Interrelationship of yield and its morphological components in annual ryegrass*

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ABSTRACT

The potential for genetic improvement of annual ryegrass (*Lolium rigidum* L.) yield through selection based on morphological factors such as leaf elongation rate has been suggested. Field experiments were conducted to study the relationship between forage yield and the morphological characters of the plants. The influence of using such characters in improving forage yield was also determined using one cycle of recurrent restricted phenotypic selection. Among plants a positive correlation ($r = 0.64$) existed between yield/tiller and leaf elongation rate, and negative correlation ($r = -0.53$) existed between yield/tiller and rate of tillering. Path coefficient analysis showed that both yield/tiller and leaf elongation rate had large positive direct effects on total yield/plant. The direct effect of yield/tiller on yield/plant was about 2.1 times as great as the direct effect of number of tillers/plant. Using leaf elongation rate as selection criterion, and the recurrent restricted phenotypic selection procedures resulted in increasing forage yield of this grass 39% over that of the original population in the selection direction for high leaf elongation rate. The data suggest that leaf elongation rate can be an efficient selection criterion in improving forage productivity of this crop.

INTRODUCTION

In lieu of breeding for yield per se to increase productivity of forage grasses, physiologists are identifying and studying morphological and physiological characters associated with the expression of herbage yield in order to assess their feasibility as selection criteria in forage breeding programs. A suitable selection criterion would be one that can be implemented at an earlier stage of plant development, yet would be maintained when plants are grown under sward conditions. In addition, the character (s) selected would need to remain stable under the variable environmental conditions under which forage crops grow (6).

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Several years ago the concept of critical leaf area index (LAI) was described by Brougham (2) to define the LAI that is necessary to achieve 95% light interception at noon. Cooper (4) has summarized the sequence of leaf area accumulation and crop growth in herbage grasses. After gremination or defoliation, crop growth rate (CGR) is limited by the small amount of leaf area available to intercept the incoming light energy. As the crop grows, assimilation per unit area of leaf is reduced because of shading, but crop growth rate increases. As a point when the leaf area index is sufficiently large to intercept all the light energy (optimum LAI), the maximum growth rate is attained. In some species this growth rate is maintained with further increases in LAI, but in others, a decline occurs which is probably associated with the increased respiratory load at the base of canopy. This leads to the conclusion that the limiting factor for forage material production by forage crops was LAI. Critical LAI depends on the size and orientation of leaves (12). Canopies of erect-leafed cultivars of perennial ryegrass (*Lolium perenne* L.) had larger optimum LAI and higher CGR than did prostrate-leafed cultivarts (12).

Three major concepts have emerged over the years of research that are considered with forage growth in the broadest sense and are related to solar energy interception and its utilization by forage plants (8). These include: 1) rapid development of leaf canopy in order to achieve 95% interception of available radiation with the radiation well distributed in the canopy, 2) a photosynthetic system that efficiently utilises that radiation, 3) a management system based on growth habit of the plant that would allow a rapid growth as well as maintain an adequate stored energy reserve.

Morphological characters associated with yield have been used as selection criteria in forage grass breeding programs to increase herbage productivity (9, 10). Such characters were usually those influencing canopy structure and thus, light interception. Therefore, selection pressure on morphological characteristics associated with high productivity usually resulted in selection of genotypes with larger leaf area (10, 17, 19). The importance of increasing radiation interception and herbage yield by characters that would increase LAI has been documented (17).

Features of grasses which determine canopy structure are variable genetically and are highly heritable in ryegrass (13) and tall fescue (*Festuca arundinacea* Schreb.) (9). Rhodes (13) has shown that genetic variation exists for leaf length in ryegrass populations. Moreover, Rhodes (11) suggested that the mechanism of canopy development would need to be a function of the management system for which it was intended. For example, Rhodes (13) reported that a selected population of long-leafed genotypes of ryegrass was more productive under infrequent cutting than was either a selected population of short-leafed genotypes or their base population. However, under frequent cutting the short leafed population was more productive. Moreover, Zarrough and Nelson (17) showed that a genotype of tall fescue selected for high yield/ tiller was superior in yield to low yield/ tiller genotype when cut every 42 days. However, the low yield/ tiller genotype was superior when cut every 14 to 28 day cutting frequencies.

