Theor Appl Genet (1985) 70:322–329

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The effects of three genes which modify leaves and stipules in the pea plant

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Received December 10, 1984; Accepted January 15, 1985
Communicated by R. Riley

Summary. The effects of three genes (*af, st* and *tl*) which modify leaf and stipule form and size in peas were investigated in families generated by crossing eight near-isogenic lines in all combinations but excluding the reciprocals. The eight parents and their equivalent phenotypes differed significantly for all characters due to the direct effects of all three genes, with their combined effects being especially influential in some instances. The effects of the recessive allele at any one of the three loci in homozygotes was to reduce plant productivity with *stst* having the most pronounced effect. The response of characters tended to be similar in direction, if not in magnitude, to any of the three genes. Partial dominance was frequently associated with the *tl* locus, and was especially obvious in *afaf Tltl* genotypes.

Key words: Peas – *Pisum* – Foliage – Partial dominance – Yield

1 Introduction

In recent years there has been increasing interest in the dried pea as a protein crop and this has stimulated efforts to improve its phenotype. Particular attention has been paid to the effects of three mutant genes which modify the foliage, with the 'wild type' being homozygous for the dominant allele in each instance: *af* which converts all leaflets to tendrils, *st* which reduces the stipule size very considerably and *tl* which converts all tendrils into leaflets. Plant breeders have made use of all three genes but only two phenotypes have some useful commercial potential, that resulting from the combination *afaf. stst,* and that due to *afaf* alone. The mass of tendrils which results from the latter gene helps considerably in supporting the crop and overcoming some of the harvesting problems (Snoad 1974, 1980).

Crops of peas carrying *afaf* do not seem to be at a yield disadvantage as compared with *AfAf* forms but the possession of very small stipules (*stst*) appears to reduce yield and some work has gone into the production of pea plants with a range of stipule sizes, both *stst* and *StSt* (Snoad and Hedley 1981). In this experiment we set out to examine the effects of the three genes *af, st* and *tl* as well as of their combined effects.

2 Materials and methods

Eight near-isogenic lines of *Pisum sativum* L. representing all possible combinations of the three genes *af, st,* and *tl* originally developed as the result of six backcrosses to an American freezing pea by Professor G. A. Marx of the New York State Agricultural Experiment Station, Geneva NY, were multiplied at the University of Naples. All eight lines were crossed in all combinations, excluding reciprocals, at the John Innes Institute, in order to generate 36 families; eight reconstituted parents and 28 recombinants. Within all but one of the eight resulting phenotypes there were a number of genotypes (Table 1).

The F1 seed was sown in a glasshouse in small peat pots in order to check the phenotype of each plant and replace any accidental selfs. The seedlings were then hardened off and planted out as soon as possible, 30 in each family, against wire netting in the experimental field at the John Innes Institute. Three blocks were planted with single plant randomisation of 10 plants from each of the 36 families in each block, making 1,080 plants in all. The plants were spaced at 20 cm, two guard row plants were sown at the end of each row and guard rows were provided at the end of each block.

During the growing season a large number of characters were recorded but only six are discussed in this paper: 1. the node of the first flower on the main stem (X1); 2. the total number of primary podding nodes on the main stem (X2); 3. the oven-dried weight of the "leaf" at the first flowering

Table 1. The 36 families generated by crossing, in half diallel fashion, the eight parental lines (underlined) with the genotype and family number given for each family. Note that there is a group of 13 families (and 7 genotypes) expected phenotypically to resemble family 1; three groups of 4 families (and 3 genotypes) expected phenotypically to resemble families, 2, 3, and 4; three groups of 1 family (and 1 genotype) expected phenotypically to resemble each of the families 5, 6 and 7. Family 8 has no phenotypically similar family. (Table 3 for example, sets out the families in each of the eight groups for the first character analysed). Group 1: Families 1, 9, 10, 11, 12, 13, 14, 15, 16, 17, 20, 22, 24, 27; Group 2: Families 2, 18, 19, 21, 31; Group 3: Families 3, 23, 25, 26, 32; Group 4: Families 4, 28, 29, 30, 34; Group 5: Families 5, 33; Group 6: Families 6, 35; Group 7: Families 7, 36; Group 8: Family 8

