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Detection of linkage and pleiotropy between characters of *Nicotiana tabacum* using inbred lines produced by dihaploidy and single seed descent

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A method for detecting and distinguishing between pleiotropy and a linkage disequilibrium as causes of genetical correlations between pairs of characters is developed theoretically and its application illustrated by the analysis of 11 characters scored on material derived from a cross between a burley and a flue cured variety of tobacco raised at two planting densities.

The method is based upon comparisons of the correlations in random samples of inbred lines extracted from the F_1 of a cross by dihaploidy and from the F_2 of the cross by single seed descent. On the basis of the significant difference of the correlation in the dihaploid and single seed descent samples from zero and from one another the pairs of characters can be divided into five categories corresponding with the presence or absence of either or both of pleiotropy and a linkage disequilibrium. Application to random samples of 60 dihaploid and 126 single seed descent families allows the unambiguous classification of most of the pairs of characters.

INTRODUCTION

Dihaploidy offers the quickest method of inbreeding from an F_1 cross between two inbred lines. In the absence of differential selection and a linkage disequilibrium the phenotypic distributions of the inbred populations derived by dihaploidy (DH), single seed descent (SSD) and pedigree inbreeding (PI) should be identical in all circumstances (Jinks and Pooni, 1981). In the presence of a linkage disequilibrium, however, SSD and PI offer more opportunity for recombination than DH's and insofar as linkages have to be broken to produce superior recombinant inbred lines SSD and PI have an advantage over DH's—a conclusion also arrived at by Riggs and Snape (1977) using computer simulation. Any disadvantages of DH's arising from this cause are, however, minimised by extracting them from the F_2 or F_3 rather than the F_1 generation (Jinks and Pooni, 1981). By comparing the means, variances and covariances of dihaploids (produced by the bulbosum technique) derived from F_1 and F_2 generations of a cross between two spring barley varieties, Snape and Simpson (1981) found evidence for the presence of linkage in important agronomic characters. These authors agreed with Jinks and Pooni (1981) that when repulsion linkages are present dihaploid lines extracted from an F_2 will contain a higher proportion of superior inbreds than those from an F_1.

It is, therefore, clear that the presence or absence of linkage and its predominant phase influences whether dihaploidy is the better method for extracting inbred lines from a biparental cross and which generation is the best source. Moreover, when making early generation predictions of the proportions of inbred lines that are expected to be better than the better parent or the F_1, if it shows heterosis, it is important to be aware of the presence of linkage and its phase because it would lead to an underestimate or overestimate of the expected proportions in the presence of repulsion and coupling linkage, respectively (Jinks and Pooni, 1982).

There are a number of methods currently available for the detection of linkage in the generations derivable from a cross between two inbred lines.

These are a) comparisons of the variances of B_1 with L_1, B_2 with L_2 and F_2 with L_3 (Perkins and Jinks, 1970); b) tests of the homogeneity of additive (D) and dominance (H) components of variation over the statistics of different rank (Mather and Jinks, 1971; 1982); and c) comparison of the variances for single characters and for phenotypic correlations between pairs of characters of dihaploids derived from the F_1 and F_2 generations and therefore of different rank (Snape and Simpson, 1981).

In this paper we shall increase the sensitivity of the last technique by comparing inbred lines produced by dihaploidy from the F_1 generation with those produced by single seed descent. At the same time we shall present genotypic as well as phenotypic correlations as an aid to interpretation.

THEORY

In the absence of pleiotropy and linkage disequilibrium between the genes controlling a pair of characters there will be no correlation between them in random samples of all possible inbred lines extractable from a cross whether by dihaploidy or SSD. In the presence of a linkage disequilibrium the characters will be correlated and the magnitude of the correlation will depend on their method of extraction insofar as this affects the opportunities for recombination.

In general the genetical correlation (r_{gAB}) between two characters A and B in the random sample of inbred lines extractable from a cross will be

$$r_{gAB} = \frac{D_{AB}}{(D_A \cdot D_B)^{1/2}}$$

where D_{AB} is the additive genetic covariance between characters A and B and D_A and D_B are their additive genetic variances.

