

Quantitative Genetic Studies at the Tetraploid and Hexaploid Levels in Alfalfa

S.M. Singh

Department of Biology, Dalhousie University, Halifax, Nova Scotia (Canada)

Summary. Two sets of diallel crosses involving seven tetraploid and five hexaploid alfalfa lines, previously selected for seed and forage yield, are studied. On the basis of combining ability and heritability estimates the following conclusion is drawn. The dominant and epistatic interactions (heterozygosity) are the major components in the expression of variability for yield and characters associated with yield in tetraploid populations. In hexaploid populations, however, there is an appreciable amount of additive variance, and the additive effect of genes along with interaction of various forms may account for the expressed variability for all the characters studied. Better genes and desirable interactions (possibly through heterozygosity) are the two essential genetic components of yield. The selection of better genes is feasible, but by itself will not produce the desired results. Future improvement may therefore depend on the utilization of heterosis and other forms of interactions. There is, in general, a very strong genetic correlation between yield and its components, and therefore, when a direct selection for yield is not feasible, the selection program may rely on a number of closely related characters.

Keywords: Combining ability – Heritability – Tetraploids – Hexaploids – Alfalfa

Introduction

The parents of commercial varieties are determined primarily by their genetic ability to possess and transmit desirable characteristics. To choose the best type of breeding program, one must determine the genetic nature of these characteristics by studying the combining ability of potential parents and the type of gene action involved in the expression of the character to be improved and others that are highly correlated to it.

In alfalfa, forage yield is considered to be an important commercial character suitable for an improvement program. Dessureaux (1970) pointed out that in the past 25 years of breeding programs in Canada, forage yield has shown only a 5 to 10% increase, most of which could have been achieved indirectly by winter hardiness and other resistant traits. The complexity of the problem may lie in the tetraploid nature of the species and the complex genetic nature of yield. The usual selection method is not practical in this species because of the rapid increase in self-sterility with increased inbreeding. Breeding for hybrid varieties is gaining popularity but it is too early to evaluate this approach. Furthermore, heterosis in tetraploids needs a better understanding. Nilsson and Anderson (1941) and Julén (1944) have reported increased vegetative yield in hexaploids. Although according to these reports the seed setting was disappointing, selection was found to be effective in increasing seed yield in successive generations (Lesins et al. 1969). Breeding through increased ploidy, therefore, may deserve further evaluation.

Our understanding of the genetic nature of agronomically important characters in alfalfa is primarily based on studies of combining ability, heterosis and reciprocal effects. The paucity of literature dealing with precise quantitative genetic estimates in alfalfa may be because the tetraploid nature of the species complicates genetic analysis and many problems are involved in the production of single crosses on a large scale. Almost no attempt has been made to study the genetic nature of hexaploids.

Bolton (1948) and others realized the importance of both general and specific combining ability in evaluating alfalfa for forage and seed yield. Kehr and Graumann (1958) and Gardener (1963) have reviewed the combining ability studies in tetraploid alfalfa. The general combining ability is found to be higher than the specific combining ability for previously unselected characters in the unselected populations. The opposite is true in the selected populations for characters used in earlier selections: Car-

nahan et al. (1960), Kehr (1961), Frakes et al. (1961), Wilcox and Wilsie (1964), Dudley et al. (1969) and Singh and Lesins (1971 a and b). At present, the selection for vigor in alfalfa involves selection for better genes and heterozygosity, as both are essential components of yield. It is desirable to discriminate between the two as heterozygosity is a non-fixable component of genetic predisposition and is difficult to maintain in the selection programs. Unfortunately, we are unable to distinguish between the two with our present knowledge and further information is needed here. Such studies would be desirable not only in tetraploid but also in hexaploid alfalfa if they are to be utilized in an improvement program. Because of the complex nature of yield and the problem of dealing with it directly in the breeding program, correlation studies are needed to establish association between yield and other traits that may be used indirectly to facilitate selection. Furthermore, the understanding of the genetic nature of these traits may be useful in choosing the breeding procedure to be followed. In this study, an attempt is made to elucidate some of the above problems. The report deals with the quantitative genetic nature of various morphological characters in tetraploid and hexaploid alfalfa, the relative magnitude of additive, dominant and epistatic genetic effects in the expression of various characters and the association between the various characters studied.

