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Relationship between Stomatal Frequencies, Yield Components and Morphological Characters in Collections of Winter Wheat Cultivars

J. F. LEDENT** and M. F. JOURET

Laboratoire d'Ecologie Végétale, 4, Louvain-la-Neuve*

Abstract. Genotypes on the Belgian national list as well as about 120 genotypes of winter wheat from the world collection were examined for the relationships of their stomatal frequencies in the flag leaf with yield, yield components and other morphological characters. Stomata were in rows, with a higher density in adaxial leaf surface. Cultivars differed significantly in both stomatal density and number of rows of stomata per unit of leaf width. Yield and morphological characters in general showed no significant correlation with stomatal frequencies. Densities in all series examined ranged from 46 to 78 stomata per mm^2 in the adaxial leaf epidermis and from 32 to 93 in the abaxial one.

Stomatal frequencies in wheat (*Triticum aestivum* L.) and more particularly in flag leaves have been studied by various workers.

JONES *et al.* (1975) reported total density of about 50 to 55 stomata per mm^2 for two cultivars with a greater density on the adaxial leaf surface (ratio of adaxial to abaxial surfaces was about 1.3). TEARE *et al.* (1971) indicated also more stomata on the adaxial side, but BALDY (1973) citing DE PARCEVAUX reported the contrary for various winter wheats.

The same author reported 40 to 80 stomata mm^{-2} in the *Triticum* genus and noted that differences between cultivars of the same origin were small. SHIMSHI and EPHRAT (1975) reported the same type of results for 6 cultivars of wheat. ANDELIĆ *et al.* (1970) and JANJATOVIĆ *et al.* (1972) reported total densities of 50 to 72 mm^{-2}. SAPRA *et al.* (1975) however gave much higher stomata densities with about 50 mm^{-2} in the abaxial face of the flag leaf of one winter wheat cultivar. There is therefore no general consensus about stomatal densities in the flag leaves of wheat. Moreover, many studies involve a limited number of genotypes. Thus it seemed interesting to check those results with a wide array of cultivars.

Relationships of stomatal frequencies with photosynthesis and yield are not obvious. JANJATOVIĆ *et al.* (1972) as well as TEARE *et al.* (1971) found no correlations between yield and stomata in wheat. WILSON and COOPER (1969) noted that in spite of marked variation in stomatal characteristics, differences in photosynthesis of *Lolium perenne* L. are more associated with differences in mesophyll than in stomata. According to HEICHEL (1971), photosynthetic rates and stomatal frequencies were inversely related in two

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* *Address:* Place Croix du Sud, 4, 1348, Louvain-la-Neuve, Belgium.

** Chargé de recherches FNRS.

cultivars of maize. Also in sugar cane, there was a negative correlation with photosynthesis (IRVINE 1975).

Most of those results were not obtained in wheat; moreover, only in a few cases were the relationships between stomatal densities and other morphological characters studied. (Negative correlations with flag leaf area have been reported by TANK and DUNN (1975) and MISKIN and RASMUSSON (1970) in *Bromus inermis* LEYSS and barley, respectively).

We present in this communication results obtained during two contrasting years, and with a wide array of cultivars. The relationships with grain yield and other morphological characters are examined.

Material and Methods

Measurements of stomatal frequencies were taken in 1975 (a normal year) and 1976 (a very dry year). The cultivars or genotypes examined were those already included or being tested for their release in the Belgian national list. There were 30 entries in 1975 and 43 in 1976. Of the 30 entries in 1975, 25 were among the entries appearing in 1976. Plots were 15×2 m in 1975 and 10×1.2 m in 1976. The sowing rate was 180 kg ha^{-1}. The distance between rows was 20 cm.

To obtain a wide range of variation, counting of stomata in 1975 was also taken on a series of 121 genotypes chosen at random from the world collection kept by the Plant Breeding Station of Gembloux. Plots were three row plots 0.60 m $\times$ 1 m.