For dihaploids derived from the F_1

$$D_{AB} = \overset{+C}{-R} \sum_{i=1}^{k_a} \sum_{s=1}^{k_b} (1-2p_{is}) d_i d_s$$

$$D_A = \sum_{i=1}^{k_a} d_i^2 \overset{+C}{-R} \sum_{i=1}^{k_a-1} \sum_{j=i+1}^{k_a} 2(1-2p_{ij}) d_i d_j$$

$$D_b = \sum_{s=1}^{k_b} d_s^2 \overset{+C}{-R} \sum_{s=1}^{k_b-1} \sum_{t=s+1}^{k_b} 2(1-2p_{st}) d_s d_t$$

(see Jinks and Pooni, 1981 and Mather and Jinks, 1982 for nomenclature).

For single seed descent inbreds derived from the same F_1 the linkage disequilibrium coefficients $(1-2p_{is})$, $(1-2p_{ij})$ and $(1-2p_{st})$ are replaced by $(1-2p_{is})/(1+2p_{is})$, $(1-2p_{ij})/(1+2p_{ij})$ and $(1-2p_{st})/(1+2p_{st})$ respectively, which are obviously smaller if there is recombination, that is, the p's are >0. Hence, in the presence of a linkage disequilibrium the absolute value of D_{AB} will be larger in the dihaploid than in the single seed descent sample of inbred lines. Furthermore, D_{AB} will be positive if there is an excess of coupling linkages ($C > R$) and negative if there is an excess of repulsion linkages ($C < R$).

Simply because there is a linkage disequilibrium between the k_a loci controlling character A and the k_b loci controlling character B it does not necessarily follow that there will be a similar linkage disequilibrium within the two (k_a and k_b) sets of loci. While, therefore, the linkage bias in D_A and D_B will be greater in the dihaploid than in the single seed descent sample of inbred lines it does not follow that it will be similar in magnitude and sign or differ between the two samples to the same extent as D_{AB}.

While, therefore, the absolute value (irrespective of sign) of D_{AB} will always be larger for the dihaploid compared with the single seed descent sample the corresponding values of D_A and D_B may be larger, the same or smaller. For example, D_A (or D_B) will be the larger for the dihaploid sample if there is an excess of coupling linkages ($C > R$), it will be the same if there is no linkage disequilibrium ($C = R$) or no linkage ($C = R = 0$) and it will be the smaller if there is an excess of repulsion linkages ($C < R$). While, therefore, the higher absolute value of D_{AB} in the dihaploid relative to the single seed descent sample of inbred lines leads to the expectation that the genetical correlation will also be higher, the genetical correlation can in fact be lower; and it will be so whenever the fall in the value of D_{AB} between the dihaploid and single seed descent samples is exceeded by a fall in the value of $(D_a \cdot D_B)^{1/2}$ because of an excess of coupling linkages between the loci within the two sets.

Any contribution that pleiotropy makes to the correlation between a pair of characters should not be affected by recombination between the gene loci controlling them. Formally, pleiotropy is indistinguishable from complete linkage ($p_{is} = 0$). Its contribution to the genetic correlation will, therefore, be the same for the SSD and DH samples of inbred lines.

If we now relate the theoretical expectations to observable properties of the correlations between pairs of characters in the SSD and DH samples of inbred lines we can recognise the

following situations:

1. No significant correlation between two characters either in the DH or SSD samples of inbred lines. This will occur when $p_{is} = 0{\cdot}5$ for $i = 1$ to k_a and $s = 1$ to k_b, that is, no linkage, or when the sum over coupling pairs $(+C)$ equals the sum over repulsion pairs $(-R)$, that is, no linkage disequilibrium. There must, of course, also be no pleiotropy or alternatively positive and negative pleiotropy must cancel out exactly.