Horst *et al.* (6) considered several morphological and physiological characters and showed that leaf elongation during early stages of regrowth was closely associated with forage yield which could be used as selection criterion for yield improvement of tall fescue. Moreover, Nelson and Sleper (9) reported that four cycles of recurrent restricted phenotypic selection for high (H) and low (L) rates of leaf area expansion (LAE) gave populations with rates of LAE of 181 and 74 mm^2 day^{-1} for the H and L directions, respectively. Moreover, Nelson and Sleper (9) showed that yield of the vegetative regrowth of tall fescue after two generations of selection in the (H) direction was 39% more than the broad-based population. However, leaf area expansion was negatively correlated with tiller density (17).

It is evident that all of these studies emphasized that plant morphology is an important determinant of productivity in forage grasses through its effect on canopy shape and light interception. Leaf area expansion is critical as it not only is the harvestable product, but also contributes to an ever increasing LAI which increases the light interception surface on the canopy until the critical LAI is reached.

In order to obtain high production of forage grasses it is essential that desirable characters which influence productivity be understood. Ultimately, the desirable attributes should be combined together to obtain high yielding cultivars. Recognizing the significance of Rhodes (13) and Zarrough *et al.* (17, 18) works, an effective selection criterion may be one associated with canopy development, as it would be associated with both radiation interception and dry matter distribution. Therefore, the objective of this experiment was to study several morphological characters of the annual ryegrass (*Lolium rigidum* L.) native to Libya and their relationship to forage yield.

MATERIALS AND METHODS

The original population consisted of 100 seeds of annual ryegrass (*Lolium rigidum* L.) taken randomly from a collection made by Dr. K. Sgaier in 1979. This collection consisted of ecotypes collected in Zawia, Tajoura, Gharabulli and the Faculty of Agriculture farm. On October 28, 1982, seeds were planted singly in the field in 20-plant rows at a distance of 25 cm within the row and 50 cm between rows at the Faculty of Agriculture Farm, Tripoli. The experimental area received an application of N (as ammonum sulphate) at the rate of 100 kg/ha post to planting. Weed population was controlled by hand cultivation and hand weeding escapes. Supplemental irrigation was given as needed throughout the experimental period to keep active growth.

Forage dry matter yield (DMY) was evaluated by cutting plants to a height of approximately 10 cm above the soil surface on April 4, 1983. The cut herbage was dried in a forced air oven at 70°C for 48 hours to determine DMY. Tillers that had extended to or above the cutting height were counted and yield/ tiller was calculated. Leaf elongation rate (LER) was measured before cutting plants. On February 28, 1983, one tiller/ plant was marked with a colored wire. To determine LER, the length of the emerging leaf blade above the youngest fully collared leaf was measured on five alternative days from March first through 13 March, 1983. One leaf was sampled per plant. Leaf length was measured from the tip of the blade to the collar of the next lower leaf which was fully developed. The regression coefficient of leaf length vs. time was used to estimate LER (mm/day). (16).

Subsequent evaluation of the correlated response in dry matter production was carried out. Moreover, a path coefficient analysis (15) was computed to characterize mechanisms involved in yield and to suggest suitable selection criteria for improving forage yield of this crop.

After the evaluation of the base population, the 10 plants with the highest leaf elongation rate (HLER) and the 10 plants with lowest leaf elongation rate (LLER), (selection pressure 10%), were selected, labelled and transplanted in pots on April 4,

1983. Each population was isolated from the other in a greenhouse for cross pollination. Seeds from intercrossed heads from each plant were threshed and kept separate to give seeds to first cycle of selection.

In Fall of 1983, these selections were evaluated in 10 plants rows. 100 plants for both the high leaf-elongation rate and low leaf elongation rate (five seedlings from each maternal plant) were planted on 13 Oct., 1983, in such a way that a single plant from each maternal parent was included in one replication (3). The five seedlings from each maternal selection permitted five replications. Forage dry matter, tiller number and leaf elongation rate were evaluated as described for the base population. On 25 March, 1983, selection of plants to furnish plants to intermate for the next cycle of selection was carried out using leaf elongation rate as a selection criterion also. One plant in each 10 plant row of each population was appropriately labelled. These plants were transplanted in 30 cm diameter plastic pots. The plants from each selection were intermated in isolation as in 1983, to give seed for the second cycle of selection (3).