Stomata were counted on flag leaf sections taken at midlength around anthesis and stored in FAA before counting. Four microscopic fields (corresponding to 0.82×0.82 mm) were counted on four leaves, on each leaf surface for the two 1975 series. In 1976, two fields were counted on eight leaves. Counting was made directly on the leaf material which was discoloured after storage in FAA. Total number of stomata, number of rows of stomata, number of veins (vascular bundles) were recorded. To assess differences between cultivar and leaf surface (adaxial and abaxial), all data were submitted to analysis of variance. Stomatal frequencies were also submitted to analysis of covariance with successively number of rows, number of vascular bundles and then both rows and bundles as covariate. Correlations were calculated between stomatal characters (frequencies, number of rows per unit of leaf width) and other morphological characters. Correlations with yield and yield component were also calculated. The morphological characters included leaf characters such as area, dry weight, leaf area duration of each of the three uppermost leaves, maximal width of each of the two uppermost leaves. Yield characters measured involved grain yield per ha, mean grain yield per culm, number of spikes m^{-2}, number of fertile spikelets, number of underdeveloped basal spikelets, mean number of grains per spikelet and mean weight per kernel.

Results

Yield and Number of Culms per ha

Grain yield per ha ranged from 5.1 to 7.4 tons in 1975 (average 6.1; $\sigma = 0.5$) and from 5.6 to 6.6 in 1976 (average 6.2; $\sigma = 0.3$). Number of spikes per square meter ranged from 362 to 534 (average 438; $\sigma = 41$) in 1975 and from 485 to 691 (average 567; $\sigma = 48$) in 1976.

TABLE 1
Distribution of stomatal densities in the flag leaf among different genotypes of winter wheat

	Stomatal density*					
	80—89.9	90—99.9	100—109.9	110—119.9	120—129.9	130—139.9
Relative number of genotypes showing that density [%]						
1. Belgian list						
1975	0**	40	50	3.3	3.3	0
1976	0	2	42	30	21	5
average 75—76	0	21	46	16.8	12.1	2.5
2. World collection						
1975	2.5	21.5	44.6	28.9	2.5	0

* Density (per mm^2); sum of adaxial and abaxial surface per leaf area.
** One cultivar (*ca.* 3.3% of the cultivars) showed a density of 77.4 in 1975.

Stomatal Densities (Frequencies)

There were differences between the two years for the genotypes in the Belgian list (Table 1). The distributions were shifted towards the right in 1976, *i.e.* there were more stomata that year. It should be noted that 1976 was an abnormally hot and dry year. The distribution of stomatal densities in the world collection is practically symmetrical. Comparison of the two 1975 series shows that most of the genotypes in the Belgian list were in the lower classes of stomatal densities. Care should be taken however as the plots from the world collection were smaller and tended to show lower plant densities.

For all the series examined, it appears that most genotypes show stomatal densities between 45 and 65/mm^2 (average of both leaf surfaces).

Analysis of variance showed that in all three series of genotypes there were significant ($P = 0.01$) differences between varieties. Moreover the density on the upper (adaxial) face was always significantly ($P = 0.01$) greater. The interaction cultivar $\times$ leaf surface was highly significant ($P = 0.01$) in the world collection. In the Belgian list, the interaction was only significant ($P = 0.05$) in 1976. Average densities for each leaf surface are presented in Table 2.

For all series, there were on an average 1.4$\times$ more stomata on the adaxial leaf surface as compared to the abaxial one. The ratio varies however between 1.24 and 1.56 in the Belgian series in 1976. It is interesting to note that the range of densities in the world collection is not wider than in the Belgian list.

Stomata in wheat are in rows which are parallel to the leaf ribs. Therefore analysis of covariance is conducted to test the differences in stomatal densities after eliminating the effect of row or vein density. Analysis of covariance gives basically the same results, indicating that the differences observed are not primarily due to differences in number of rows of stomata. It appears however that the relationship between stomatal density and either number

TABLE 2
Stomatal densities in adaxial or abaxial epidermis of the flag leaf (per mm²)

	Average density*			Maximum density		Minimum density		
1. Belgian list	Upper face	Lower face	Upper face/ /lower face	Upper face	Lower face	Upper face	Lower face	LSD**
1975	59.7	41.3	1.4	73.6	48.0	45.8	31.8	6.2
1976	65.8	47.2	1.4	78.5	51.5	58.0	39.9	5.2
2. World collection								
1975	61.5	44.1	1.4	71.3	53.5	50.4	32.2	7.4

* Average, maximum and minimum are established over all genotype in one series.
** LSD 5% comparison of means per genotype.

of veins or number of rows of stomata (per unit of leaf width) is highly significant in all series.