2. A significant correlation between two characters the magnitude of which does not differ between the DH and SSD samples of inbred lines. This will occur when there is pleiotropy or what is in practice indistinguishable from it, a very tight linkage ($p_{is} \simeq 0$). It will also occur if there is a linkage disequilibrium in which the change in D_{AB} between the DH and SSD samples of inbred lines is of the same magnitude and direction as the change in $(D_A \cdot D_B)^{1/2}$. This, as we have already seen, can only be achieved if there is an excess of coupling linkages among the genes controlling one or both characters.

3. A significant correlation between characters in the DH sample but not in the SSD sample. This will occur when there is a linkage disequilibrium but no pleiotropy. Since the effect of the smaller linkage disequilibrium in the SSD sample is not detectable the initial linkage disequilibrium in the F_1 gametes and hence in the dihaploids derived from them must be small. A reduction of the correlation in the SSD sample to non-significance would also arise if there were a marked increase in the value of $(D_a \cdot D_B)^{1/2}$ between the DH and SSD samples as would result, for example, from an excess of repulsion linkages between the genes controlling one or both characters.

4. A significant correlation between two characters in both the DH and SSD samples but the correlation in the DH sample is significantly the larger of the two. This will occur with a linkage disequilibrium which is significantly reduced but, as expected, unless it is relatively small, not completely removed in the SSD sample. It is not, however, possible to rule out the presence of pleiotropy because its contribution would remain unchanged between the DH and SSD samples of inbred lines.

5. The last category includes all those, at first sight, anomalous situations in which the correlation in the SSD sample is significant and larger than that in the DH sample. It includes, for example, the situation where the correlation for the SSD sample is significant but that for the DH sample is not and where the correlation for the SSD sample is significantly greater than that for the DH sample irrespective of whether the latter is significant. The only situation in theory in which D_{AB} for the DH sample can be smaller than that for the SSD sample other than as a result of sampling error is an apparent linkage equilibrium among the F_1 gametes that leads to linkage disequilibrium in the later generations. This can happen either when linkages in one phase are predominantly stronger than those in the other phase or when pleiotropy and linkage disequilibrium oppose each other exactly. Recombination in the later generations leads to the elimination of weaker linkages thus allowing the disequilibrium due to stronger linkages and/or pleiotropy to express itself. While this can lead to significant correlations for the SSD sample their magnitude will be small. Alternatively, the correlation can be larger because $(D_A \cdot D_B)^{1/2}$ for the SSD sample is much smaller than that for the DH sample and, as we have noted earlier, this must imply coupling linkages among the genes controlling one or both characters. If D_{AB} does not change between the two samples we have, therefore, pleiotropy for the genes controlling the two characters and if D_{AB} is smaller in the SSD sample we have a linkage disequilibrium. But as the SSD correlation is significant we cannot rule out pleiotropy also. The pairs of characters which fall into this category probably, therefore, are anomalous members of categories 2 or 4.

EXPERIMENTAL DATA

The experimental data are taken from two random samples of inbred lines of *Nicotiana tabacum* extracted from a cross between varieties SCR and *S*3 by dihaploidy (60 lines) and by single seed descent (126 lines). The dihaploid lines were produced by culturing anthers from an F_1 plant followed by chromosome doubling through colchicine treatment of normal plantlets. The single seed descent lines were mostly F_8 but some were F_7 and F_6. Further details of the source of the material, the experimental design and the characters scored are given by Jinks, Chowdhury and Pooni (1985).

In this paper we shall analyse the 11 characters recorded on a completely randomised field experiment of 60 dihaploid lines (DH) and 126 single seed descent lines (SSD) grown at the normal planting density (ND) and on 59 of those DH lines and all 126 SSD lines grown at double the normal density (DD).

