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Relationships between Grain Yield and Morphological Characters in the Winter Wheat Genotypes of the Belgian National List

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Abstract. Yield per shoot and to a much lesser extend yield per unit area were related to morphological characters. The flag sheath was better related to shoot yield than were any of the three uppermost leaf laminae. Among these the areas of the two lower leaves showed a better relationship to the yield than did the flag leaf lamina. Variation in main shoot yield was associated mainly with variation in grain number. More attention should be given to morphological character related to spike development before anthesis.

Numerous studies have been conducted to study the relationship between morphological characters and yield. Typical examples are works by SIMPSON (1968), SMOČEK (1968), HSU and WALTON (1971).

It is difficult to generalize results from these types of experiments. Indeed the characters measured differ from one experiment to the other. Material and experimental conditions (fields, glasshouse) differ widely. For these reasons two series of experiments were conducted. A first series of experiments were conducted strictly on a within genotype basis, under a wide variety of experimental conditions (LEDENT 1974, 1977a).

The results were unexpectedly very consistent: grain number per spikelet was the main yield component (a result also found by HSU and WALTON 1971), second or third leave laminae and flag sheath were among the morphological characters most closely related to yield (the results concerning flag sheath correspond also to those of SIMPSON 1968, and HSU and WALTON 1971).

To check if the results reached in that first series of experiments were applicable to differences between genotypes, and therefore would have the same value in plant breeding, other series of experiments were conducted. One was conducted in small plots on genotypes chosen at random from a world collection. These results have been presented elsewhere (LEDENT 1977b).

Cultivars chosen at random from the world collection are not necessarily among those best adapted to the local conditions. Moreover the small plots used allowed only the consideration of culm yield and not yield per unit area.

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Another series of experiments was therefore conducted in bigger plots, limit ing the range of variation to the forty or so cultivars in the Belgian national list, or being tested for their inclusion in that list.

MATERIAL AND METHODS

Trials for the official testing of cultivars in the national list were used for the measurements in 1975 and 1976. In 1975 the trial was located at the Plant Breeding Station of Heverlee on sandy-loamy soil, and in 1976 it was at the Plant Breeding Station of Gembloux on loamy soil. Plots were 15×2 m in 1975 and 10×1.2 m in 1976. In both years the trial was laid out in completely randomized blocks, with four replications. There were 32 cultivars or lines in 1975 and 43 in 1976. The sowing rate was 180 kg ha^{-1}, and the nitrogen dressing was given in three parts: 20, 30, 50 kg ha^{-1} in 1975 and 42, 26, 24 in 1976 (application at sowing in early March and in late April). A complete list of the characters measured is presented in Table 1.

Yields per unit area were determined on whole plots. Dry weights, leaf areas, culm yield and culm yield components were measured on 40 shoots. Stomata were counted on flag leaf sections, taken at or about anthesis. In 1975, four fields (0.82×0.82 mm each) were counted on eight leaves. These fields were midway along the length of the flag leaf. Counting was made directly on the leaf material which was discoloured after storage in F.A.A. Leaf areas were measured with an Hayashi automatic leaf area meter.

As in the previous studies mentioned above, the complete matrix of correlations between characters was calculated and the characters ranked according to their closeness of relationship with yield (ranking according to absolute value of correlation coefficient with yield). To take into account the whole pattern of interrelationships, the whole matrix was submitted to factor analysis (method of principal components, rotations using the varimax method: DAGNELIE 1975). Multiple regressions on yield and yield components (with subsets or morphological characters as independent variables) and stepwise regressions were also calculated. Characters were ranked according to the absolute value of their coefficient of partial correlation or regression with yield.

Each of those methods has its advantages and its shortcomings. Hence their simultaneous use to analyse the results.

Choice of Morphological Characters to be Related to Yield

All the characters measured were chosen among those easily measured, which had a reasonable chance to show some relationship to grain yield per shoot (culm yield).

The choice was, of course, influenced by the results of the previous studies mentioned above. The main reasons which originally guided our choice are briefly summarized below.