Although there are some shifts in the distribution of stomatal density between 1975 and 1976 in the Belgian series, there is some constancy in the results. Indeed for the 25 genotypes appearing in both years, there appears to be a highly significant ($P = 0.01$) correlation between the densities observed in 1975 and those observed in 1976. Correlation coefficients are $r = 0.740$ for the adaxial and $r = 0.795$ for the abaxial leaf surface. There are therefore consistent cultivar differences. Most of the densities observed are higher than many of those reported in the literature for wheat. It is difficult to explain the reasons for this discrepancy.

Number of Rows of Stomata

Although, as noted above, differences in stomatal densities were not basically due to differences in number of rows of stomata per unit of leaf width, there are also highly significant ($P = 0.01$) differences between varieties for the latter character in 1975 (both series) but not in 1976. There are also significantly more rows on the adaxial leaf surface than on the abaxial one. Moreover the interaction genotype $\times$ leaf surface is significant ($P = 0.05$) for both series in 1975. However, the differences between surfaces are only slight (ratio of adaxial to abaxial leaf surface between 1 and 1.1).

Correlation of Stomatal Frequencies with Yield

The correlations of stomatal densities (adaxial + abaxial epidermes) with yield are mostly negative and non-significant whether grain yield per culm or yield per ha is concerned (practically all correlations are 0.2 in absolute value).

The highest correlations with yield were in the Belgian list with $r = -0.257$ (N.S.) and $r = -0.265$ (N.S.) for the correlation with yield per ha and $r = -0.313$ (N.S.) and $r = -0.226$ (N.S.) for the correlation with culm yield (in 1975 and 1976 respectively). Correlations with yield components are most often lower. One exception occurs in the world series when

there is a significant correlation with the number of underdeveloped spikelets ($r = 0.286$ significant at $P = 0.01$ level). A second exception involves mean weight per kernel and the stomatal density on the abaxial leaf surface in the Belgian series of 1975 ($r = -0.428$ significant at $P = 0.05$ level).

Correlations between Total Density and Morphological Characters

In the Belgian list in 1976, as well as in the world collection, most correlations are again non-significant. In 1976, the only significant ($P = 0.05$) correlation involves the stomatal density and culm height ($r = -0.386$). In the world collection, there are significant ($P = 0.05$) but weak correlations with the second leaf dry weight and with the leaf area duration of the third leaf.

In the Belgian list of 1975, more significant ($P = 0.05$) relationships appear, and involve basically the first leaf: its area ($r = -0.426$) and leaf area duration ($r = -0.435$).

Moreover some correlations which are not significant when total density is considered appear to be significant when density per leaf surface is involved. Such a result was also observed by TANK and DUNN (1975) with *Bromus inermis*. Indeed the stomatal density on the abaxial epidermis is negatively related to the second and third leaf areas and dry weight as well as to the leaf area duration of the second leaf (correlations are all -0.4 after rounding off) and the correlation is significant at the $P = 0.05$ level.

In conclusion, it could be said that some significant correlations appear, but there is no consistency from year to year or from series of genotypes to other series of genotypes. No generalization is possible.

There appears to be considerable variation in stomatal densities between winter wheat genotypes. The range of variation found in the genotypes of the Belgian national list is quite similar to the range found in the entries of the world collection. There are variations from year to year, but there is constancy in the varietal differences. Stomata in winter wheat are in rows on both leaf surfaces with more stomata in the adaxial epidermis.

There are significant differences between cultivars in number of rows of stomata per unit of leaf width but those differences do not account for the differences in stomatal densities. Stomatal densities show low, non-significant negative correlations with yield. The correlations with other morphological characters are mostly loose and there is no constancy from year to year.

There is no general negative correlation between leaf area (flag leaf in this case) and stomatal density: such a correlation was observed only in one of the three series of cultivars examined.

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