1	9	10	11	12	13	14	15
Af St Tl	*Af St Tl*	*Af St Tl*	*Af St Tl*	*Af St Tl*	*Af St Tl*	*Af St Tl*	*Af St Tl*
Af St Tl	*af St Tl*	*Af st Tl*	*Af St tl*	*af st Tl*	*af St tl*	*Af st tl*	*af st tl*
	2	16	17	18	19	20	21
	af St Tl	*af St Tl*	*af St Tl*	*af St Tl*	*af St Tl*	*af St Tl*	*af St Tl*
	af St Tl	*Af st Tl*	*Af St tl*	*af st Tl*	*af St tl*	*Af st tl*	*af st tl*
		3	22	23	24	25	26
		Af st Tl	*Af st Tl*	*Af st Tl*	*Af st Tl*	*Af st Tl*	*Af st Tl*
		Af st Tl	*Af St tl*	*af st Tl*	*af St tl*	*Af st tl*	*af st tl*
			4	27	28	29	30
			Af St tl	*Af St tl*	*Af St tl*	*Af St tl*	*Af St tl*
			Af St tl	*af st Tl*	*af St tl*	*Af st tl*	*af st tl*
				5	31	32	33
				af st Tl	*af st Tl*	*af st Tl*	*af st Tl*
				af st Tl	*af St tl*	*Af st tl*	*af st tl*
					6	34	35
					af St tl	*af St tl*	*af St tl*
					af St tl	*Af st tl*	*af st tl*
						7	36
						Af st tl	*Af st tl*
						Af st tl	*af st tl*
							8
							af st tl
							af st tl

Table 2. An analysis of variance of the eight parents to estimate the effects of the genes *af*, *st* and *tl* upon the six characters

	D.F.	Node of first flower (X1)	No. of podding nodes (X2)	Leaf wt. at 1st fl. node (X3)	Yield at 1st fl. node (X4)	Plant yield (X5)	Harvest index (X6)
Total	186						
Block	2	2.156	6.603*	783	0.860	336.7	343.76***
Genotype	7	9.331***	18.600***	102,089***	6.543***	4,393.2***	451.75***
Bl×Gen	14	3.902	2.023	523	1.143**	181.6	69.36*
Af	1	21.295***	6.690	146,485***	0.953	2,209.3***	1,823.56***
St	1	10.299*	85.009***	17,739**	12.683***	17,003.1***	294.49**
Tl	1	6.032	0.197	266,914***	16.906***	1,371.0***	126.23
Af×St	1	0.256	3.987	4,665	0.499	1,645.2***	144.24
Af×Tl	1	4.478	2.548	178,588***	6.883***	9.0	49.65
St×Tl	1	1.289	2.430	174	0.116	1,149.3**	1.14
Af×St×Tl	1	9.460*	0.803	1,367	0.152	123.3	71.36
Residual	163	2.325	2.048	2,618	0.559	173.2	39.72

* $P = 5.0$–1.0%; ** $P = 1.0$–0.5%; *** $P < 0.5\%$

Table 3. The mean values and their standard errors in the eight phenotypic groups for the first three characters analysed (X1, X2 and X3)