RESULTS

Means and coefficients of variation obtained in the first year of the initial space planting of the original population for four agronomic traits are presented in Table 1. Forage yield within the original population ranged from 2.5 to 24.4 gm/ plant with a mean of 19.2 gm/ plant and C.V. of 43.7% (Table 1). Moreover the original population showed large variability in number of tillers/ plant, yield/ tiller and leaf elongation rate (Table 1).

Table 1 — Variation for leaf elongation rate, number of tillers/ plant, yield/ tiller and forage yield/ plant among plants of the original population.

Character	Range	Mean	C.V. (%)
Leaf elongation rate (mm/day)	8.9 − 21.2	15.3	50.9
Tillers/ plant (No.)	7 − 51	21	41.8
Yield/ tiller (mg)	357.1 − 3485.7	1257.6	56.3
Forage yield/ plant (gm)	2.5 − 24.4	19.2	43.7

The frequency distribution of individual leaf elongation rate in the original population is shown in Fig. 1. The distribution shows significant ($p < 0.05$) skewness due to an excess of low leaf elongation rate individuals. The assymmetry of the distribution may be due to different causes, the most obvious one being directional dominance of high leaf elongation rate.

The correlation between number of tillers/ plant and forage yield/ plant was negative and significant ($r = -0.76$, $p < 0.01$) (Table 2). However, positive and significant correlation were observed for yield/ tiller and leaf elongation rate with forage yield/ plant. The determination coefficients show that 88% of the between plant variability for forage yield is associated with leaf elongation rate. Moreover, leaf elongation rate was associated positively with yield/ tiller and in negative manner with number of tillers/ plant.

