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Correlations and heritability of the characters determining the seed yield of the long-raceme alfalfa (*Medicago sativa* L.)

Zbigniew BODZON

Plant Breeding and Acclimatization Institute, Radzików, Błonie, Poland

Abstract. Phenotypic correlation coefficients and heritability of the characters controlling seed yield of long-raceme forms of alfalfa was determined. It was found that seed yield per plant, which was positively correlated with 10 out of 12 analysed characters, depended upon the number of pods per raceme and the number of seeds per pod. Variability of these characters determined about 60% of the variability of seed yield. Multiple linear regression and phenotypic correlations show that simultaneous selection for increased pod number per raceme and increased seed number per pod and raceme length resulted in enhanced seed yield potential. The share of the additive genetic effects in the phenotypic variance for number of pods per raceme was low and about 21-23%, while for number of seeds per pod and per raceme amounted to about 50%. The expected genetic progress in recombination breeding for number of seeds per pod and number of seeds per raceme will be of medium magnitude, while one cannot expect any rapid and considerable progress in the number of pods per raceme. Considering the high positive correlation between raceme length and number of pods and seeds per raceme, one should conclude that raceme length can be an important criterion in selection of plants showing a high seed productivity.

Key words: alfalfa, correlations, heritability, long raceme, multiple regression, seed yield.

Introduction

One of the most important aims of alfalfa breeding is to increase seed yield. The main causes of low seed productivity are: the poor pod setting (as only 40 to 60 % of the flowers set pods), and the low number of seeds per pod (usually 3 to 4). Both characters depend on weather conditions, particularly temperature

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Correspondence: Z. BODZON, Plant Breeding and Acclimatization Institute, Radzików, 05-870 Błonie, Poland; e-mail: z.bodzon@ihar.edu.pl

and insolation, but also on the sum and distribution of rainfall during the flowering period, pod setting and seed ripening (SIMON 1984, 1997, DJUKIČ, KRALJEVIČ-BALALIČ 1993, KATEPA-MUPONDWA et al. 1996). Considerable improvement of seed yield may be achieved by observing the recommendations concerning regionalisation of seed industry and proper plant husbandry (WILCZEK 1981, SKALSKA 1993, SIMON 1997).

According to several authors, the average number of inflorescences on stems, and of flowers in racemes, are sufficient to produce satisfactory yields of alfalfa seeds (WILCZEK 1981, SKALSKA 1993, DYBA, ROGALSKA 1995). Investigations aimed at increasing seed yield indicate that improvement of pod and seed setting is possible by breeding (JARANOWSKI, DYBA 1983, BOCSA, PUMMER 1994, 1997).

In breeding for improved seed yield it is particularly important to determine the effect of generative and morphological characters on seed yield and of their interrelations and heritability. These properties determine the effectiveness of selection for better pod and seed setting.

The presented results concern phenotypic correlation coefficients and heritability of the characters responsible for seed yield of long-raceme forms of alfalfa. The long-raceme character is controlled by a single recessive gene *lp* (BODZON 1998). The knowledge of general genetic patterns in new long-raceme forms is essential for alfalfa breeding.

Material and methods

The experimental material consisted of 7 long-raceme BC_2, constituting the components of the new synthetic population RAH 100.

These long-raceme hybrids were made by crossing 7 clones, being the basic breeding material of the cultivar Radius, with four lines I_2 2002/1, used as donors of both the long-raceme character and a high number of pods per raceme. The gene *lp* was introduced by backcrossing to the genotypes of the Radius clones. Two cycles of backcrossing were performed, which resulted in obtaining 7 long-raceme BC_2 hybrids.

The analysis was performed both in the first and the second year of full utilisation (the second and third years of growth) in a field trial set in a completely randomised block design in 3 replicates. Field trials were performed at Radzików in 1992-1993, on a podzolic soil formed on glacial till and assigned to the third class in the Polish system. The plot size was 10 m^2, row distance was 0.8 m, and plant density amonuted to 8 per m^2.