Materials and Methods

The tetraploid material of *Medicago sativa* L. was developed at the University of Alberta, Edmonton, Canada by Dr. K. Lesins, where selection was primarily based on high seed and forage yield. The selection was carried out in Edmonton, where, due to the scarcity of bees, cross pollination was found to be only around 2%. Lines from single selected plants were tested in field tests and seven lines were chosen on the basis of their high seed and forage yielding ability. These were used in one complete set of diallel crosses including reciprocals. All the crosses were made following complete emasculation using 57% alcohol and a vacuum pump. Greenhouse-started seedlings from forty-two intercrossed and seven selfed tetraploid genotypes together with a check variety (Grimm) and a male sterile line (to evaluate cross pollination) were single planted in eight replications. There were ten plants in a row, 90 cm. apart, the distance between rows being 90 cm.

The hexaploid material was developed from the selected tetraploids by crossing them with their octoploids and selecting plants with hexaploid chromosomes (for details see Lesins et al. 1975). They were tested in field trials and five lines with good seed and forage yields were selected to be used in a partial diallel crossing. Ten intercrosses and five selfed hexaploid genotypes were produced, started in the greenhouse, and planted, like the tetraploids, in the same field. Two border rows 90 cm. apart surrounded the total experimental area.

The following characters were studied:

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|--------------------------|---------|
| 1. Growth in Spring (kg) | = T_1 |
| 2. Growth in Fall (kg) | = T_2 |
| 3. Total yield (kg) | = T_3 |
| 4. Seed yield (gms) | = T_4 |

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|--|---------|
| 5. Number of seeds per pod | = T_5 |
| 6. Dry matter per plant (kg) | = T_6 |
| 7. Plant height at maturity (cm) | = T_7 |
| 8. Percentage of pod set during crossing | = T_8 |
| 9. Number of seeds per pod set during crossing | = T_9 |

Measurements for these characters were made on individual plants. Growth in Spring represents the fresh vegetative weight of the first cutting taken in the first week of July and growth in Fall is the vegetative weight of the second cutting taken in the first week of September. Total yield was obtained by taking the total of the two cuttings taken from the first four replications. The other four replications were used for seed test where seed yield, number of seeds per pod, plant height and dry matter per plant were recorded.

Diallel cross analysis was done following Griffing's (1956) method, (model I) that partitioned the total variance into general combining ability (GCA), specific combining ability (SCA) and reciprocal effects. Heritability estimates were based on Lush (1949), with necessary modifications. Associations between characters were established using correlation calculations suggested by Al-Jibouri et al. (1958). The two sets (tetraploid and hexaploid) were treated in the same way in all details except that there were no reciprocals for the hexaploids.

Results

1. Genetic Estimates

a. *Combining ability.* The analysis of variance for all the characters in both populations gave highly significant F values. Components of genetic variances estimated by diallel cross analysis are presented in Table 1.

The variances due to general combining ability (GCA) are significant at the 1% level of probability for all the characters studied in tetraploids. In hexaploids, however, significant variances for general combining ability were noted for growth in fall, total forage yield, seed yield and number of seeds per pod. The same estimates for per cent of pod set during crossing and number of seeds per pod set during crossing could not be tested statistically for significance. However, the obtained values are high enough to be considered as significant. In general, these estimates are considerably higher in tetraploids than hexaploids for all characters, except percent of pod set during crossing and the number of seeds in them. GCA variance for seed yield in tetraploids was twelve times that of hexaploids. On the other hand, the GCA variance for number of seed per pod set during crossing for hexaploids was approximately four times higher than tetraploids.

Like the GCA variances, SCA variances were also significant for all the characters studied in tetraploids. In hexaploids, however, SCA variances were significant for growth in Fall, total forage yield, seed yield, number of seeds per pod and plant height. Again, the statistical significance for percentage of pod and seed setting could not be tested in hexaploids but their values are

Table 1. The combining ability analysis of various characters in the tetraploid and hexaploid populations