	Family	*Af.*	*St.*	*Tl.*	Node of first flower	No. of podding nodes on main stem	Dry wt of "leaf" at first flowering node (mg)
					Mean ± SE	Mean ± SE	Mean ± SE
Group 1	1	D	D	D	14.04 ± 0.19 a	7.40 ± 0.24 a	66.20 ± 2.93 ab
	9	H	D	D	14.03 ± 0.24	7.59 ± 0.27	75.17 ± 4.44
	10	D	H	D	14.17 ± 0.19	7.57 ± 0.47	77.73 ± 5.48
	11	D	D	H	14.12 ± 0.34	7.40 ± 0.31	73.80 ± 4.01
	12	H	H	D	14.17 ± 0.34	7.35 ± 0.34	64.83 ± 4.16
	16	H	H	D	14.59 ± 0.22	7.17 ± 0.25	66.62 ± 3.03
	13	H	D	H	14.21 ± 0.18	7.89 ± 0.25	77.64 ± 4.52
	17	H	D	H	14.46 ± 0.32	7.23 ± 0.31	74.04 ± 4.31
	14	D	H	H	14.74 ± 0.21	8.08 ± 0.15	84.17 ± 3.82
	22	D	H	H	14.79 ± 0.17	7.54 ± 0.24	69.43 ± 3.74
	15	H	H	H	14.96 ± 0.23	7.04 ± 0.24	76.96 ± 4.74
	20	H	H	H	14.10 ± 0.23	7.73 ± 0.15	78.37 ± 4.92
	24	H	H	H	15.21 ± 0.18	7.54 ± 0.19	73.39 ± 2.79
	27	H	H	H	13.96 ± 0.21	7.68 ± 0.25	68.46 ± 3.81
Group 2	2	R	D	D	14.52 ± 0.39 a	7.27 ± 0.39 a	55.48 ± 4.24 ab
	18	R	H	D	14.83 ± 0.35	6.97 ± 0.35	51.59 ± 2.89
	19	R	D	H	14.68 ± 0.28	7.46 ± 0.36	77.89 ± 5.87
	21	R	H	H	14.79 ± 0.32	7.10 ± 0.38	83.87 ± 5.71
	31	R	H	H	15.00 ± 0.27	6.06 ± 0.38	86.16 ± 5.58
Group 3	3	D	R	D	14.73 ± 0.32	5.96 ± 0.33 b	51.10 ± 3.07 ab
	23	H	R	D	14.07 ± 0.32	6.34 ± 0.26	49.49 ± 3.04
	25	D	R	H	14.36 ± 0.32	6.32 ± 0.30	50.93 ± 3.18
	26	H	R	H	14.87 ± 0.35	6.57 ± 0.24	52.83 ± 3.09
	32	H	R	H	14.20 ± 0.33	5.89 ± 0.32	48.18 ± 3.31
Group 4	4	D	D	R	14.20 ± 0.30	7.42 ± 0.20 a	74.49 ± 4.87 b
	28	H	D	R	14.32 ± 0.27	7.25 ± 0.25	79.61 ± 4.14
	29	D	H	R	14.29 ± 0.29	7.61 ± 0.17	81.04 ± 4.64
	30	H	H	R	15.21 ± 0.24	7.54 ± 0.21	83.00 ± 4.70
	34	H	H	R	14.07 ± 0.28	7.55 ± 0.18	78.97 ± 4.53
Group 5	5	R	R	D	14.29 ± 0.32 a	5.57 ± 0.33 b	36.89 ± 2.32 a
	33	R	R	H	14.72 ± 0.31	5.76 ± 0.40	54.60 ± 4.67
Group 6	6	R	D	R	14.93 ± 0.22 a	7.21 ± 0.24 a	198.72 ± 16.10 c
	35	R	H	R	14.73 ± 0.35	6.57 ± 0.30	146.17 ± 11.13
Group 7	7	D	R	R	14.45 ± 0.28 a	6.32 ± 0.37 b	65.35 ± 4.58 ab
	36	H	R	R	14.55 ± 0.26	6.28 ± 0.23	64.10 ± 4.50
Group 8	8	R	R	R	15.86 ± 0.38 b	5.39 ± 0.32 b	159.07 ± 16.15 c

D = Dominant allele; H = Heterozygous; R = Recessive allele. Mean values for the eight parental lines (underlined) not followed by the same letter are significantly different at the 5% level of probability according to Duncan's Multiple Range Test

node (stipules excluded) (X3); 4. the oven-dried weight of seed developed at the first flowering node (X4); 5. the oven-dried weight of seed developed per plant (X5); 6. the Harvest Index – the ratio of economic to total biological yield (X6).

Two groups of data have been examined: 1. the eight parental lines (Families 1–8); 2. all families (Families 1–36) in which 27 genotypes are represented.

Because the eight parental lines used in this experiment have been continuously selfed after only six generations of back-crossing, it is always possible that some differences between recombinants could be due to residual heterozygosity and/or genetic drift. For this reason only highly significant differences are taken into account.

Before proceeding with a detailed analysis of each of the six selected characters, block differences and block by genotype interactions were checked.