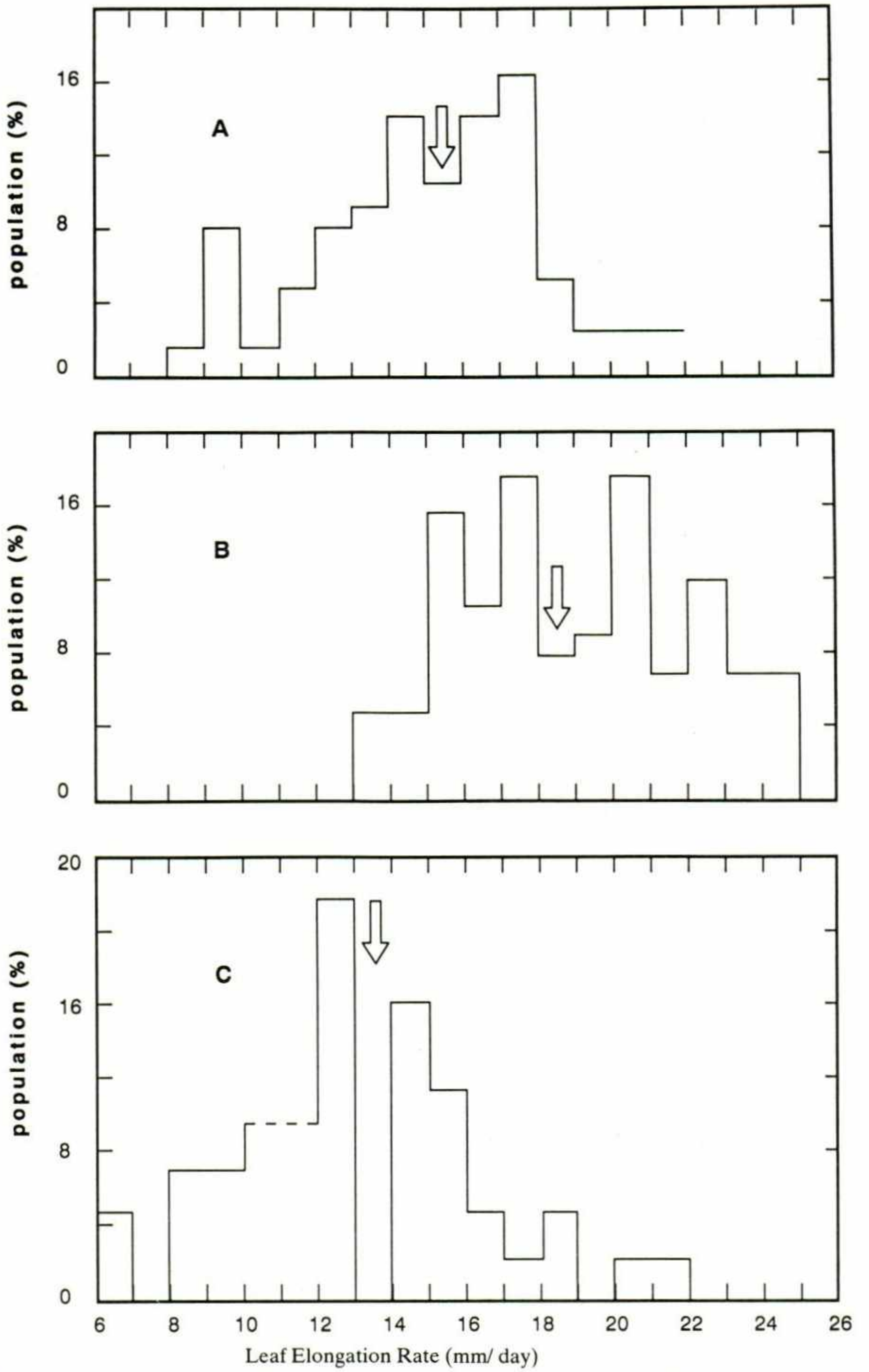

Fig. 1. Frequency distribution of individual plant values for leaf elongation rate (LER) determined on the original population (A) and after one cycle of recurrent restricted phenotypic selection for (B) and low (C) LER. Arrow indicates the mean.

The correlation coefficients between various characters, as well as with forage yield itself (Table 2), are generally in conformity with those obtained by other workers in perennial ryegrass (5) and in tall fescue under sward condition when tiller production reached its equilibrium and had stablized (17). However, Sleper *et al.* (14), and Zarrough *et al.* (17) reported that a close relation existed between number of tillers and forage yield before equilibrium tiller production was reached, where a greater difference in genetic expression for tillering could be expected than under sward condition.

Table 2 — Within original population intercharacter correlations based on individual plant data.

	(1)	(2)	(3)	(4)
Character				
(1) Forage yield/ plant (g)	–			
(2) Tillers/ plant (No.)	– 0.76**	–		
(3) Yield/ tiller (mg)	0.94**	−0.53**	–	
(4) Leaf elongation rate (mm/day)	0.79**	−0.48**	0.64**	–

** indicates significance at the 0.01 probability level.

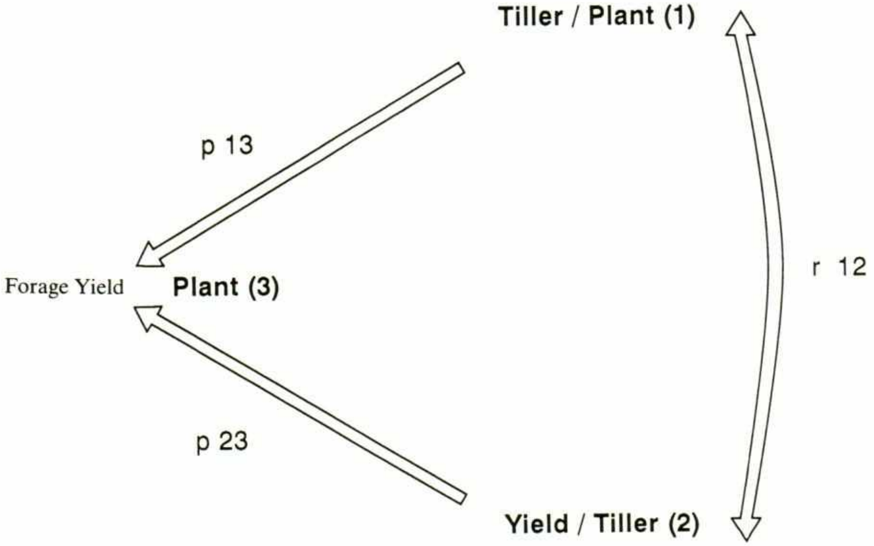

Fig. 2. Path diagram showing direct and indirect effects of components on forage yield/ plant. Unidirectional arrows represent coefficients (direct effects) and bidirectional arrow represents correlation coefficient.

The concept of yield component has not been considered to a great degree in forage grasses. However, forage yield is a direct function of number of tillers/ plant and yield/ tiller (14). A technique to identify the direct and indirect effects of each on forage yield/ plant is path coefficient analysis (15). Further, path coefficient analysis permits an examination of the relative importance of the yield components as genetic determinants of forage yield.

