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THE EFFECT OF DIRECT AND INDIRECT MASS SELECTION ON PLANT CHARACTERS IN PROSO MILLET

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Abstract: Mass selection for increased and decreased expression of five agronomic characters using two selection units was conducted in a heterogeneous population previously mass selected for seed characteristics of proso millet (*Panicum miliaceum* L.). Mean comparison between the unselected control and mass-selected populations showed asymmetrical response to selection; the shift in means and variances in undesirable direction being much greater than in desirable direction. It seemed that scaling effect and unequal gene frequencies were responsible for the asymmetry observed in the population studied. Overall selection was the most promising selection criteria in regarding overall desirability of the populations.

Index Words: Proso millet, *Panicum miliaceum* L., direct vs. indirect selection, mass selection, asymmetry of response.

KUMDARI'DA DİREK VE DOLAYLI TOPLU SELEKSİYONUN BİTKİ KARAKTERLERİ ÜZERİNE ETKİSİ

Özet: Daha önce tane özellikleri yönünde toplu seleksiyona tabi tutulmuş heterojen bir kumdarı (*Panicum miliaceum* L.) populasyonunda iki seleksiyon birimiyle beş tarımsal özellikte azalan ve artan yönde toplu seleksiyon uygulanmıştır. Kontrol populasyon ile toplu seleksiyon uygulanan populasyonların mukayesesi, seleksiyon etkisinin asimetrik olduğunu göstermiştir: ortalama ve varyansdaki değişme negatif yönde uygulanan seleksiyonda pozitif seleksiyona nazaran çok daha belirgindir. Toplu seleksiyon uygulanan populasyonlarda görülen asimetrinin seleksiyonla populasyon ortalamasındaki değişmeye bağlı olarak varyansın değişmesi ve gen frekansının eşit olmamasından kaynaklandığı kanısına varılmıştır. Populasyonların bütün özellikler bakımından arzu edilen yönde iyileştirilmesine, önemli özelliklerin birlikte dikkate alınmasının en yararlı seleksiyon kriteri olduğu belirlenmiştir.

Anahtar kelimeler: Kumdan, *Panicum miliaceum* L., direk-dolaylı seleksiyon, toplu seleksiyon, asimetrik response.

Introduction

The ultimate interest of the breeder is often the progress to be expected from selection exerted on economically important traits. Therefore, the time and cost associated with selection encourage breeders to consider more effective procedures that will maximize genetic improvement per unit of time with maximum allocation of available resources (1). Among selection methods available to plant breeders mass selection in heterogeneous bulk population is supposed to be the cheapest, quickest, and presumably oldest method in modifying gene frequencies in desirable directions (2).

The improved techniques and proven results reported by Gardner (3) increased breeders interest in mass selection and during the past three decades, mass selection has been used extensively for the improvement of several traits including yield in both self- and cross-pollinated species. In self-pollinated crops, mass selection is a way of increasing the frequency of favorable genes during the segregation period of inbreeding (4). Eliminating material showing less fitness and lower productivity through mass selection is expected to enhance the chance of selecting superior recombinants in later generations (5).

Mass selection may be practiced in two distinct ways; direct mass selection refers to exposing selection pressure upon the trait for which improvement is sought, while indirect mass selection implies selecting for one trait through the expression of another genetically related trait (6), (7). The gain expected from direct mass selection would be directly proportional to the degree of reliability of phenotype in predicting genotype of the attribute being selected (2). With the use of indirect mass selection, however, genetic correlations between traits to be selected and traits to be improved have to be considered as well (8). Indirect selection is commonly used in plant breeding because the primary characters are often difficult or costly to measure directly during the selection process (9). The main limitation to indirect selection is finding efficient selection criteria and existence of negatively correlated responses to selection for some characters. If positive genetic correlations exist, indirect mass selection may be advantageous and preferable for traits with low heritabilities, such as yield, or for traits that require detailed work and more money, such as protein or oil content (10).

The success of mass selection, to some extent, would be expected to correspond with; whether it operates on increased or decreased expression of a character. Mass selection may be applied from either a positive or negative (or both) approach; positive if it involves selecting and bulking of desired genotypes, negative if it involves discarding or culling undesirable genotypes from a population (1). Some mass selection techniques may be more efficient in eliminating undesirable genotypes rather than in retaining desirable ones. The results published by Rattunde et al. (11) in pearl millet (*Pennissetum americanum* L.) indicated that divergent mass selection for harvest index and threshing ratio were effective only for identifying genetically undesirable plants for these traits.

