinctly but slightly irregular (Table XIV).

Fig. 2. *M. litoralis*. Irregular pod shown from the side. The change of coiling direction and the turning point can be plainly seen (higher part in the figure L, lower part R).

Table XIV. Frequency of irregularities in coiling direction.
Pods from various R-plants

No. of regular right pods	No. of irregular pods	No. of regular left pods	No. of examined pods
1216	38 ¹⁾	4	1258
Pods from various L-plants			
0	4 ²⁾	1513	1517

1) In various degrees irregular.

2) Slightly irregular

Table XV. Offspring from irregular pods produced by R-plants

Offspring	Pods with 1 change of direction				Confused pod		L-pods		Offspring from regul. right pods of resp. plants	
	R part		L part		No. R's	No. L's	No. R's	No. L's	No. R's	No. L's
	No. R's	No. L's	No. R's	No. L's						
Nos. 263-267	0	1	3	1					9	3
269					3	2			17	10
300	1	0	2	1 ¹⁾					6	2
302							3	3	10	2
304(-305)							6	0	9	1 ²⁾ , 3 inter-RL

1) of 6 seeds 5 were in the L-part; 2 plants died before flowering. 2) The only plant of Nos. 304-305, 305b 1, considered to be left-handed, flowered very late and produced at last, at the end of September, 2 left-handed pods.

Table XV represents the results. Three kinds of irregularities are distinguished in the table: 1. pods with one change of direction; 2. "confused pods" with several changes of direction and 3. entirely left pods. At the same time a few regular pods of the respective right-handed plants which had furnished the aberrant ones were investigated (last column of the table). The figures, though naturally

small, show that the divergencies were phenotypical. Even the offspring of the two left pods examined show no response to their aberrant shape. No. 304, the offspring of one of the left pods, found on an *RL*-plant of F_2 , consisted of 6 plants, all right-handed. But the tendency to irregularities seems to be heritable. For instance, the same strain, Line 304–305, derived from a plant (173a) which had besides a left pod several other irregularities, continued not only to produce irregular pods but also included 3 inter-R/L plants.

Similarly, 5 plants obtained from an irregular pod found on a left-handed plant were all left-handed, showing that here too the aberration was of phenotypical nature.

On the basis of the above findings, the irregularities do not appear to be due to gene mutations. More probably the plants, irrespective of their genotype, *RR*, *RL*, or *LL*, are endowed with the potentiality to realize both alternatives. Which of them will actually be realized, is genetically controlled. But disturbances in the developmental pattern may occur—such as changes in the relation of developmental rates or relative shifts of the involved thresholds—which lead to changes in the direction of coiling. The degree of divergence would depend upon the stage in which the disturbance sets in, in an ovary or, much earlier, in a flower primordium. However, it is difficult to explain in concord with this assumption, why the three genotypes (*RR*, *RL*, and *LL*) differ in the frequency and degree of irregularities, particularly why the dominant homozygotes produce them much more frequently and more strikingly divergent than the recessive ones. A detailed discussion will be given later with ampler experimental material at hand.

Summary. *Medicago litoralis* ROHDE includes right-handed and left-handed races. Reciprocal crosses were carried out with the following results.

1. Right dominates over left.
2. Reciprocal crosses are identical.
3. In F_2 simple segregation takes place.
4. A considerable deficit of L-plants was observed in F_2 when the female parent of the cross was left-handed.
5. Aberrant pods in which one or more changes in coiling direction take place were sometimes observed on R-plants (*RL* and *RR*) and very seldom on L-plants. On the former sporadically even entirely L-pods occurred; they were found frequently on so-called inter-R/L plants. Such drastic reversal of the spiral was never found in L-plants where the irregularities were of slight degree. So far the examined deviations were all of phenotypical nature.

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