RESULTS

The phenotypic and genotypic correlations between all 55 pairwise combinations of 11 characters for the DH and SSD samples of inbred lines in the normal and double densities are given in tables 1 and 2. These are classified in table 3 in two ways, into three groups according to whether the SSD correlation is significantly smaller than, significantly larger than or not significantly different from the DH correlation and into four groups according to whether both, one or neither of the

Table 1 Phenotypic (top right) and genotypic (bottom left) correlations between all pairs of characters for the DH sample (60 families) and the SSD sample (126 families) of inbred lines at the normal density

Character	Sample	*H*1	*H*2	LL	LB	FT	HFT	FH	TY	LN	SY	LY
*H*1	DH		0·86 *	0·27	0·19	−0·58	0·37	0·38	0·25	0·01	0·36	0·01
	SSD		0·82	−0·24	−0·20	−0·58	−0·10	0·07	−0·06	−0·39	0·13	−0·34
*H*2	DH	0·88		0·40	0·33	−0·73	0·35	0·38	0·39	−0·09	0·52	0·10
	SSD	0·85		−0·05	−0·20	−0·74	0·03	0·14	−0·02	−0·51	0·18	−0·33
LL	DH	0·24	0·35		0·80	−0·08	0·80	0·84	0·87	0·59	0·82	0·82
	SSD	−0·39	−0·26		0·62	−0·02	0·57	0·60	0·77	0·37	0·71	0·69
LB	DH	0·12	0·25	0·80		−0·15	0·58	0·60	0·80	0·35	0·77	0·74
	SSD	−0·30	−0·40	0·57		0·15	0·54	0·57	0·70	0·45	0·60	0·69
FT	DH	−0·58	−0·75	−0·01	−0·08		0·15	0·09	−0·08	0·43	−0·21	0·15
	SSD	−0·58	−0·76	0·07	0·26		0·31	0·14	0·01	0·56	−0·12	0·21
HFT	DH	0·44	0·38	0·83	0·60	0·18		0·99	0·71	0·79	0·70	0·62
	SSD	−0·09	−0·01	0·58	0·55	0·35		0·93	0·60	0·63	0·61	0·46
FH	DH	0·44	0·40	0·87	0·62	0·13	0·99		0·73	0·77	0·72	0·64
	SSD	0·07	0·08	0·60	0·57	0·19	0·95		0·69	0·58	0·74	0·49
TY	DH	0·18	0·33	0·89	0·82	0·01	0·75	0·76		0·57	0·97	0·90
	SSD	−0·17	−0·22	0·77	0·70	0·12	0·64	0·72		0·54	0·95	0·88
LN	DH	0·07	−0·03	0·69	0·43	0·47	0·85	0·82	0·69		0·49	0·63
	SSD	−0·40	−0·55	0·47	0·54	0·60	0·67	0·61	0·66		0·44	0·58
SY	DH	0·31	0·47	0·84	0·78	−0·13	0·74	0·76	0·98	0·61		0·77
	SSD	0·04	0·01	0·70	0·58	−0·03	0·67	0·79	0·95	0·59		0·68
LY	DH	−0·05	0·05	0·88	0·79	0·25	0·67	0·68	0·93	0·73	0·82	
	SSD	−0·04	−0·51	0·74	0·75	0·31	0·47	0·48	0·89	0·65	0·71	

* Where there is no significant difference between the DH and SSD samples the correlations are bracketed.

Table 2 Phenotypic (top right) and genotypic (bottom left) correlations between all pairs of characters for the DH sample (59 families) and the SSD sample (126 families) of inbred lines at the double density