Proso millet is extensively cultivated in India, China, Russia, and also in the Middle East including Iran, Iraq, Syria, Turkey, Afghanistan, and Romania (12). Proso millet has been found to have the highest conversion of limited water supply into grain of any domestic crop known (13). Proso has a nutritive value comparable to that of other cereals. It is somewhat higher in protein than rice (*Oryzea sativa* L.), maize (*Zea mays* L.), sorghum (*Sorghum bicolor* L.Moench), and oat (*Avena sativa* L.) crops (14), (15), (16). In spite of its immense potential in poor, hot, and moisture-limited areas of the World, little attention has been paid in the past towards genetic improvement of proso millet. So far no information is available regarding the feasibility of mass selection techniques in proso millet breeding. Therefore, any contribution to our limited knowledge in formulating an effective breeding procedure for proso millet is of value. The present study was carried out to evaluate the effectiveness and practical utility of direct and indirect mass selection in advancing heterogeneous bulk populations of proso millet.

Material and Methods

The material used to initiate this study was a heterogeneous population of Dawn proso millet which is a white seeded proso with a compact panicle and short stature (17). A mass selection scheme based upon seed characteristics, such as seed size, seed density, and color was imposed upon a heterogeneous population of Dawn. Sample seed from Dawn was stratified into different fractions using various sieve screening, gravity table separation, and seed blower separation. The sample seed was divided into two sub-samples, largest 37% and largest 50%, using appropriate round holed sieves. With the gravity table, the sample seed was sorted into the largest 1%, 13%, 33%, 51%, and 72%. The South Dakota Seed Blower produced three classes, the largest 15%, largest 35%, and largest 50%. Separations obtained from the seed blower and gravity table were made through repeated sampling and readjustment. In addition, visual white seed separation was made by hand. An unsorted sample was used as a control. The same seed source was used for all the experiments to avoid sampling differences.

Sorted and unsorted populations (12 entries) were planted in pots in the greenhouse in a randomized complete block design with five replications in early spring in 1991. On the average, 20 plants per treatment per rep were grown in five pots each having four plants, resulting in 100 plants per entry. Data were collected on these individual plants (approximatey a total of 1200 individual plants) for days to flowering, panicle type, plant height, panicle exertion, and seed weight (each plant was individually harvested).

In the summer of 1991, individual plants from the greenhouse experiment were subjected to a second cycle of selection and field evaluation. The field experiment compared the effect of the criterion of selection (the traits), the units of selection (individual vs line), and the direction of selection (desirable vs undesirable) as well upon the efficiency of mass selection in proso millet. Plants and/or lines with compact panicle, short stature, short panicle exertion, early in flowering, and high seed weight were designated as "desirable selections" (DS). Conversely, selections which appeared markedly deficient for the attributes listed were termed "undesirable selection" (US). Individual plants and lines were selected separately for several agronomic traits as well as overall expression in both desirable and undesirable directions. Among 12 entries evaluated in the greenhouse experiment, designated as lines, desirable and undesirable four lines in the expression of each trait were selected, 13 plants from each. Harvested seeds from these selected plants of each line were bulked to form line selections. A total of 12 lines were obtained for six selection criterion, two lines of each, desirable line selection (DLS) and undesirable line selection (ULS). At the same time, 52 individual plants from the whole population were selected for each selection criterion in both directions, desirable individual selection (DIS) and undesirable individual selection (UIS). Thus, selected proportion was about 4% in both cases, 52 individual plants were selected out of 1200 for each treatment. Individual plant selection was made equally from each replication, 10-11 plants from each, to avoid block effect. Equal number of seeds were taken from each selected plant at random and mixed to give equal representation of selected plants in the next cycle. Selections for overall expression were obtained by selecting sequentially for panicle type, plant height, days to flowering, seed weight and panicle exertion in both directions. An unsorted sample of seed from the original source population was used as a check (CK).