Figure 2 shows the direct and indirect effects of the yield components on forage yield/ plant. When forage yield/ plant was partitioned into direct and indirect effects contributed from number of tillers/ plant component, the direct effect (p 13) was negative relationship between number of tiller and yield/ tiller (Table 3). The direct effect of yield/ tiller on forage yield/ plant was large and positive (Table 3).Thus, these data suggested that under the conditions of this experiment forage production was influenced about 2.1 times more by variations in yield/ tiller than by variations in number of tillers/ plant (Table 3).

Table 3 — Path coefficient analysis of the direct and indirect influences of number of tillers/ plant and yield/ tiller on forage yield/ plant in the original polulation of annual ryegrass.

Type of effect	Coefficient
Effect of number of tillers/ plant on forage yield/ plant	
Total correlation, r_{13}	-0.76^{**}
Direct effect, P_{13}	-0.36
Indirect effect, $r_{12}\ P_{23}$	-0.40
Effect of yield/ tiller on forage yield/ plant	
Total correlation, r_{23}	0.94^{**}
Direct effect, P_{23}	0.75
Indirect effect, $r_{12}\ P_{13}$	0.19

** indicates significance at 0.01 probability level.

Differences between the high and low leaf elongation rate populations derived, respectively, by intercrossing among the high and low leaf elongation rate selections were significant for all characters (Table 4). Population selected for high leaf elongation rate outyieled population selected for low leaf elongation rate, and had the lowest number of tillers/plant (Table 4). Moreover, the high leaf elongation rate population had about 43% faster leaf elongation rate as compared to the low leaf elongation rate population (Table 4, Fig. 1). The coefficient of variation in Table 4 shows that the high leaf elongation rate was less variable than the low leaf elongation rate population in most measured traits. The high coefficients of variation observed for number of tillers/ plant, and yield/ tiller was probably due to environmental or genetic variation or both. However, the contribution of each component in this variation was not known. Correlation coefficients between the measured characters as well as with yield itself obtained from the first cycle of selection data (Table 5) are comparable to the data obtained from the original population.

Means expressed as percentage of original population are shown in Table 6. The data presented in this table suggest that selection for high leaf elongation rate was effective in improving forage productivity of annual ryegrass. These data indicated that one cycle of recurrent restricted phenotypic selection for high leaf elongation rate increased forage productivity by 39% over the original population (Table 5).

Table 4 — Range, mean and C.V. of leaf elongation rate and some other morphological characters. Within high and low leaf elongation rate (LER) population.

Character	Population		Range	Mean	C.V. (%)
Leaf elongation rate (mm/ day)	High	LER	13.0 — 25.9	18.7	16.4
	Low	LER	6.5 — 18.8	13.1	26.0
Tillers/ plant (NO.)	High	LER	11.0 — 38	18	32.5
	Low	LER	10 — 47	23	42.9
Yield/ tiller (mg)	High	LER	686.8 — 3654.6	1569.3	43.7
	Low	LER	208.0 — 1473.7	751.6	64.5
Forage yield/ plant	High	LER	12.7 — 48.9	26.6	39.8
(gm)	Low	LER	3.5 — 33.0	14.5	37.6

Table 5 — Correlation coefficients for forage yield/ plant and morphological characteristics within the first cycle of selection.

Character	(1)	(2)	(3)	(4)
(1) Forage yield/ plant (g)	—			
(2) Tillers/ plant (No.)	—0.60**	—		
(3) Yield/ tiller (mg)	0.83**	—0.51**	—	
(4) Leaf elongation rate (mm/ day)	0.56**	—0.47**	0.61**	—

** indicates significance at the 0.01 probability level.

Table 6 — Means expressed in percentage of original population (Co) for character determined on first cycle of selection of high and low leaf elongation rate (LER) population.

Character	Mean in % of Co. Population	
	Higher LER	Low LER
Leaf elongation rate	122.2	85.6
Tiller/ plant	85.7	109.5
Yield/ tiller	124.8	59.7
Forage yield/ plant	138.5	75.5

DISCUSSION

This experiment was conducted under low plant competition to allow plants to express their maximum genetic potential. Under sward conditions plant competition might mask the genetic potential for yield and its components.