Six generative characters were evaluated and included number of pods per raceme, number of seeds per raceme, number of seeds per pod, 1000-seed weight, seed weight per raceme and seed yield per plant. Also six morphological characters were evaluated and included raceme length, number of flowers per raceme, plant height, number of main stems, number of nodes and of racemes per main stem.

Interrelations among the observed characters were studied by phenotypic correlation coefficients. Also, on the basis of multiple linear regression analysis, the effects of 6 characters conditioning the seed yield, namely number of pods per raceme, number of seeds per pod, 1000-seed weight, raceme length, number of flowers per raceme, and number of racemes per stem were studied. This study was done on samples of 90 plants taken at random from 3 plots (30 plants per plot). Correlation among characters and multiple linear regression was applied separately within each of the 7 BC_2 hybrids.

A single plant was taken at random from each BC_2 cross combination. These plants were cloned, thus giving 7 clones, which in turn were crossed in 1991, according to the diallel crossing system using Griffing method 3. The resulting F_1 progenies were studied in the first and the second year of full utilisation in a completely randomised block design with 3 replicates. The analysis of data concerning the generative characters, i.e. number of seeds per raceme, number of seeds per pod, number of pods per raceme, and raceme length, was followed on the basis of the random Griffing model (GRIFFING 1956, UBYSZ-BORUCKA et al. 1985).

The heritability coefficients were calculated, both in a narrow (h_A^2) and broad (h_G^2) sense. Also the values of expected genetic progress R were calculated, assuming the following selection intensities: 10%, 20%, 30%, 50%, and 80%.

Results

Multiple linear regression was applied to estimate the effects of generative and morphological characters on seed yield per plant. In all BC_2 hybrids it depended upon the number of pods per raceme and the number of seeds per pod, both in the first and the second year of full utilisation. The variance of these characters determined the variance of the yield of seeds per plant from ca 59.7% to ca 65.4% in the first year, and from ca 57.4% to ca 62.0% in the second year. All other independent variables had no effect on seed yield per plant (the dependent variable).

The mean values of the correlation coefficients for 12 generative and morphological characters obtained in the first and second year of utilisation are presented in Table 1. The seed yield per plant of all the long-raceme BC_2 hybrids was positively correlated with all generative and morphological characters tested in this experiment. The only exception was the lack of correlation with the number of nodes per stem in both years.

Interdependence of the number of pods per raceme and the number of seeds per pod, i.e. the characters determining seed yield, was not statistically confirmed. Similarly, correlation coefficients between number of seeds per pod and raceme length as well as those between the number of seeds per pod and the number

Table 1. The matrix of mean phenotypic correlation coefficients between 12 characters within BC_2 alfalfa populations (clones Radius × I_2 2002/1). Data above the diagonal are for 1992, below for 1993