The results are presented in four ways: 1. an analysis of variance (ANOVA) for the eight parents, which accounts for blocks and genotypes, their interaction and the effects of the three gene loci singly and in all combinations (Table 2); 2. a similar ANOVA for all 36 families but in which the effects of the nine genotypes represented more than once in each phenotypic group are also taken into account. There is also an analysis of the differences between each of the three loci when homozygous for the dominant allele or heterozygous (Table 4); 3. the mean values and their standard errors for each of

Table 4. An analysis of variance of the 36 families which estimates gene effects, interactions and the effects of heterozygosity

	D.F.	Node of first flower (X1)	No. of podding nodes (X2)	Leaf wt. at 1st fl. node (X3)	Yield at 1st fl. node (X4)	Plant yield (X5)	Harvest index (X6)
Total	926						
Block	2	3.950	41.687***	4,348*	0.724	6,058***	426.643***
Family	35	4.454***	9.282***	26,730***	3.119***	4,212***	202.851***
Genotype	26	4.420***	11.684***	35,790***	4.108***	5,451***	258.012***
Replicated genotypes	9	5.705***	2.341	545	0.263	632*	43.482
Bl×*Gen*	52	1.910	2.264	441	0.599	256	52.146*
Af	2	18.400***	10.515***	91,490***	0.944	15,767***	1,839.705***
St	2	7.975*	117.574***	29,320***	24.893***	43,023***	45.953
Tl	2	3.962	4.872	133,700***	14.269***	4,187***	432.744***
Af×*St*	4	1.393	3.587	4,893***	1.301	1,559***	117.962*
Af×*Tl*	4	1.380	2.631	89,230***	3.283***	146	200.931***
St×*Tl*	4	1.083	0.793	4,812***	0.584	1,129***	52.526
Af×*St*×*Tl*	8	3.567	1.229	3,219***	0.570	436	73.243
AfAf v *Afaf*	1	1.496	0.211	1,902	1.701	341	119.744
StSt v *Stst*	1	9.811*	0.132	4,534*	2.399	1,670*	77.102
TlTl v *Tltl*	1	0.530	4.837	35,090***	8.114***	7,604***	431.481***
Residual	837	2.132	1.746	1,002	0.528	286	39.453

* $P = 5.0–1.0\%$; ** $P = 1.0–0.5\%$; *** $P < 0.5\%$

the six characters in each family together with a Duncan's Multiple Range Test (DMRT) for the eight parental lines only (Tables 3 and 6); 4. the differences exposed by ANOVAs for each character within each of the seven phenotypic groups; the eighth group having but one representative (Table 5).

3 Results

Node of first flower (X1)

1 Parents. There were highly significant differences between the genotypes (Table 2) but DMRT suggests that it is only family 8 (*afaf. stst. tltl*) which differs significantly from the others by flowering approximately one node later (Table 3). A similar finding has been reported by Wehner and Gritton (1981). The ANOVA shows that it is the *af* locus which is most influential in modifying the node at which flowering is initiated.

2 All families. Significant differences between the families are evident and the influence of the *af* locus is again indicated (Table 4), flowering tending to be delayed when the mutant allele at the *af* locus is homozygous (Table 3). Only within phenotypic Group 1 are significant differences seen between the genotypes (Table 5) but these need to be treated with caution because families 15, 20, 24 and 27, which are theoretically identical, are obviously different. This difference is also indicated by the significant value for replicated genotypes in the ANOVA (Table 4). These deviations may be due to experimental error or they may indicate the residual heterozygosity or genetic drift to which reference has already been made.

Number of podding nodes on the main stem (X2)

1 Parents. The genotypes differ very significantly and the differences are principally due to the effects of the mutant allele at the *st* locus in homozygotes which reduces the number of podding nodes developed as can be seen in parents 3, 5, 7, and 8 (Tables 2 and 3; Fig. 1).

2 All families. From Table 4 it can be seen that whilst *st* is the most important locus influencing this character, *af* also has a very significant effect. The smallest number of podding nodes being developed in *afaf. stst* genotypes as in Groups 5 and 8 (Table 3). There are no very significant differences between genotypes in the seven phenotypic groups (Table 5).

