

My observations agree in nearly all respects with those of H. and O. Tedin, but some details remain to be settled. A modest addition to their findings can be mentioned: in addition to z, genes a and b also restore normal hilum structure in ar plants. I have also introduced wa, a marker for genes ar and oh, and n and was, markers for z, into the system. Importantly, the material now at hand is "tamed", being represented by fertile dwarf lines which are easy to cultivate and in which the gene expressions are clear. A number of the lines are near isogenic for one or more relevant genes and thus are particularly favorable for demonstrating gene action and interaction. Finally, the material is well suited as parents for new crosses with genes in the am-1 and am-2 system, a project which is now underway.

1. Tedin, H. 1920. Hereditas 1:68-97.
2. Tedin, Hans and Tedin, Olof. 1928. Hereditas 11:1-62.

LINKAGE RELATIONSHIPS AMONG MARKERS IN CHROMOSOME 3 AND En, A GENE CONFERRING VIRUS RESISTANCE

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Two excellent seedling markers, apu and tac, recently were reported to be situated in chromosome 3, linked with st (4). The data did not reveal, however, if apu and tac lie towards the b or the M end of the chromosome, so new linkage tests were performed using b as an additional marker. F<sub>2</sub> populations from the following crosses were scored in the field in 1984 (only the relevant genes being listed):

A B St apu Tac x A b st Apu tac (and reciprocal)  
a B St apu tac x b st Apu Tac  
a B St apu tac x A b st Apu Tac

The analysis (Table 1) confirms the placement of apu and tac in chromosome 3 and localizes tac in the M end of the chromosome. Although the orientation of apu is somewhat unclear from these data, the overall body of evidence indicates that apu also lies on the M side of st.

These findings, together with results from previous studies of chromosome 3 (2, 3), make it evident that suitable seedling markers are favorably spaced over nearly the entire length of the chromosome. This set the stage for three further linkage tests conducted in the greenhouse in the fall of 1984. They were designed to establish the relationships among morphological markers, certain isozyme markers, and the gene En conferring resistance to pea enation mosaic virus (PEMV).

Initially we determined the relationship between three morphological markers, st, apu, and tac, and two isozyme markers, Lap-2 and Aat-c (Table 2). Gel electrophoresis was performed using methods previously described (5). Linkage between Aat-c and Lap-2 is evident. Moreover, both isozyme markers showed linkage with tac and both evidently lie distal to tac.

In the second and third greenhouse experiments the F2 populations segregated for resistance (En) and susceptibility (en) to PEMV. Gritton and Hagedorn (1) and D. W. Barton (unpublished) earlier had found linkage between En and st. En was believed to be in the M arm of chromosome 3, but because there was no certainty of this, we used a line carrying a morphological marker (chi-6) known to be located distal to b. (2). The cross had the formula:

En Tac Apu st chi-6 x en tac apu St Chi-6

Seedling F2 plants were inoculated in the two-three leaf stage by rubbing the leaves with a known culture of PEMV. A week later the plants were inoculated again to ensure against escapes. Analysis of this cross revealed that En and tac are rather tightly linked (- 8 units), verifying that the En locus resides in the M end of chromosome 3 (Table.3).

The third of the three greenhouse experiments involved the cross: Aat-c(S) Lap-2(S) En st chi-6 bulf x Aat-c(F) Lap-2(F) en St Chi-6 Bulf. In this case the M end of chromosome 3 was marked only with isozyme variants and the b end was marked by morphological genes. The relationships among the genes segregating in this cross (Table 4) were consistent with expectation. However, the St-En relationship is probably anomalous because the genes were in repulsion and the population size was small. Although both Aat-c and Lap-2 showed linkage with En, neither was sufficiently close to be considered a useful marker for En. However, as described elsewhere in this volume (6), Adh-1, Acp-3 and Gal-3 also map to this general region of chromosome 3. One of these loci should show close linkage with En.

Considering past and present evidence, our best current estimate of the relative order and distance among the markers discussed herein is as follows:

Aat-c-11-Lap-2-17-Tac-8-En-22-Apu-10-St-27-B-20-Bulf-8-Chi-6

1. Gritton, E. T. and D. J. Hagedorn. 1980. PNL 12:26-27.
2. Marx, G. A. 1982. PNL 14:43-46.
3. Marx, G. A. 1983. PNL 15:47.
4. Marx, G. A. 1984. PNL 16:46-48.
5. Weeden, N. F. and G. A. Marx. 1984. J. Heredity 75:365-370.
6. Weeden, N. F., G. A. Marx, and E. Pagowska. 1985. PNL 17:75-76.

Table 1. Joint segregation of st, apu, and tac in F<sub>2</sub> populations grown in the field in 1984.