Character	Pod no. per raceme	Seed no. per raceme	Seed no. per pod	1000-seed weight	Seed weight per raceme	Seed yield per plant	Raceme length	Flower no. per raceme	Plant height	Main stem no. per plant	Node no. per main stem	Raceme no. per stem
Pod no. per raceme		0.80*	–0.10	0.12	0.63*	0.74*	0.57*	0.65*	0.30*	0.16	0.26	0.35*
Seed no. per raceme	0.86*		0.66*	0.02	0.75*	0.90*	0.64*	0.57*	0.37*	0.35*	0.30*	0.39*
Seed no. per pod	–0.16	0.72*		0.06	0.60*	0.84*	–0.16	–0.13	0.09	0.23	0.02	0.01
1000-seed weight	0.15	0.07	0.03		0.89*	0.74*	0.15	0.11	0.31*	0.18	0.12	0.11
Seed weight per raceme	0.72*	0.80*	0.54*	0.84*		0.76*	0.37*	0.33*	0.15	0.10	0.13	0.09
Seed yield per plant	0.68*	0.84*	0.76*	0.82*	0.80*		0.40*	0.39*	0.32*	0.38*	0.05	0.52*
Raceme length	0.65*	0.67*	–0.11	0.18	0.32*	0.35*		0.81*	0.44*	0.34*	0.09	0.28
Flower no. per raceme	0.73*	0.50*	–0.09	0.06	0.30*	0.32*	0.88*		0.38*	0.44*	0.13	0.37*
Plant height	0.22	0.33*	0.04	0.20	0.09	0.36*	0.37*	0.31*		0.11	0.25	0.44*
Main stem no. per plant	0.09	0.32*	0.16	0.14	0.12	0.33*	0.25	0.36*	0.16		0.15	0.36*
Node no. per main stem	0.30*	0.38*	0.05	0.08	0.04	0.10	0.14	0.08	0.31*	0.06		0.07
Raceme number per stem	0.39*	0.33*	0.06	0.06	0.17	0.43*	0.23	0.30*	0.50*	0.27	0.13	

* significant at P = 0.05.

of flowers per raceme, were insignificant in both years. On the other hand, the two characters, i.e. the number of pods per raceme and the number of seeds per pod, were positively and significantly correlated with the number of seeds per raceme and with seed weight per raceme.

The number of seeds per raceme, i.e. the product of the number of pods and the number of seeds per pod, was in both years highly and positively correlated both with seed yield per plant and with the raceme length. It was also positively correlated with all other generative and morphological characters, except 1000-seed weight.

Seed weight per raceme was positively correlated with all generative characters, raceme length and the number of flowers per raceme, in both years of utilisation.

Also in both years no negative correlations were found between seed yield per plant or any generative character and the characters decisive for yield of green matter, like plant height, number of main stems and of nodes formed on stems.

Characters significantly influencing the seed yield per plant, i.e. number of pods per raceme, number of seeds per pod and number of seeds per raceme, were studied in F_1 hybrids produced by intercrossing seven BC_2 clones in the first and second year of full utilisation under field conditions.

The variance components concerning the variability of the effects of GCA (σ_g^2), of SCA (σ_s^2), of reciprocal crossing (σ_r^2), and of standard error of the mean (σ_g^2) the are given in Table 2.

Table 2. Estimates of variance components for characters determining seed yield per plant of alfalfa F_1 hybrids obtained by crossing clones in a diallel crossing system using Griffing method 3

Component of variability	Year	Pod no. per raceme	Seed no. per pod	Seed no. per raceme
σ_g^2	1992	1.2184*	0.0405*	57.030*
	1993	1.1492*	0.0414*	46.023*
σ_s^2	1992	1.2826*	0.0121*	14.219*
	1993	1.1571*	0.0133*	12.998*
σ_r^2	1992	0.6583	0.0178	30.661*
	1993	0.8526	0.0216	24.313*
σ_e^2	1992	0.5010	0.0111	10.720
	1993	0.6322	0.0139	9.413

* significantly different from zero.

Significant deviations from zero were found for variance components concerning the effects of combining ability, both general and specific, in all studied characters in both years of utilisation. Therefore, in the population of long-raceme hybrids, variance appeared both additive and due to dominance of the characters conditioning the seed yield per plant. The variance component responsible for the effects of reciprocal crossings in relation to the number of seeds per raceme, both in the first and the second year of utilisation, also differed significantly from zero. On the other hand, the variance component σ_r^2 of all other characters did not differ significantly from zero. It means that the female parents transmitted the genetic material controlling the number of seeds per raceme also via non-nuclear way. This conclusion is important for the choice of components to be crossed in recombination breeding.

The estimates of heritability coefficients of the analysed characters in a narrow and broad sense, as well as the genetic progress expected in the next generation obtained from 10%, 20%, 30%, 50% and 80% of the parental population, are presented in Table 3.