Table 5. Difference between the families in each of the phenotypic groups for the six characters recorded (X1 to X6)

	X1	X2	X3	X4	X5	X6
Group 1	***	*	**	–	***	***
Group 2	–	–	***	–	***	–
Group 3	–	–	–	–	*	–
Group 4	*	–	–	–	**	–
Group 5	–	*	***	***	**	***
Group 6	–	–	**	–	–	–
Group 7	–	–	–	–	–	–

* $P = 5.0–1.0\%$; ** $P = 1.0–0.5\%$; $P < 0.5\%$

Dry weight of "leaf" at first flowering node (X3)

1 Parents. The parents differ significantly (Table 2) and this can equally be discerned from Table 3 and Fig. 1. All three loci are obviously influencing leaf weight with the combined effects of *af* and *tl* also being of significance (Fig. 1).

2 All families. It is clear that *afaf* tends to reduce leaf weight, that *stst* has a similar effect but that *tltl* increases it (Table 3). Even more striking are the combined effects of the three loci (Table 4) so that when both *af* and *tl* are present the leaf weight is increased disproportionately although this value is reduced when *st* is also present.

An analysis of the phenotypic groups shows that there are highly significant differences between the genotypes in four of them; 1, 2, 5 and 6 (Table 5). The data suggest that these differences are associated with heterozygosity at the *tl* and *st* loci (Table 3) and these observations are borne out by the general ANOVA, especially for *tl* (Table 4). For example, in Groups 2 and 5 heterozygosity at the *tl* locus raises leaf weight in comparison with *TlTl*. In Group 6 there is a reduction in leaf weight in *Stst* plants in comparison with *StSt*. There is therefore a clear indication of partial dominance rather than heterosis at the *tl* locus with suggestions of a similar phenomenon influencing *st*. In both cases this effect can be seen most clearly in *afaf* plants.

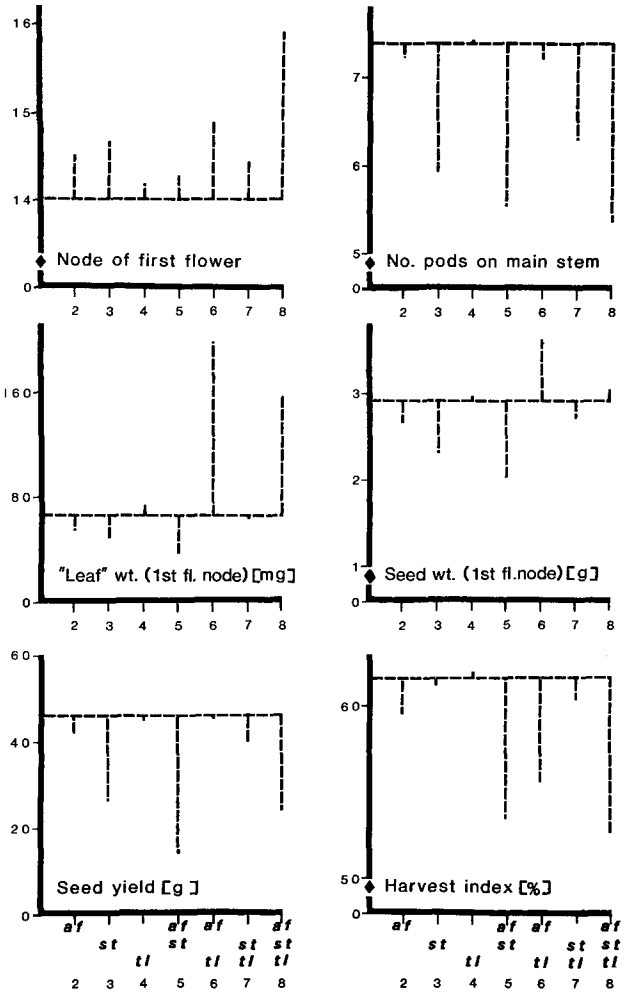

Fig. 1. Illustrating the effects of the three genes singly and in all combinations upon the six characters measured in the eight parental lines only. The results are presented as deviations from the triple dominant form which is shown as a horizontal line in each diagram