It is well known that the upper leaves make the greatest contribution to grain filling (EVANS *et al.* 1975). Hence the measurements of the leaf areas of the three uppermost leaves (those which are still green and photosynthesizing at anthesis) to assess the assimilatory surface available for grain filling. The span of life of those leaves, after anthesis, *i.e.* their duration as active assimilatory organs should also influence the amount of carbohydrate available for grain filling, and the duration of the grain filling period. Therefore we have calculated coefficients such as leaf area duration (leaf area × duration), which have been shown to be related to yield (see for instance WELBANK *et al.* 1966). Specific leaf weights (ratio of leaf weight to leaf area) were included because they were shown in several cases (see for instance WILSON and COOPER 1967) to be related to photosynthetic rates.

Dry weights of leaves were measured primarily because they are more easily measured than areas. Moreover the previous studies mentioned above indicated a better relationship to yield with weight instead of areas.

Recently it has also been suggested (CHARLES-EDWARDS 1978) that leaf dry weight could be a better indicator of metabolic volume than leaf area. The flag leaf sheath makes a considerable contribution to grain filling through its photosynthetic capacity (see for instance PUCKRIDGE 1972). Some time before ear emergence the spike is completely enclosed within the sheath, which determines to some extent its environment. Moreover the sheath developing at the same time as the young spike during the weeks preceding boot stage may be sensitive to the same stress and therefore its size may be correlated with spike size. To make the difference between an effect of shoot length and therefore sheath length on sheath size and weight, the sheath thickness (see Table 1) was calculated.

Consideration of the period of ear growth preceding ear emergence or even flag leaf complete emergence has been also one of the main reasons why assimilatory surfaces of the second and third uppermost leaves have been included. Leaf width affects leaf area, but could also affect the number of bundles available for translocations or the interveinal distance.

The reason why yield components were measured is obvious as each component is determined at different times, and possibly by different physiological processes.

RESULTS AND DISCUSSION

Due to the amount of original data only a brief summary may be presented. Means over both years are presented for some of the most typical characters in Table 2. Results for only the genotypes present in both years (15) are given. It should be noticed that the range of yields observed in the complete data is wider than the range found in Table 1 (5092—7400 kg ha^{-1} in 1975 and 5631—7718 kg ha^{-1} in 1976).

Simple Correlations with Yield

1) Yield in grain per ear. Significant correlation coefficients ($P = 0.05$) with yield are presented in Table 1.

Except for the well known negative relationship between density (number of spikes/m^{-2}) and yield of grain per ear, grain number showed the closest relationship to yield per ear, as found in other studies (LEDENT 1974, 1977a, 1977b). In 1975, the number of kernels per spikelets ranked next, well before the number of spikelets per ear. In 1976, both characters showed practically the same rank. In both years mean weight per kernel ranked far behind. Among the vegetative characters, the flag sheath (G_1 and to a lesser extent DG or G_1L; Table 1) were particularly well ranked, as in the within-genotypes studies mentioned in the introduction.

Contrary to the results of studies with the world collection (LEDENT 1977b),

TABLE 1
Characters studied and correlations with yield

	Characters studied	Correlations[1] with yield per ear		Correlations[1] with yield/m^2	
	Components	1975	1976	1975	1976
GN	Grain number per ear	0.822(1[3])	0.766(2)	0.532(1)	—
N	Number of spikes/m^2	−0.644(2)	−0.835(1)	—	—
NEp_1	Number of fertile spikelets	0.450(8)	0.601(4)	—	—
GNEp	Mean number of kernels per spikelet	0.519(3)	0.590(5)	0.403(3)	—
G_1W	Mean dry weight per kernel	—	0.308(16)	—	—
	Leaf characters[2]				
	Leaf area A_2	—	0.523(7)	—	—
	Leaf dry weight L_2	0.504(5)	0.512(8)	—	—
	L_3	0.460(7)	0.346(14)	—	—
	Maximal width W_1	—	0.509(9)	—	—
	W_2	—	0.452(11)	—	—
	Leaf area duration				
	LAD_2	—	0.322(15)	—	—
	LAD_3	—	0.404(12)	−0.372(4)	—
	$LAD_{1,2,3}$	—	0.302(17)	—	—
	Specific leaf weight				
	SLW_2	0.419(10)	0.458(10)	—	—
	SLW_3	0.425(9)	—	—	—
	Stomatal frequency × leaf area (flag leaf)	—	—	−0.502(2)	—
	Other vegetative characters				
G_1	flag sheath dry weight	0.518(4)	0.648(3)	—	—
G_1L	flag sheath length	0.463(6)	0.388(13)	—	—
DG	sheath thickness (G_1/G_1L)	0.381(11)	0.580(6)	—	—