Gene pair & F <sub>2</sub> identities	XY	Xy	xY	xy	Total	X	Y	Linkage	Recomb.	S.E.
St-Apu										
B284-519-528	171	65	57	1	294	4.4*	1.02	17.3**	14.8	5.7
540-547	122	50	56	0	228	0.02	1.45	18.72**	<13	
550-554	54	38	36	0	128	0.67	1.50	24.50**	<13	
					650					
St-Tac										
B284-519-547	181	53	37	21	292	4.11*	0.01	4.52*	40.9	3.9
540-547	131	55	58	5	249	0.01	0.11	11.86**	28.8	5.7
550-554	70	34	34	5	143	0.39	0.39	6.15*	33.6	7.3
					684					
St-B										
B284-519-528	162	36	24	18	240	7.20**	0.80	12.10**	33.8	3.9
540-547	121	18	21	22	182	0.18	0.89	24.91**	25.7	3.9
550-554	66	9	11	19	105	0.71	0.16	33.15**	20.2	4.5
Apu-Tac										
B284-519-528	157	70	61	4	292	1.17	0.02	15.22**	25.0	5.4
540-547	145	30	20	29	224	1.17	0.21	32.51**	25.7	3.5
550-554	68	20	19	18	125	1.41	1.94	11.35**	34.4	5.5
					641					
Apu-B										
B284-519-528	141	44	45	10	240	0.56	0.80	0.60 ns		
540-547	93	35	37	1	166	0.39	0.97	8.70**	18.2	7.4
550-554	41	25	25	1	92	0.52	0.52	12.08**	17.4	10.0
					498					
Tac-B										
B284-519-528	147	43	39	12	241	1.89	0.61	0.04 ns		
540-547	97	32	40	8	177	0.42	0.54	1.39 ns		
550-554	55	22	20	6	103	0.00	0.26	0.31 ns		
					521					

Table 2. Joint segregation analysis in the F<sub>2</sub> population for pairwise comparisons of the loci Apu, Tac, Aat-c and Lap-2.

Gene pair	Number of plants with designated phenotypes <sup>1/</sup>									N	Joint Chi-square	Recomb. fract.	S.E.
	-/-	-/H	-/+	H/-	H/H	H/+	+/-	+/H	+/+				
Apu-Tac	12		19				18		76	125	4.89	37.0	7.6
Apu-Aat-c	5	15	9				28	42	23	122	1.89ns	-	-
Apu-Lap-2	6	17	6				22	43	28	122	1.47ns	-	-
Tac-Aat-c	3	9	18				31	48	15	124	23.15	26.0	4.5
Tac-Lap-2	19	11	0				9	51	34	124	41.36	17.0	3.6
Aat-c-Lap-2	0	7	27	3	47	7	25	8	0	124	126.18	11.0	2.1

<sup>1/</sup> Designations: recessive phenotype or homozygous slow=(-); heterozygous=(H), dominant phenotype or homozygous fast=(+).  
(Population C284-223-228)

Table 3. Joint segregation analysis in the F<sub>2</sub> population for pairwise comparisons among Tac, En, Apu, St,<sup>2</sup> and Chi-6.

Gene pair	XY	Xy	xY	xy	Total	Chi-square			Recomb. fract.	S.E.
						X	Y	Joint		
St-Tac	92	47	33	4	176	1.48	1.48	7.92**	30.5	6.7
St-En	90	49	35	2	176	1.48	1.48	13.09**	21.6	7.1
St-Apu	84	55	37	0	176	1.48	3.67	23.27**	< 13	-
Apu-Chi-6	92	29	46	9	176	3.67	1.09	1.71ns	-	-
Apu-Tac	99	22	26	29	176	3.67	1.48	29.45**	29.2	4.2
Apu-En	104	17	21	34	176	3.67	1.48	55.31**	22.4	3.6
Chi-6-Tac	96	42	29	9	176	1.09	1.48	0.82ns	-	-
Chi-6-En	96	42	29	9	176	1.09	1.48	0.82ns	-	-

(Population: C284-477 and 481)

Table 4. Joint segregation analysis in F<sub>2</sub> population for pairwise comparison of loci Aat-c, Lap-2, En, St, Bulf, and Chi-6.

Gene pair	Number of plants with designated phenotypes <sup>1/</sup>									N	Joint Chi-square	Recomb. fract.	S.E.
	-/-	-/H	-/+	H/-	H/H	H/+	+/-	+/H	+/+				
St-Chi-6	15		14				12		93	134	22.93	24.0	
St-Bulf	15		14				14		91	134	19.75	26.0	
St-En	0		29				33		71	133	12.24	-	
St-Aat-c	3	14	10				31	46	22	126	5.17ns	-	
St-Lap-2	9	15	3				19	48	30	124	5.04ns	-	
Chi-6-Bulf	23		4				6		101	134	80.51	8.0	
Chi-6-En	4		23				29		79	133	1.81ns	-	
Chi-6-Aat-c	3	11	10				31	49	22	126	5.41ns	-	
Chi-6-Lap-2	7	14	3				21	49	30	124	3.13ns	-	
Bulf-En	3		26				30		74	133	4.16ns	-	
Bulf-Aat-c	6	12	7				28	48	25	126	0.19ns	-	
Bulf-Lap-2	4	16	5				24	47	28	124	2.19ns	-	
En-Aat-c	14	14	4				20	46	28	126	7.41	36.0	
En-Lap-2	4	9	19				24	54	14	124	23.70	26.0	
Aat-c-Lap-2	2	8	23	4	46	10	22	9	0	124	91.73	15.0	

<sup>1/</sup> Designations as described in Table 2.  
(Population C284-478-480)