Character	Sample	*H*1	*H*2	LL	LB	FT	HFT	FH	TY	LN	SY	LY
*H*1	DH		0·88 *	0·38	0·35	−0·73	0·23	0·45	0·29	−0·13	0·41	0·02
	SSD		0·83	−0·16	−0·26	−0·80	−0·15	0·14	−0·13	−0·51	0·07	−0·42
*H*2	DH	0·89		0·59	0·52	−0·70	0·48	0·64	0·46	0·01	0·59	0·14
	SSD	0·86		0·17	0·01	−0·75	0·20	0·43	0·13	−0·32	0·34	−0·20
LL	DH	0·33	0·54		0·83	−0·10	0·80	0·86	0·83	0·57	0·82	0·74
	SSD	−0·35	−0·02		0·79	0·12	0·63	0·62	0·83	0·49	0·80	0·75
LB	DH	0·30	0·47	0·82		−0·25	0·59	0·69	0·79	0·41	0·79	0·68
	SSD	−0·44	−0·19	0·75		0·26	0·58	0·54	0·78	0·46	0·72	0·73
FT	DH	−0·75	−0·70	−0·06	−0·23		0·15	−0·06	−0·06	0·36	−0·17	0·19
	SSD	−0·83	−0·77	0·25	0·41		0·37	0·07	0·18	0·62	0·02	0·40
HFT	DH	0·25	0·49	0·84	0·60	0·20		0·93	0·74	0·72	0·74	0·63
	SSD	−0·18	0·13	0·62	0·59	0·45		0·92	0·69	0·67	0·70	0·56
FH	DH	0·49	0·65	0·90	0·70	−0·01	0·95		0·80	0·68	0·82	0·64
	SSD	0·12	0·38	0·57	0·50	0·15	0·93		0·71	0·53	0·78	0·48
TY	DH	0·26	0·41	0·86	0·81	0·01	0·75	0·80		0·65	0·98	0·90
	SSD	−0·26	−0·04	0·86	0·80	0·32	0·69	0·68		0·63	0·96	0·90
LN	DH	−0·12	0·04	0·67	0·48	0·40	0·81	0·75	0·75		0·57	0·72
	SSD	−0·60	−0·39	0·58	0·55	0·71	0·71	0·55	0·72		0·52	0·69
SY	DH	0·38	0·54	0·84	0·81	−0·11	0·76	0·83	0·98	0·67		0·79
	SSD	−0·04	0·19	0·80	0·73	0·15	0·73	0·79	0·97	0·62		0·74
LY	DH	0·00	0·11	0·80	0·71	0·25	0·66	0·66	0·93	0·82	0·83	
	SSD	−0·53	−0·34	0·84	0·80	0·52	0·58	0·47	0·94	0·79	0·81	

* Where there is no significant difference between the DH and SSD samples the correlations are bracketed.

Table 3 Categorisation of the 55 phenotypic correlations between 11 characters taken in pairs based upon tests of significance

Significant differences	SSD sig^n DH sig^n	SSD sig^n DH n.s.	SSD n.s. DH sig^n	SSD n.s. DH n.s.
		Normal density		
SSD < DH	8 (4)	0	7 (3)	} 1*
SSD > DH	0	2 (5)*	0	
SSD = DH	24 (2)	4 (5)	3 (2 or 1)	6 (1)
		Double density		
SSD < DH	5 (4)	0	7 (3)	1 (3)
SSD > DH	2 (5)	3 (5)	0	1 (5)
SSD = DH	30 (2)	2 (5)	0	4 (1)

sig^n = $P < 0{\cdot}05$. * Equal in value, opposite in sign.
n.s. = $P > 0{\cdot}05$.
* Most category (5) pairs conform with some or all of the criteria of categories (2) and (4).

SSD and DH correlations are significant. All tests of significance were carried out on the phenotypic correlations. On the basis of this classification we can readily identify the five categories defined earlier on the basis of the theoretical expectations.

At each density 46 of the 55 pairs of characters fall unambiguously into categories 1 to 4 (tables 4, 5, 6 and 7). Of the six pairs of characters in category 1 at the normal density four are in the same category at the double density (table 4). These four, therefore, show no evidence of either pleiotropy or a linkage disequilibrium at either density. The remaining 51 pairs show evidence of pleiotropy or a linkage disequilibrium at one or both densities.

Half or more of the 55 pairs of characters fall into category 2 (table 5). Of the 30 (or 38 if we include the anomalous category 5 cases in table 3) pairs of characters in this category at the double density and 26 (or 32) at the normal density, 25 are common to both densities. All six discrepancies between the two densities fall into category 4. All 31 pairs, therefore, are compatible with pleiotropy as the sole or major cause of the correlation. Although less likely, we cannot, however, rule out a linkage disequilibrium balanced in such a way as to produce little or no change in the correlation between the DH and SSD samples of inbred lines.