The entries were grown at the High Plains Agricultural Laboratory of the University of Nebraska under dryland conditions in 1991. The experimental design was a split-plot with four replications. The six selection criterion (days to flowering, panicle type, plant height, panicle exertion, seed weight, and overall expression) were allotted to main plots and the five selection procedures (individual and line selections in both directions, and the control) were allotted to subplots. The seed material was space drilled in one-row plots, each 6 m long, spaced 75 cm. apart. 100 individual plants were sampled at random from each entry. The following attributes were evaluated on each individual plant; days to flowering: number of days from sowing to the day when the spike on the main culm was fully exerted from the flag leaf sheath; plant height: length in cm from the base of the culm to the tip of the spike of the tallest culm after heading; panicle type: visually graded as 0 for compact (dense panicle with short branches), 10 for open (dropping panicle with long branches), and 5 for semi-open; panicle exertion: length in cm from the flag leaf to the base of the panicle; seed weight: weight in grams of fifty seeds from each individual plant.

Statistical analyses were computed using the Statistical Analysis System (SAS), version 6.03. The analyses of variance were calculated and comparisons among treatment means were made through planned contrasts using the general linear models procedure (Proc GLM) in SAS. Changes in means and variances of the attributes in the selected populations were determined to evaluate the effectiveness of the selection procedures.

Results

The results of analysis of variance for various plant characteristics indicated the presence of highly significant variability in the populations (Table 1). There were no significant differences in terms of selection criteria for all of the traits. The test, however, indicated that the effect of the unit and direction of selection was highly significant for all of the traits studied, except panicle type. The interaction of selection criteria with unit and direction of selection was also highly significant for days to flowering, plant height, and seed weight indicating that the effect of selection criterion was not uniform across selection unit and direction.

The effect of the criterion of selection may be diminished or neutralized by selecting in two opposite directions with two different selection units. A selection criterion can be effective in changing the mean when selecting for desirable expression of that trait. But it may not exert any shift on the mean when selection is for undesirable expression of the trait. Therefore, the data were reanalyzed considering selection only in one direction at a time to eliminate the effect of two directional selection on the effect of selection criteria. The results, however, were in agreement with that of the overall analysis when selection was applied in the desirable direction. The test showed significant differences for the unit and the direction of selection, but no differences with regard to the selection criteria. On the contrary, corresponding analysis for undesirable selection indicated significant effect of selection criteria for days to flowering and plant height.

Table 1. Analysis of variance of the traits studied in direct and indirect mass selection in two directions.

Source of variation	Panicle type	Days to flowering	Panicle exertion	Plant height	Seed weight
	Mean squares				
Blocks	0.9	323.4**	202.8**	17721.1**	0.043*
Criterion(C)	9.9	91.1	12.1	862.9	0.007
Error(a)	6.1	31.6	24.2	566.6	0.009
Units(U)	2.8	590.6**	102.9**	7590.5**	0.046**
CK vs DS	2.4	111.9	125.4*	550.0	0.001
CK vs US	0.5	1567.5**	240.5**	9999.4**	0.052**
DLS vs DIS	7.3	13.0	13.9	405.7	0.007
ULS vs UIS	0.9	214.6**	157.0**	2984.2**	0.065**
C x U	2.3	31.5**	12.7	839.1**	0.006**
Error(b)	2.8	14.6	21.2	206.9	0.003

* and ** F values exceed the 5 and 1% level of probabilities.

The mean of the selected populations averaged across selection criteria and units were significantly different than that of the control population for all of the traits, except panicle type, when selecting in undesirable direction. Corresponding planned contrasts for desirable selection, however, indicated that mass-selected populations significantly differed from the control only for panicle exertion. Interestingly, similar results were obtained from the comparison of selection units (individual plants or line selection) in both directions. There was no response to desirable selection irrespective of whether the selection unit was individual plant or line. With regard to undesirable selection, however, there was significant discrepancy between individual-plant and line selection for all of the traits evaluated.

Selecting plants with short stature (direct selection) and selection for overall desirability resulted in shorter plants compared to the others (Table 2). On the other hand, the tallest population was obtained from light-seeded plants.The highest response to selection to improve seed weight was observed from retaining late flowering plants. Interestingly, selecting light-seeded plants produced late flowering population, which was in conflict with the indirect effect of days to flowering on seed weight. The shift in mean of panicle exertion was in desirable direction; mass selection usually reduced panicle exertion irrespective whether it operated in negative or positive direction.

Table 2. Means of characters recorded following direct and indirect mass selection in two direction.