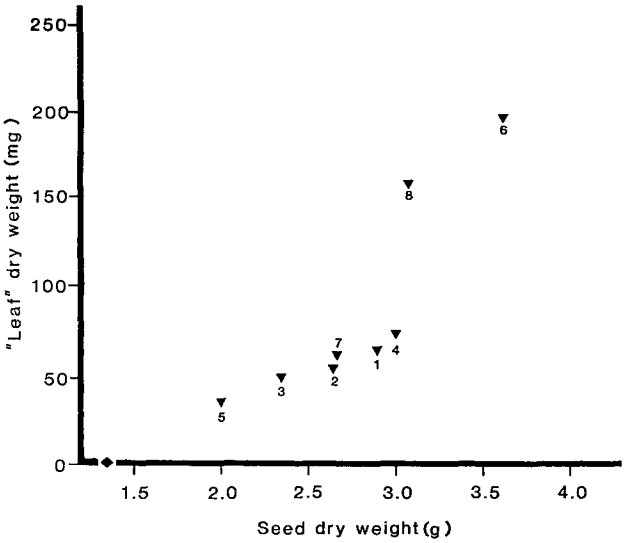

Fig. 2. Relationship between the dry weights of the "leaf" and the seed developed at the first flowering node in the eight parental lines

Dry weight of seed at the first flowering node (X4)

1 Parents. There are significant differences between the parents but the results need to be treated with caution because of a significant block by genotype interaction (Table 2). Even so the ANOVA suggests that both *tl* and *st* loci influence the amount of seed produced at this node and that the combined effect of the two genes *af* and *tl* is also important. Seed production tends to be lowest in parents 3 and 5 (Table 6 and Fig. 1).

2 All families. Seed production tends to be reduced when the mutant allele at the *st* locus is homozygous but there is some compensation for the *st* effect in *AfAf. tltl* or *afaf. tltl* families (Table 6). In contrast, the productivity of the node is increased significantly in the *afaf. StSt. tltl* genotype (Family 6). There is, therefore, a similarity between the effects of these three loci upon

Table 6. The mean values and their standard errors in the eight phenotypic groups for the last three characters analysed (X4, X5 and X6)

	Family	*Af.*	*St.*	*Tl.*	Dry wt of seed at first flowering node (g)	Dry wt of seed harvested per plant (g)	Harvest index (%)
					Mean ± SE	Mean ± SE	Mean ± SE
Group 1	1	D	D	D	2.91 ± 0.18 c	46.09 ± 2.62 d	61.75 ± 0.58 b
	9	H	D	D	2.95 ± 0.13	58.83 ± 3.24	62.00 ± 1.07
	10	D	H	D	3.11 ± 0.09	53.82 ± 3.72	62.23 ± 0.85
	11	D	D	H	3.07 ± 0.16	60.38 ± 4.53	60.80 ± 1.70
	12	H	H	D	2.77 ± 0.18	46.99 ± 4.03	58.54 ± 1.86
	16	H	H	D	2.68 ± 0.12	43.20 ± 3.01	56.73 ± 1.44
	13	H	D	H	2.98 ± 0.14	65.86 ± 5.07	63.00 ± 0.81
	17	H	D	H	2.94 ± 0.16	60.52 ± 4.42	63.09 ± 1.21
	14	D	H	H	2.89 ± 0.15	59.54 ± 4.59	63.58 ± 0.94
	22	D	H	H	2.71 ± 0.17	50.37 ± 2.83	60.86 ± 1.22
	15	H	H	H	2.80 ± 0.18	55.92 ± 3.92	62.05 ± 1.26
	20	H	H	H	3.03 ± 0.14	52.68 ± 3.97	61.79 ± 1.29
	24	H	H	H	2.92 ± 0.13	62.55 ± 3.69	62.05 ± 0.98
	27	H	H	H	2.78 ± 0.09	45.75 ± 3.40	61.45 ± 1.18
Group 2	2	R	D	D	2.65 ± 0.15 bc	42.77 ± 2.75 d	59.53 ± 1.47 b
	18	R	H	D	2.55 ± 0.15	33.90 ± 2.83	60.06 ± 1.17
	19	R	D	H	2.98 ± 0.17	51.36 ± 2.71	58.65 ± 1.11
	21	R	H	H	2.58 ± 0.15	42.87 ± 2.59	60.45 ± 0.91
	31	R	H	H	2.73 ± 0.19	42.98 ± 3.27	56.73 ± 1.18
Group 3	3	D	R	D	2.33 ± 0.13 ab	27.18 ± 2.30 b	61.27 ± 1.39 b
	23	H	R	D	2.19 ± 0.15	32.67 ± 3.08	59.90 ± 1.48
	25	D	R	H	2.45 ± 0.12	36.23 ± 2.53	64.55 ± 1.04
	26	H	R	H	2.31 ± 0.13	35.15 ± 2.12	61.18 ± 1.24
	32	H	R	H	2.46 ± 0.09	28.29 ± 2.19	63.29 ± 1.53
Group 4	4	D	D	R	2.99 ± 0.17 c	45.31 ± 3.79 d	62.02 ± 1.30 b
	28	H	D	R	3.10 ± 0.15	58.44 ± 4.05	61.16 ± 1.44
	29	D	H	R	3.50 ± 0.09	62.42 ± 3.11	60.98 ± 1.27
	30	H	H	R	3.04 ± 0.12	59.03 ± 4.11	60.89 ± 1.02
	34	H	H	R	3.10 ± 0.14	60.30 ± 4.29	61.47 ± 0.92
Group 5	5	R	R	D	2.04 ± 0.13 a	14.61 ± 1.88 a	53.57 ± 2.11 a
	33	R	R	H	2.63 ± 0.16	20.46 ± 1.48	59.78 ± 0.72
Group 6	6	R	D	R	3.62 ± 0.14 d	45.58 ± 2.64 d	55.66 ± 0.65 a
	35	R	H	R	3.30 ± 0.12	38.31 ± 3.29	54.72 ± 1.30
Group 7	7	D	R	R	2.66 ± 0.17 bc	40.18 ± 3.39 d	60.28 ± 2.16 b
	36	H	R	R	2.40 ± 0.14	36.97 ± 2.69	62.23 ± 1.74
Group 8	8	R	R	R	3.07 ± 0.17 c	24.16 ± 1.44 b	52.60 ± 1.16 a