Seven pairs of characters fall into category 3 at each density but only four are common to both densities (table 6). The six discrepancies between the two densities are distributed over the other four categories but all with one exception (one category 1) are consistent with a linkage disequilibrium as the major or sole cause of the correlation.

Eight pairs of characters at the normal density and five at the double density fall into category 4 with only two pairs being common to both densities (table 7). However, all the nine discrepancies fall into cateogries 2 (six pairs) and 3 (two pairs) and therefore have in common either pleiotropy, a linkage disequilibrium or both. The remaining discrepancy *H*1 and LB at the normal density is the anomalous case marked with an asterisk in table 3 where neither correlation is significant from zero. But they differ significantly from each other because they take opposing signs.

Table 4 Genetic correlations for the combinations of pairs of characters which fall into category 1, no pleiotropy, no linkage disequilibrium

Character	Density	Sample	FT	FH	TY	SY
*H*1	ND	DH			0·18	
		SSD			−0·17	
	DD	DH			{ 0·26 }*	
		SSD			{ −0·26 }	
LL	ND	DH	−0·01			
		SSD	0·07			
	DD	DH	−0·06			
		SSD	0·25			
LB	ND	DH	−0·08			
		SSD	0·26			
	DD	DH	{ −0·23 }*			
		SSD	{ 0·41 }			
FT	ND	DH		0·13	0·01	−0·13
		SSD		0·19	0·12	−0·03
	DD	DH		−0·01	0·01	−0·12
		SSD		0·15	0·32	0·15

* The bracketed correlations do not conform with the criteria for category 1 and therefore differ between planting densities.

CONCLUSIONS

Ninety per cent of the pairs of characters show a significant correlation indicative of a linkage disequilibrium and pleiotropy and 84 per cent do so consistently over both planting densities. Linkage and pleiotropy are, therefore, important determinants of the range of combinations of characters extractable from the cross of varieties S3 and SCR.

The attempts to classify the correlations according to the most likely underlying cause, for example, linkage disequilibrium, pleiotropy or both have, in the majority of cases, led to an unambiguous classification which is consistent over the two planting densities. With one exception all the differences between densities are of the kind where in one density pleiotropy or a linkage disequilibrium is detected while in the other density both are detected. While these differences may

Table 5 Genetic correlations for the combinations of pairs of characters which fall into category 2, pleiotropy

Character	Density	Sample	*H*2	LB	FT	HFT	FH	TY	LN	SY	LY
*H*1	ND	DH	0·88		−0·58						
		SSD	0·85		−0·58						
	DD	DH	0·89		−0·75						
		SSD	0·86		−0·83						
*H*2	ND	DH			−0·75		0·40				
		SSD			−0·76		0·08				
	DD	DH			−0·70		0·65				
		SSD			−0·77		0·38				
LL	ND	DH		{0·80}*				0·89	0·69	0·84	0·88
		SSD		{0·57}				0·78	0·47	0·70	0·74
	DD	DH		0·82				0·86	0·67	0·84	0·80
		SSD		0·75				0·86	0·58	0·80	0·84
LB	ND	DH				0·60	0·62	0·82	0·43	{0·78}	0·79
		SSD				0·55	0·57	0·70	0·54	{0·58}	0·75
	DD	DH				0·60	0·70	0·81	0·48	0·81	0·71
		SSD				0·59	0·50	0·80	0·55	0·72	0·80
FT	ND	DH							0·47		
		SSD							0·60		
	DD	DH							{0·40}		
		SSD							{0·71}		
HFT	ND	DH					{0·99}	0·75	{0·85}	0·74	0·67
		SSD					{0·95}	0·64	{0·67}	0·67	0·47
	DD	DH					0·95	0·75	0·80	0·76	0·66
		SSD					0·93	0·69	0·71	0·73	0·58
FH	ND	DH						0·76	{0·82}	0·76	0·68
		SSD						0·72	{0·61}	0·79	0·48
	DD	DH						0·80	0·75	0·83	0·66
		SSD						0·69	0·55	0·79	0·47
TY	ND	DH							0·69	0·98	0·93
		SSD							0·66	0·95	0·89
	DD	DH							0·75	0·98	0·93
		SSD							0·72	0·97	0·94
LN	ND	DH								0·61	0·73
		SSD								0·59	0·65
	DD	DH								0·67	0·82
		SSD								0·62	0·79
SY	ND	DH									0·82
		SSD									0·71
	DD	DH									0·84
		SSD									0·81