Criterion	Unit	Characters				
		Panicle type	Days to flowering (days)	Plant height (cm)	Panicle exertion (cm)	Seed weight (g)
Panicle exertion	DIS	0.48	27.9	53.0	9.3	0.340
	DLS	0.24	28.8	52.4	10.4	0.350
	UIS	0.28	31.3	62.2	9.8	0.317
	ULS	0.17	30.1	56.0	10.2	0.335
Days to flowering	DIS	0.27	28.7	54.4	10.4	0.337
	DLS	0.35	28.0	52.5	10.4	0.343
	UIS	0.36	28.8	50.5	9.3	0.343
	ULS	0.38	28.5	52.0	9.5	0.359
Plant height	DIS	0.44	28.8	49.3	9.2	0.343
	DLS	0.31	29.0	50.6	9.8	0.345
	UIS	0.11	31.5	55.9	9.0	0.345
	ULS	0.28	29.7	62.4	9.8	0.311
Overall expression	DIS	0.07	28.7	50.1	10.0	0.341
	DLS	0.35	28.7	47.1	9.2	0.346
	UIS	0.26	31.2	59.0	8.5	0.314
	ULS	0.53	30.1	58.9	10.4	0.346
Panicle type	DIS	0.34	28.6	51.4	9.4	0.347
	DLS	0.43	28.0	51.0	10.2	0.356
	UIS	1.02	30.9	61.2	9.2	0.331
	ULS	0.74	29.4	54.4	9.6	0.341
Seed weight	DIS	0.36	29.1	54.3	9.7	0.349
	DLS	0.13	28.9	50.1	9.3	0.341
	UIS	0.95	31.4	64.6	9.2	0.319
	ULS	0.54	31.1	60.9	9.2	0.326
Control(CK)		0.49	28.0	52.5	10.3	0.346

The results from the analysis of treatment variances were given in Table 3. The effect of selection criteria on variances of the populations was significant only for days to flowering. The effect of unit and direction of selection, however, was significant for all the plant characteristics, except for panicle type. The results in Table 3 showed asymmetrical response to mass selection as evidenced by variance comparison of desirable and undesirable selection with the control population. Mass selection in desirable direction did not indicate a significant change in variance of any trait. On the contrary, mass selection in undesirable direction exposed significant differences for the variance of days to flowering, plant height, and panicle exertion. Significant interaction of selection criteria with the unit and direction of selection was also observed for all the attributes (Table 3).

Treatment variances for the traits evaluated in unselected control and mass-selected populations are given in Table 4. In general, the lowest variances for most of the attributes were recorded in overall expression in desirable direction.

Table 3. **Mean squares from the analysis of treatment variances.**

Source of variation	Characters				
	Panicle type	Days to flowering	Plant height	Panicle exertion	Seed weight
	Mean squares				
Blocks	2.2	11.5	1841.1	22.5	0.55
Criteria(C)	7.7	21.3**	7124.2	98.3	0.28
Error (a)	9.9	6.5	3077.9	23.7	0.22
Units(U)	3.8	168.1**	54389.4**	145.7**	0.43**
CK vs DS	4.1	22.5	6066.7	20.1	0.87
CK vs US	0.1	200.4**	81008.5**	275.8**	1.03
C x U	7.4*	19.4*	9479.8**	40.7*	0.20**
Error (b)	4.0	9.3	1955.4	20.6	0.07

*and ** F values exceed the 5 and 1% levels of probability.

Discussion

Response to selection was somewhat asymmetrical, the change in undesirable direction being much greater than in desirable direction. Asymmetrical responses to selection have also been observed in corn (18), and in sorghum (19). Ten cycles of divergent mass selection for ear length in maize showed asymmetrical response (18). Realized gain for decreased ear length was twice as great as for increased ear length. Demonstrating identical results for grain protein in sorghum, Ross et al. (19) concluded that breeding sorghum grain for low protein percentage is more tenable than breeding for high protein which is more likely to be the objective.

Falconer (7) discusses the following as some of the possible causes of asymmetrical response to selection in two-way selection experiments: 1) scaling effect; 2) unequal gene frequencies; 3) differences in genetic and environmental variation.