D = Dominant alleles; H = Heterozygous; R = Recessive allele. Mean values for the eight parental lines (underlined) not followed by the same letter are significantly different at the 5% level of probability according to Duncan's Multiple Range Test

seed production and upon the amount of "leaf" produced at the same node (X3).

This similarity suggests that there could be a positive correlation between the two characters and this relationship can be seen in Fig. 2. However, it is obvious that the linear relationship which applies to Families 1–5 and 7 does not apply to Families 6 and 8 which are in a class of their own. In a sense these last two families are less "efficient" at seed production than might have been predicted by extrapolation from the data for the other six families.

Only in Group 5 are there differences between genotypes in the phenotypic groups (Table 5). This is an additional indication of partial dominance at the *tl* locus, seen by examination of the data in Table 6 and confirmed by the general ANOVA (Table 4). Thus heterozygosity of *tl* (Family 33) results in an increase in seed yield when compared with the effect of the wild

type allele at the *tl* locus in homozygotes (Family 5). Again it should be noted that this effect is most pronounced in *afaf* genotypes.

Dry weight of seed harvested per plant (X5)

1 Parents. There are significant differences between the genotypes in the total amount of seed produced (Table 2) with the major deviants being parents 3, 5 and 8 in which yield is reduced due to the effects of the mutant allele at the *af* and/or *st* locus in homozygotes (Table 6 and Fig. 1). The importance of the three loci and of the combined effects of *af* and *st* are indicated in the ANOVA (Table 2).

2 All families. All three loci are of significance in determining plant yield with the combined effects of *af. st* and *st. tl* also being highly significant (Table 4). Within the phenotypic groups there are significant differences measured in groups 1, 2, 4 and 5 (Table 5). In group 1, as was found with the node of first flower, families 15, 20, 24 and 27 appear to differ which may be a further indication of residual heterozygosity, or, the result of genetic drift. In groups 2, 4 and 5 the differences appear to be associated with heterozygosity at the *tl* and *st* loci with the greater emphasis being upon *tl* (Tables 4 and 6).