The positive correlation between leaf elongation rate and yield/ tiller suggests that if selection pressure was placed on leaf elongation rate, yield/ tiller would eventually be altered in a productive manner. However, the negative correlation between leaf elongation rate and number of tillers/ plant suggests that improvement of both yield components simultaneously would be difficult. Moreover, the data obtained from this experiment indicated that the plants differed in the pattern by which they developed tillers and their leaf elongation rates, but provided no information on the internal mechanisms for the control of either tillering or leaf elongation rate. However, from the review by Langer (7) the following possible explanation is offered to account for the difference in tiller production. Tiller buds are formed in the axils of most leaves suggesting that difference in rate of leaf initiation may alter rate of tiller formation. Genetic differences have been reported in the rate of leaf appearance in tall fescue (16) and in perennial ryegrass (5). Begg and Wright. (1) concluded that initiation and development of leaves constitued the first priority for assimilates. Therefore, differences in tillering rate may be associated with the failure of tiller buds to develop as a consequence of preferential translocation of photosynthates to leaf primordia. Thus, it appears as one select for rapid leaf elongation rate, there may be an increased demand from that sink and therefore, fewer tillers were produced. Zarrough *et al.* (18) reported that selection for high leaf elongation rate was accompanied by a decrease in both rate of leaf appearance and site usage. Thus the high tillering rate in a population of tall fescue characterized by having low leaf elongation rate and high tiller number was brought about by a combination of higher rate of leaf appearance and utilization of tillering site.

Difference in the rate of leaf elongation between the high and low leaf elongation rate selections might be associated with differences in the rate of cell division, elongation or both. Nelson *et al.* (8) reported that a genotype with a faster rate of leaf elongation produced more cells per day in the leaf meristem and the cells expanded to a greater length when compared to a genotype characterized by low leaf elongation rate.

Path coeficient analyses have shown that yield/tiller was about 2.1 times more important in determining forage yield than tiller number. Zarrough *et al.* (18) reported that genetic differences altered the equilibrium tiller density and the time required to achieve this equilibrium in tall fescue. Moreover, genotype of tall fescue that achieved higher yield, largely via increased number of tillers did not have a forage yield advantage after equilibrium tiller production was achieved. Once equilibrium tiller density was reached, forage yield was closely related to yield/ tiller (17). Under those conditions, the highest yielding genotype of tall fescue was the one characterized by low tiller number and high yield/ tiller. Thus, it might be concluded that in this experiment tiller production was stabilized and became limited. In this case the plant exploited increased genetic potential for expression of yield/ tiller which consequently increased yield potential.

Sleper *et al.* (14) studied the components associated with yield/ tiller and reported that leaf elongation rate was the most important character associated with variability in yield/ tiller in tall fescue. It is evident from the results of this experiment that divergent selection for high and low leaf elongation rate was effective in producing two differentiated populations. Populations selected for high leaf elongation rate had about 84% more yield compared to the population selected for leaf elongation rate.

The results of this experiment suggest that leaf elongation rate might be a good indicator for forage yield and an effective selection criterion in a breeding program for yield improvement. Measurement of this character at an early stage of growth is relatively easy, accurate and would allow the screening of a large population. Moreover, it would serve as an indicator of canopy development and photosynthate distribution. Although this trait possesses some of the characters of an ideal selection criterion, information on the additive genetic variances and its heritabilities is lacking. Evaluation of material under sward conditions for better understanding of the correlated response in yield, and stability of leaf elongation rate as a selection tool for forage yield improvement is required.