In the present study, the same degree of selection pressure was applied to the same selection criteria in both directions of selection. It is more likely that scaling effect and unequal gene frequencies in the initial population played major roles on the asymmetry of response. The most common cause of scaling effect is that the variance may change as a result of the change of mean, which is in agreement with the result of this study. Consequently, selection differential will differ between the upward and downward selected plants or lines; so does the response to selection.

Unequal gene frequencies in the initial population mass-selected may also be a cause for the asymmetry of response. The initial population was previously mass-selected through three methods of mechanical mass selection for seed size and density. Populations selected for high density seed were more skewed in undesirable direction than that for seed size. It seems that mechanical mass selection may result in a change in the gene frequencies away from symmetrical values. Thus, in a two-way selection experiment in that kind of population, gene frequencies may move toward a symmetrical value in one direction, but move away from symmetrical in another direction of selection (7).

Table 4. Treatment variances for plant attributes in unselected and selected populations for several traits in two directions.

		Characters				
Criterion	Unit	Days to flowering	Panicle type	Plant height	Panicle exertion	Seed weight
Panicle exertion	DIS	6.4	3.7	142.8	15.0	0.0009
	DLS	4.2	0.9	65.6	9.3	0.0008
	UIS	11.5	1.4	188.6	18.6	0.0011
	ULS	12.8	0.9	136.1	14.1	0.0010
Days to flowering	DIS	10.6	1.3	99.8	19.9	0.0007
	DLS	4.8	1.6	61.1	11.4	0.0004
	UIS	7.0	1.6	79.3	12.7	0.0008
	ULS	5.8	2.8	56.1	9.7	0.0005
Plant height	DIS	5.7	2.7	73.0	9.1	0.0003
	DLS	6.8	1.9	102.9	9.3	0.0006
	UIS	14.6	0.6	198.3	18.8	0.0009
	ULS	11.9	1.2	147.4	10.6	0.0012
Overall expression	DIS	3.5	0.3	88.9	10.0	0.0003
	DLS	3.7	1.9	67.4	8.1	0.0004
	UIS	13.4	0.9	197.2	14.3	0.0012
	ULS	9.6	3.5	245.0	10.1	0.0011
Panicle type	DIS	8.7	1.6	74.5	10.4	0.0005
	DLS	4.9	2.0	64.4	10.3	0.0004
	UIS	12.9	6.3	185.1	17.3	0.0011
	ULS	9.2	3.1	140.0	19.5	0.0007
Seed weight	DIS	10.1	4.0	60.3	20.5	0.0004
	DLS	6.2	0.5	88.2	12.9	0.0005
	UIS	12.1	2.1	250.5	15.2	0.0012
	ULS	11.7	3.5	252.9	21.4	0.0014
Control		7.5	2.4	101.9	11.1	0.0007

Another possible explanation is that, due to genotype by environment interaction, the genetic and environmental variation may be skewed in opposite directions. In the present study, mass selection was performed in a population grown in a greenhouse which was an adverse environment. The resulting set of populations, however, were evaluated in field conditions, a more favorable environment. Different sets of genes may be effective in different selecting and testing environments; some desirable genes even would be either neutral or negative in their effects in a poor environment. If selected plants are grown in a more favorable environment, the skewness in genetic and environmental variation may be a possible source of asymmetry of response.

There was no appreciable effect of the selection unit on any trait in desirable selection. In the case of selection in undesirable direction, selecting individual plants alone moved the means and variances to a more undesirable direction. The line selection makes use of both the family mean and the within-family deviation and thus, it may be considered as a combined selection. It is expected that within-line selection would eliminate a large component of environmental variance from the variation on which selection was operated. However, individual plant selection was greatly effected by environmental variation and thus, produced more outlier plants for each character.

The result of the present two-way selection experiments suggest that mass selection, either direct or indirect, would be more effective usually for identifying inferior plants in their phenotypic expression. Consequently, mass selection, as tested in this study, looks like a feasible and practical aproach in purifying contaminated commercial varieties of proso millet.

Overall selection was the most promising selection criteria in regarding overall desirability of the populations. Overall selection is the process of selection of each trait in turn and independently in a given population at the same time. In this aspect, it looks like independent culling levels, but differs from it as retaining best and worst plants instead of rejecting all individuals that are below a certain value for each character. Since overall selection operates on several traits simultaneously, it may reduce undesirable correlated responses and give the most rapid improvement, but it is a more complex system than single trait selection.

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