Characters		Variance due to				
		GCA ($\sigma^2 g$)		SCA ($\sigma^2 s$)		Reciprocal effect ($\sigma^2 r$)
		Tetraploid DF 6	Hexaploid DF 4	Tetraploid DF 21	Hexaploid DF 10	Tetraploid DF 21
Growth in Spring (kg)	T ₁	0.0648**	0.0103	3.9740**	0.0092	0.0098
Growth in Fall (kg)	T ₂	0.0306**	0.0283**	3.3350**	0.0184**	0.0048
Total forage yield (kg)	T ₃	0.1560**	0.0770**	14.5900**	0.0442**	0.0218
Seed yield (gm)	T ₄	178.8500**	14.1852**	1936.8900**	23.1009**	22.6560
Number of seeds per pod	T ₅	0.6030**	0.1459**	48.0860**	0.0925**	0.0225
Dry matter per plant (kg)	T ₆	0.0049**	0.0033	0.7080**	0.0024	0.0024
Plant height (cm)	T ₇	416.4890**	13.0790	54534.5000**	95146.3400**	12.2800
% pod set during crossing	T ₈	468.4000**	504.1720 ≠	91.5800**	357.9440 ≠	99.2000**
Number of seeds per pod set	T ₉	3.9860**	14.9210 ≠	0.5573**	1.6170 ≠	0.7449

** highly significant

≠ could not be tested for significance

Table 2. Estimates of the general and specific combining ability effects of the tetraploids and hexaploids

Characters		$1/G\hat{\Sigma}g_i^2$		$1/S\hat{\Sigma}s_{ij}^2$	
		Tetraploids	Hexaploids	Tetraploids	Hexaploids
Growth in Spring (kg)	T ₁	0.0045	0.0011	0.0537	0.0056
Growth in Fall (kg)	T ₂	0.0022	0.0010	0.0028	0.0131
Total yield (kg)	T ₃	0.0066	0.0288	0.1263	0.0289
Seed yield (gm)	T ₄	12.7746	2.0144	19.1267	13.3991
Seeds/pod	T ₅	0.0431	0.0285	0.3018	0.0507
Dry matter/plant (kg)	T ₆	0.0004	0.0527	0.0003	0.0029
Plant height (cm)	T ₇	29.6350	1.8674	2.7121	29.8350
% pod set	T ₈	36.5420	41.2394	31.3531	16.3734
No. of seed set during crossing	T ₉	0.1200	0.1780	0.2520	0.1715

G = D.F. for general combining ability

S = D.F. for specific combining ability

high enough to be considered significant. The values of the SCA variances are higher in tetraploids for most characters except percentage of pod and seeds per pod set during crossing, where the hexaploids showed higher values than the tetraploids.

The reciprocal differences could only be studied in tetraploids because only partial diallel crossing was executed with hexaploids. The variances due to reciprocal differences, presented in Table 1, are not significant except for percent pod set during crossing. Further analysis, therefore, is performed assuming no such differences in reciprocal crosses.

Estimates of GCA and SCA effects are presented in Table 2 and suggest that such estimates are higher in tetraploid than in hexaploid populations. In general, the values of SCA effects are greater than the GCA effects in both

populations except for plant height in tetraploids and percent pod set during crossing in hexaploids.

b. *Heritability.* The heritability estimates, in both the broad and narrow sense, for the characters studied in both populations are given in Table 3.

It is evident from this table that the narrow sense heritability values are very low for all characters except percentage of pod set and number of seeds per pod set during crossing as compared to its broad sense values. The narrow sense estimates for hexaploids, lower than its broad sense values, are considerably higher than for tetraploids. It may be pointed out that narrow sense heritability estimates the additive, while broad sense heritability represents the total genetic variance.

Table 3. Heritability estimates

Characters		% heritability – broad sense ($\sigma^2 G/\sigma^2 p$)		% heritability – narrow sense ($\sigma^2 A/\sigma^2 p$)	
		Tetraploid	Hexaploid	Tetraploid	Hexaploid
Growth in Spring (kg)	T ₁	72.0	51.0	1.4 (0.03)*	26.9 (0.56)*
Growth in Fall (kg)	T ₂	70.8	92.3	0.9 (0.02)	12.9 (0.27)
Total forage yield (kg)	T ₃	79.5	85.6	1.5 (0.03)	50.7 (1.04)
Seed yield	T ₄	86.0	94.7	8.2 (0.17)	34.1 (0.70)
Seeds per pod	T ₅	75.4	86.6	1.3 (0.03)	48.8 (1.01)
Dry matter/plant (kg)	T ₆	71.9	40.0	0.6 (0.01)	27.7 (0.57)
Plant height (cm)	T ₇	88.0	84.4	0.7 (0.02)	0.01 –
% of pod set during crossing	T ₈	80.4	–	63.8 (1.32)	– –
No. of seeds per pod set	T ₉	80.8	–	71.0 (1.46)	– –