Harvest index (X6)

1 Parents. There are highly significant differences between the genotypes, which are marginally affected by a possible block × genotype interaction. There is no doubt, however, about the significance of the *af* locus in influencing harvest index with *st* playing a part too (Table 2). It would appear that in homozygotes the mutant allele at either locus tends to reduce the harvest index (Fig. 1).

2 All families. Significant differences between the families are due principally to the effects of *af, tl* and to their combined effects and to a lesser extent to *af* and *st.* (Table 4).

Differences between the genotypes in each of the phenotypic groups are confined to Groups 1 and 5 (Table 5) and these differences can be associated with heterozygosity at the *tl* locus (Tables 4 and 6).

4 Discussion

There are significant differences between the eight parental lines for all six characters that have been examined. These differences may be due to the direct effects of one to all three of the genes *af, st* and *tl* with their combined effects being especially influential in some instances (Fig. 1).

The effects of any of the three genes acting singly tend to be towards reduction in the plants' productivity, with the mutant allele at the *st* locus in homozygotes having the most pronounced effect. The effect of *st* in reducing productivity is also noticeable when it acts in the presence of the other two loci. It has previously been considered that *st* only affected stipule size but it appears from this evidence that it can influence leaf size too.

Generally speaking, where a gene affects a character the responses are similar in direction if not in magnitude in all eight parents; i.e., increasing the node of first flower, reducing the number of pods on the main stem, reducing the yield of seed, etc. Only in *afaf* and *tltl* plants is this trend reduced or even reversed (Fig. 1).

The greatest reductions in seed productivity are always associated with the combination of the mutant alleles at the *af* and *st* loci in homozygotes and the greatest compensation for this reduction is observed when *tltl* is combined with *afaf.* The most obvious phenotypic change associated with these genotypes is in apparent photosynthetic areas with *afaf. stst. TlTl* being the lowest and *afaf. StSt. tltl* being the highest. This is likely to be of significance when plants, such as those used in this experiment, are grown under good, well-spaced conditions and are subject to minimal competition.

The implications of these results to the plant breeder are clear if wire-grown plants are used for selection or competition between plants is minimal. In these circumstances no single gene or gene combination studied in this experiment is likely to increase plant yield and in practice it would seem that some combinations are distinctly deleterious. This is in complete accord with earlier observations on the yielding capacity of these particular genetic stocks (Gritton 1972; Snoad et al. 1976).

However, even in a crop environment where the potential of a spaced plant is never attained it has already been demonstrated that some of these genotypes have a commercial potential (Snoad 1974; Monti and Frusciante 1978; Wehner and Gritton 1981; Kielpinski and Blixt 1982). Unfortunately, experiments comparing crop-grown genotypes have concentrated upon measurements of final yield and upon the efficiency of yield partitioning without any analysis of the components of yield, and only a few of the eight phenotypes have been utilised (Hedley and Ambrose 1981). What is required now is to extend the present study to plants growing as crops where competition intrudes, increases with time and influences plant development and then to determine more precisely what are the effects of, and the interactions between, the three genes.

Of particular practical interest would be the possible pleiotropic effects of *st* since the *afaf. stst* plant grown as a crop exhibits the best standing ability of all the genotypes and therefore has most appeal to the

breeder of dried peas in those environments where plant lodging is a serious problem.

Close examination of the present data points clearly to there being partial dominance associated with the *tl* locus which affects the leaf weight at the first flowering node, the yield at that node, total yield and harvest index. There are only marginal suggestions of a similar effect at the *st* locus and no indication of partial dominance at the *af* locus. However, *af* does seem to play a part in that partial dominance associated with the *tl* locus is most clearly discerned in *afaf* genotypes.

Interestingly, heterozygosity of *tl* can be observed phenotypically because in *AfAf. Tltl* plants the ends of many of the tendrils, instead of being cylindrical in cross section, tend to be slightly flattened and even spatulate and/or forked (Lamprecht 1974). This same effect can be observed in *afaf. Tltl* plants too where many of the extra tendrils show this modified development. The modification to photosynthetic area is so small as to be nonsignificant.

Acknowledgement. We are particularly grateful to Mr. Jeremy Franklin of the Food Research Institute, Norwich for help in the use of GENSTAT for analysing the data.

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