The heritability coefficients (in a narrow sense) for number of pods per raceme were low in both years of utilisation. These results indicate that the share of the additive genetic components in the phenotypic variance of the number of pods per raceme in the long-raceme population amounted to 21.3% and 22.9% in the two years. Thus the expected breeding progress concerning this character would be from about 1.7 with selection intensity 10% and about 0.3 with selection intensity 80%. The value of the broad-sense heritability coefficient indicates that the share of genetic non-additive effects in the genotypic variance was twice as great as that of additive effects.

Table 3. Estimates of narrow-sense (h_A^2) and broad-sense (h_G^2) heritability coefficients for characters conditioning seed yield of alfalfa and the expected genetic progress (R) at different selection intensities

Character	Year	h_A^2	h_G^2	*R* (%)				
				10	20	30	50	80
Pod no. per raceme	1992	0.213	0.621	1.66	1.29	1.07	0.74	0.32
	1993	0.229	0.644	1.68	1.31	1.09	0.75	0.32
Seed no. per pod	1992	0.520	0.764	0.51	0.40	0.33	0.23	0.10
	1993	0.490	0.739	0.50	0.39	0.22	0.22	0.09
Seed no. per raceme	1992	0.551	0.850	16.67	13.04	10.80	7.45	3.16
	1993	0.543	0.877	14.94	11.69	9.68	6.68	2.84

Narrow-sense heritability estimates for numbers of seeds per pod were 0.52 in the first year of investigations and 0.49 in the second year. Therefore, the variability for this character due to the additive effects of genes consisted of about a half of the total phenotypic variation in the population of long-raceme hybrids. The expected magnitude and the rate of genetic progress in recombination breeding will be at medium level, and, depending upon the intensity of selection, this gain may range from 0.5 to 0.1, if the proportion of individuals selected from the parental population would be 10% to 80%, respectively. In the case of the number of seeds per pod, the share of genotypic variance in phenotypic variance was 76.4% and 73.9% in two years of investigations, respectively, and was greater than the share of additive genetic effects because of a significant share of non-additive effects.

The share of additive variance effects in the phenotypic variance of number of seeds per raceme was 55.1% and 54.3% in the two years of investigations. The expected genetic progress resulting from selection would be, according to the results from the first year, from ca 16.7 to ca 3.2, depending on the selection intensity. On the other hand, the expected progress in the number of seeds per raceme, according to the results obtained in the second year, would range from about 14.9 to 2.8 at the selection intensity 10% and 80%, respectively. Due to non-additive effects the share of genotypic variance in total phenotypic variation for this character was 85.0% and 87.7%, respectively, in the two years.

Discussion

The quantitative characters determining seed productivity are polygenically controlled. This is why, determining of the effects of these characters on seed yield, their heritability and interrelations, is decisive for the effectiveness of selection for increased seed yield.

The analysis of multiple linear regression of the BC_2 hybrids proved that seed yield per plant depends on the number of pods per raceme and the number of seeds per pod. The variability of these characters determines about 60% of total variability of seed yield per plant. The other generative and morphological characters did not have any significant effect on seed yield per plant. Dependence of seed yield on the number of pods per raceme was also shown by RAUSCH (1964) and POMOGAIBO (1981).

Seed yield per plant in long-raceme hybrids was positively correlated with all studied generative and morphological characters except the number of nodes on stems. A positive correlation of seed yield per plant with the number of flowers and pods per plant was also found in short-raceme forms by MRA KOVA and VACEK (1981), VACHUNKOVÁ et al. (1981) and POMOGAIBO (1981). Also PUZIO-ID KOWSKA (1993) found high, positive correlation coefficients of seed yield per plant with the number of racemes per stem, number of pods per raceme and number of seeds per pod. A high correlation of seed yield with number of seeds per pod was also confirmed by BOCSA and BUGLOS (1983) and ROSELLINI et al. (1990).