* Note: Values in brackets indicate the genetic gain expected on the respective values of heritability

2. Correlations

The simple, genotypic, and phenotypic correlations between all possible combinations of the seven characters studied in the tetraploid and hexaploid populations are given in Table 4. The genotypic correlations are in general higher than the phenotypic and simple correlation values. Forage yield shows high values for the three correlations with growth in Spring and growth in Fall. In other combinations involving forage yield, although genotypic and phenotypic correlations are significant, simple correlations are usually not significant. Seed yield has significant values at all three levels in combination with seeds per pod, dry matter per plant and height. Other combinations involving seed yield show significant values for genotypic and phenotypic correlations but simple correlations are not significant. A strong correlation between Spring and Fall growth may indicate that growth rate is genetic and fast growers in Spring continue to be fast growers in Fall. Other combinations showing strong correlations, at least at the genotypic level, are: Spring growth with seed yield and plant height; Fall growth with seed yield and plant height; seeds per pod with forage yield and dry matter per plant. These relationships are observed in tetraploid as well as hexaploid populations. In general, the simple correlations were observed to be quite low when compared to the genotypic and phenotypic values and were not significant.

Discussion

1. Genetic Estimates

In the tetraploid population, highly significant GCA and SCA variances were observed for all the characters studied. Similar results were observed by Evans et al. (1966)

for plant width, plant height, largest stem, crown width, vigor, leaf to stem ratio and leaf hopper yellowing; by Wilcox and Wilsie (1964) for Fall growth, total yield and Spring vigor; by Theurer and Elling (1964) for total yield; by Dudley (1963) for plant height, plant width, Spring growth, recovery and leaf hopper yellowing. It suggests that even after selection, genetic factors responsible for GCA (mainly additive) and SCA (mainly interactions) are both present in appreciable amounts. One could, therefore, expect that by selecting the vigorous and high yielding lines one selects for both better genes and heterozygosity (or dominance and epistatic combinations) and that they both are essential contributors for not only yield but also for the characters that contribute to yield. In general, the SCA variance was higher than the GCA variance for most of the characters. A similar trend is also exhibited by SCA and GCA effects. This corroborates the results obtained by Evans et al. (1966) and Kehr (1961), and indicates that selection has been effective in accumulating at least part of the gene combinations responsible for GCA. Variance for gene combinations responsible for SCA is highly significant and suggests that heterozygosity and interactions in the expression of the characters used in earlier selections directly or indirectly, are important. In the case of the two characters not used in earlier selection, namely, percentage of pod set and seeds per pod set during crossing, the variance for GCA was higher than the variance for SCA. For the characters not used in previous selection, similar results were obtained by Kehr and Gardener (1960), Theurer and Elling (1964), Wilcox and Wilsie (1964) and Evans et al. (1966). Here the basic pattern seems to be that although the GCA and SCA components are significant, the SCA is pronounced for characters utilized directly or indirectly in previous selection while the GCA is higher for characters not used in earlier selections. Reciprocal differences were absent for most of the characters. Percentage pod set during crossing had a

Table 4. The simple (r), genotypic (rg) and phenotypic (rph) correlations between seven characters of tetraploid and hexaploid population

		T ₁	T ₂	T ₃	T ₄	T ₅	T ₆	T ₇
T ₁	r	—	0.27	0.87	0.05	0.01	0.17	0.08
	rg	—	1.12	1.05	1.04	0.41	0.23	1.02
	rph	—	0.82	0.93	0.72	0.73	0.31	0.64
T ₂	r	0.53	—	0.55	0.10	0.09	0.15	0.18
	rg	0.78	—	1.01	0.92	0.95	0.20	0.71
	rph	0.78	—	0.97	0.86	0.96	0.16	0.64
T ₃	r	0.93	0.78	—	0.07	-0.08	0.19	0.01
	rg	0.97	0.95	—	0.93	1.08	0.21	0.78
	rph	0.96	0.92	—	0.85	0.85	0.18	0.67
T ₄	r	-0.01	0.01	-0.01	—	0.32	0.08	0.28
	rg	0.77	0.74	0.99	—	0.85	0.51	0.47
	rph	0.61	0.63	0.87	—	0.81	0.32	0.45
T ₅	r	-0.10	-0.08	-0.09	0.20	—	0.04	0.26
	rg	0.43	0.27	0.38	0.38	—	0.19	0.39
	rph	0.29	0.20	0.28	0.39	—	0.21	0.37
T ₆	r	-0.13	0.01	-0.11	0.34	0.03	—	0.22
	rg	0.67	0.46	0.57	0.61	0.56	—	-0.69
	rph	0.48	0.35	0.46	0.46	0.42	—	0.34
T ₇	r	0.03	0.03	-0.02	0.18	-0.11	0.43	—
	rg	0.28	0.41	0.35	0.23	0.22	0.41	—
	rph	0.22	0.34	0.30	0.22	0.16	0.41	—