LITERATURE CITED

1. Begg, J.E. and M.J. Wright. 1984. Relative effectiveness of top and basal leaves for the regrowth of vegetative shoots in red canary grass *(Phassalaris arundinacea* L.). Crop Sci. 4: 607-609.
2. Brougham, R. W. 1956. Effect of intensity of defoliation on regrowth of pasture. Aust. J. *Agric. Res.* 7: 377-387.
3. Burton, C.L. 1974. Recurrent restricted phenotypic selection increases forage yield of Pensacola Bahiagrass. *Crop Sci.* 4: 831-835.
4. Cooper, J. P. 1970. Potential production and energy conversion in temperate and tropical grasses. *Herb. Abstr.* 40: 1-5.
5. Edwards, K. J. and J.P. Cooper. 1983. The genetic control of leaf development in *Lolium.* 2. Response of selection. Heredity. 18: 307-317.
6. Horst, G.L., C.J. Nelson, and K.H. Asay, 1978. Relationship of leaf elongation to forage yield of tall fescue genotypes. *Crop Sci.* 18: 713-719.
7. Langer, R.H.M. 1963. Tillering in herbage grasses. *Herb Abst.* 33: 141-148.
8. Nelson, C.J., J.J. Volenec, K.M. Zarrough, and J.H. Coutts. 1982. *Tall fescue physiology and yield potential.* In Norbert Gaborcik (ed.) Proceedings of Symposium on tall fescue. P. 6-28. Grassld. Res. Inst., Banska Bystrica, Czechoslovakia.
9. —— and D. A. Sleper. 1981. Using leaf area expansion rate to improve yield of tall fescue XIV Int. Grassld. Cong., Lexington, Ky., U.S.A. 199p.
10. Rhodes, I. 1971. The relationship between productivity and some components of canopy structure in ryegrass (*Lolium* spp.) 4. canopy characters and their relationship with sward yield in some intropopulation selection. *J. Agric. Sci.,* Camb. 84: 345-351.
11. ——, 1973 b. Relationship between canopy structure and productivity in herbage grasses and its implication to plan breeding. *Herb. Abst.* 43: 129-133.
12. ——, 1971 b. The relationship between productivity and some components of canopy structure in ryegrass (*Lolium* spp.) 2. Yield, canopy structure and light interception. *J. Agric. Sci.*, Camb. 77: 283-292.
13. ——, 1969. The relationship between productivity and some components of the canopy structure in ryegrass (*Lolium* spp.) 1. Leaf length. *J. Agric. Sci.,* Camb. 73: 315-319.
14. Sleper, D.A., C.J. Nelson, and K.H. Asay. 1977. Dialled and path coefficient analysis of tall fescue (*Festuca arundinacea* schreb) regrowth under controlled conditions. *Can. J. Genet. Cytol.* 19: 557-564.
15. Wright, S. 1921. Correlation and causation. *J. Agric. Sci.* (Washington, D. C.) 20: 557-585.
16. Zarrough, K.M., C.J. Nelson, and D.A. Sleper. 1984. Interrelationship between

rates of leaf appearance and tillering in selected tall fescue populations. *Crop Sci.* 24: 565-569.
17. ——, ——, and J. H. Coutts. 1982. a. Relationship between tillering and forage yield of tall fescue. I. Yield. *Crop Sci.* 22: 333-337.
18. ——, ——, and ——, 1982 b. Relationship between tillering and forage yield of tall fescue. II. *Patterns of tillering. Crop Sci.* 22: 338-342.
19. ——, ——, 1980. Regrowth of genotypes of tall fescue differing in yield/ tiller. *Crop Sci.* 20: 540-544.

العلاقة بين الانتاج
ومكوناته الظاهرية في الزيوان الحولي

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المستخلص

لقد اقترحت إمكانية التحسين الوراثي لمحصول العلف في الزيوان الحولي من خلال الانتخاب للعوامل الظاهرية مثل معدل استطالة الأوراق. ولقد أجريت تجارب حقلية لدراسة العلاقة بين محصول العلف والصفات الظاهرية للنبات. ولقد تم تحديد تأثير استعمال مثل هذه الصفات على تحسين محصول العلف باستعمال دورة واحدة من الانتخاب على أساس الشكل الظاهري المحدد والمتكرر. وكان هناك ضمن النباتات ارتباط ايجابي بين وزن الفرع ومعدل استطالة الأوراق، وارتباط سالب بين وزن الفرع ومعدل التفريع.

ولقد دلّ التحليل لهذه النتائج على أن لكل من وزن الفرع ومعدل استطالة الأوراق تأثيراً مباشراً كبيراً وموجباً على وزن النبات. وكان التأثير المباشر لوزن الفرع على وزن النبات يقدر بحوالى 2.1 مرة أكبر من التأثير المباشر لعدد الفروع للنبات الواحد. ولقد أدى استعمال معدل استطالة الأوراق كدليل للانتخاب وباستعمال خطوات الانتخاب على أساس الشكل الظاهري المحدد والمتكرر الى زيادة إنتاجية هذا المحصول بحوالى 39% مقارناً بالعشيرة الأصلية في حالة الانتخاب في اتجاه معدل عال لاستطالة الأوراق.

ولقد أوضحت النتائج أن معدل استطالة الأوراق يمكن أن يكون دليل انتخاب فعال في تحسين انتاجية هذا المحصول.