The positive correlation of raceme length with the number of pods per raceme is consistent with the results of MARTURA (1996). GUY et al. (1973) found a positive correlation of raceme length with the number of pods per raceme, and of the number of seeds per pod with 1000-seed weight and seeds yield per raceme.

The listed numerous correlations indicate that selection for improved seed yield of long-raceme forms should consist in selection of plants with the longest racemes and at the same time the highest number of pods per raceme and seeds per pod. HUYGHE et al. (1998, 1999) found that plants characterised by a high seed yield gave also a high number of seeds per raceme. The increase in the number of seeds per raceme resulted both from the increased number of pods and seeds per pod. JARANOWSKI and DYBA (1983) are of the opinion that selection for improved seed yield should be based on simultaneous selection for several characters closely connected with seed yield. The characters being the most decisive for the seed yield potential are: the number of seeds per pod, number of pods per raceme, 1000 seed weight and the number of racemes per stem (BOCSA, PUMMER 1994, DYBA, ROGALSKA 1995). Also ROTILI et al. (1998) demonstrated a high correlation of seed yield with the number of formed pods and seeds. Selection for seed yield should, according to their opinion, consider these two characters simultaneously.

Positive correlation coefficients between raceme length and numbers of pods and seeds per raceme documented in the present work indicate that raceme length can be an important criterion in selection of plants showing a high seed productivity.

Since the generative characters and characters decisive for yield of green matter of long-raceme hybrids are not negatively correlated, one can be sure that selection towards a higher seed yield may not decrease forage productivity. Our observations are consistent with the results of VERONESI et al. (1984), VERONESI and FALCINELLI (1987), and BOCSA and PUMMER (1997). Moreover, a positive correlation of seed yield and green matter was reported by SINGH (1978) and VERONESI et al. (1986).

It should be emphasised that correlations found in our work in long-raceme forms were generally similar to those found by the authors studying the short-raceme forms.

Basing on the analysis of variance of the characters determining seed yield per plant, a significant deviation from zero was found for variability components between both halfsibs (GCA effect) and parental pairs (SCA effect). This indicates that in the long-raceme BC_2 hybrids, both additive and dominant genes control seed yield per plant.

Similar results with respect to the number of seeds per raceme were obtained by HAALAND et al. (1975), who reported also that variability of the effects of general combining ability is more important for expression of this character than the effects of specific combining ability. PETERSON and BARNES (1983) and HE and CAMPBELL (1994) were of the same opinion. These authors maintain that the number of formed pods and seeds and the number of seeds per pod are determined both by additive and non additive gene action, but the variability of additive effects is more important for expression of these characters.

We found that the share of variability of additive effects in the total phenotypic variability of the number of seeds per pod and of the number of seeds per raceme in long-raceme hybrids slightly exceeded 50%. On the other hand, the share of additive genetic components in the phenotypic variance of the number of pods per raceme was at the level of 21-23%. It means that the magnitude and the rate of genetic progress in recombination breeding, which can be expected in the number of seeds per pod and in the number of seeds per raceme, will be of medium magnitude. On the other hand, one cannot expect any rapid and considerable progress in the number of pods per raceme.

Conclusions

The seed yield per plant of the long-raceme BC_2 hybrids depended upon the number of pods per raceme and seeds per pod. The variability of these characters determined about 60% of the total variability of seed yield per plant. It was found that simultaneous selection towards an increase in the number of pods per raceme, the number of seeds per pod, and raceme length, leads to an increase in seed yield. Positive correlation coefficients of raceme length with seed yield per plant and with the number of pods and of seeds per raceme indicate that this character may be an important criterion of selection of plants having a high seed productivity. The expected genetic gain for the number of pods per raceme and, indirectly, for seed yield per plant will be small. A greater progress in the recombination breeding of the long-raceme alfalfa may be expected for the number of seeds per pod and seeds per raceme.

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