r significant at 0.16

rg and rph — significant at 0.27

Note: r values above the diagonal represent the hexaploid, and below the diagonal, the tetraploid population

T₁ = growth in Spring (kg)T₂ = growth in Fall (kg)T₃ = total forage yield (kg)T₄ = seed yield (gm)T₅ = seeds per podT₆ = dry matter per plant (kg)T₇ = plant height at maturity (cm)

significant value for variance due to reciprocal differences. This would be expected if lines have differential pod setting ability and therefore, variable seed yield.

In the hexaploid population, both GCA and SCA variances were not significant for growth in Spring and dry matter per plant. Although the SCA value for plant height was significant, the GCA value was not significant. Estimates for other characters were significant. Basically, these estimates are comparable to some of the estimates for tetraploids. Here, in general, the GCA values are higher than the SCA, except for seed yield and plant height, where SCA estimates are higher than in GCA. This may be because the hexaploids were selected for seed yields and general vigor. Also, the tetraploid parents of the hexaploids were selected on the basis of their seed-setting ability.

Heritability, in the broad and narrow sense, was taken as another indicator of the fixable and non-fixable components of genetic variance. The narrow sense heritability indicated the additive or fixable component of the total

genetic variance, which is represented by the broad sense heritability. The tetraploid population in general showed high (70-88%) value for broad sense but quite low (0.7-8.2%) value for narrow sense heritability for the characters affected by earlier selection. It seems as if almost all of the additive components have already been utilized and that further improvement in this population may only be possible by utilizing the non-additive components of genetic variation. In contrast, the narrow sense value is quite high for percentage pod set and number of seeds set per pod during crossing (63.8% and 71.0%), which is 80 to 88% of the value for broad sense heritability. This indicates that at least 80% of the total genetic variance for these characters is additive. Note that these characters were never used in previous selections.

In hexaploids, both the broad and narrow sense heritabilities are fairly high. The narrow sense heritability and, therefore the additive genetic components, account for 48 ± 20 percent of the total genetic variation for all the characters except plant height, where the narrow sense value is

very low. The basic difference in the two populations, tetraploid and hexaploid, becomes obvious. In tetraploids, most of the variation is confined to heterozygosity and other interactions, and therefore, further improvement in the traits contributing to yield may not be possible by the selection of better genes. This is also indicated by the expected genetic gains that range from only 1% for dry matter per plant to 17% for seed yield. Other characters show a value of only 2 or 3%. In hexaploids however, an appreciable amount of genetic variation is additive. Therefore, further improvement by selection will be expected, as indicated by the values of genetic gains. In conclusion, the abundance of dominance and epistatic interactions seems to be the major cause of the expression for variation of most of the characters in tetraploids, and additive action of genes along with various interactions may account for the expression of characters studied in hexaploids.

2. Correlations

The observation that in general the genotypic correlations were higher than the phenotypic and simple correlations in both the tetraploid and hexaploid populations agree with reports of Dudley and Hansen (1961) in alfalfa and of others in many different crop plants. It may be due to the following: The combinations may be controlled by similar action of genes or chromosomes, the environmental sources of variation may have little influence on the expression of associations or genotypic associations are higher as a result of previous selection and the environmental influence lowers the values of phenotypic correlations. Almost all of the associations observed here could be interpreted as cause and effect relationships and are self-explanatory.

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Dr. S.M. Singh
Department of Zoology
University of Western Ontario
London, Ontario
Canada N6A 5B1