* The bracketed correlations do not conform with the criteria for category 2 and therefore differ between planting densities.

Table 6 Genetic correlations for the combinations of pairs of characters which fall into category 3, a linkage disequilibrium

Character	Density	Sample	LL	LB	HFT	FH	TY	SY
*H*1	ND	DH	{0·24}*		0·44	0·44	{0·18}	{0·31}
		SSD	{−0·38}		−0·09	0·07	{−0·17}	{0·04}
	DD	DH	0·33		{0·25}	0·49	0·26	0·38
		SSD	−0·35		{−0·18}	0·12	−0·26	−0·04
*H*2	ND	DH	0·35	0·25	0·38		0·33	0·47
		SSD	−0·26	−0·40	−0·01		−0·22	0·01
	DD	DH	0·54	0·47	{0·49}		0·41	{0·54}
		SSD	−0·02	−0·19	{0·13}		−0·04	{0·19}

* The bracketed correlations do not conform with the criteria for category 3 and therefore differ between planting densities.

Table 7 Genetic correlations for the combinations of pairs of characters which fall into category 4, pleiotropy and a linkage disequilibrium

Character	Density	Sample	LL	LB	HFT	FH	LN	SY
*H*1	ND	DH	0·24	{0·12}*				
		SSD	−0·38	{−0·30}				
	DD	DH	{0·33}	0·30				
		SSD	{−0·35}	−0·44				
*H*2	ND	DH			{0·38}			{0·47}
		SSD			{−0·01}			{0·01}
	DD	DH			0·49			0·54
		SSD			0·13			0·19
LL	ND	DH		0·80	0·83	0·87		
		SSD		0·57	0·58	0·60		
	DD	DH		{0·82}	0·84	0·90		
		SSD		{0·75}	0·62	0·57		
LB	ND	DH						0·78
		SSD						0·58
	DD	DH						{0·81}
		SSD						{0·72}
HFT	ND	DH				0·99	0·85	
		SSD				0·95	0·67	
	DD	DH				{0·95}	{0·80}	
		SSD				{0·93}	{0·71}	
FH	ND	DH					0·82	
		SSD					0·61	
	DD	DH					{0·75}	
		SSD					{0·55}	

* The bracketed correlations do not conform with the criteria for category 4 and therefore differ between planting densities.

reflect genuine differences in the genetical control of the covariation in the two environments, that is, genotype × environment interaction, the differences between the correlations are in general so small that the inconsistency over environments is more likely to be merely sampling error.

Examination of the classification of the pairs of characters (tables 4, 5, 6 and 7) shows that they fall into simple patterns. For example:

1. Of the 10 character density pairs showing no evidence of pleiotropy or a linkage disequilibrium nine involve flowering time.

2. The eight characters which measure aspects of size and yield, namely, leaf length, leaf breadth, leaf number, leaf yield, height at flowering time, final plant height, stem yield and total yield, all show a substantial pleiotropic component but rather weak or no evidence of a linkage disequilibrium.

3. All 14 character density pairs showing evidence of a linkage disequilibrium involve the characters which measure the early growth of the plants, namely, the height of the plant at 44 days (*H*1) and 9 weeks (*H*2) after planting in the field.

4. Negative correlations are in a minority and all involve the three characters *H*1, *H*2 and FT as one of the pairs, the largest negative correlations being between FT and *H*1 and *H*2.

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