[1] Only coefficients statistically significant ($P = 0.05$) are presented. Degrees of freedom 1975 : 30; 1976 : 41.
[2] Flag, second and third uppermost laminae indicated by subscripts 1, 2, 3; three subscripts indicate a summation over leaves. Although leaf characters were measured for each of these leaves, only those showing significant relationships ($P = 0.05$) to yield are presented.
[3] Rank according to absolute value of correlation coefficient (in parentheses).

leaf area durations ranked very poorly. The relationship of area durations to yield of grain per ear were not significant in 1975. Similarly, however, the second and third uppermost leaves were better related to culm yield than the flag leaf. This holds also true for the leaf dry weights or the specific leaf weights, which were better ranked than the flag leaf area itself, a result also found in the study on the world collection.

Table 2

Means over 1975 and 1976 of several morphological characters for genotypes included in both years trials

Genotype	Yield ha [kg]	Yield ear [g]	L_1 [g]	L_2	L_3	G_1	A_1 [cm^2]	A_2	A_3	W_1 [cm]	d_1^+ [days]	G_1W [mg]	GNEp
1	6078	1.49	118	122	84	171	26.0	30.3	24.8	1.61	33	41.3	2.19
2	6053	1.70	114	119	90	184	23.7	29.6	25.8	1.60	33	43.6	2.24
3	5919	1.48	100	103	78	166	21.6	25.8	22.4	1.60	35	34.9	2.21
4	6075	1.86	101	124	98	198	22.3	28.1	25.8	1.52	32	41.4	2.30
5	6429	1.27	91	86	64	124	20.5	24.1	20.0	1.43	36	33.6	2.22
6	6128	1.61	114	116	89	200	24.3	29.0	24.9	1.49	32	38.1	2.42
7	6339	1.77	121	119	84	210	23.3	26.5	21.4	1.56	36	36.7	2.52
8	5865	1.46	114	122	84	178	22.7	28.0	22.3	1.64	34	41.1	2.12
9	6240	1.82	136	131	99	200	29.4	29.4	27.8	1.66	33	44.2	2.48
10	6325	1.84	116	123	93	190	24.6	29.5	25.4	1.80	35	40.7	2.46
11	5884	1.48	107	108	78	146	22.1	27.6	22.4	1.38	36	36.6	2.44
12	6671	1.78	128	122	89	178	26.2	29.8	24.2	1.52	34	43.7	2.46
13	6740	2.02	112	122	90	195	22.8	28.1	24.2	1.81	32	37.8	3.06
14	6518	1.53	110	130	100	193	22.2	30.3	25.1	1.63	34	39.2	2.25
15	6565	1.78	136	124	86	192	27.2	28.7	21.6	1.80	35	40.6	2.37

+ : d_1 , duration of flag leaf after anthesis (time between anthesis and flag leaf senescence); for other symbols see Table 1. Areas and weight are expressed on per culm basis.

2) Yield per unit area. In general correlations with yield per unit area were much weaker than with culm yield. They were also more variable from year to year (Table 1). In 1975 the number of kernels per spike dominated, but in 1976, leaf area durations did.

In both years the leaf area durations of the second and third leaves were better correlated with yield than that of the flag leaf. The sign of the relationship varied from year to year however and no general conclusion can be drawn. The same holds true for the yield components: the component most significantly related to yield in 1975 was grain number but in 1976 it was mean grain weight (G_1W).

Factor Analysis

Factor analysis is a way to determine the main common trends of variations (the factors) appearing for instance in a correlation matrix. The loadings of the morphological characters in the various factors indicate the closeness of their relationship with the factors. Thus factors with high loading on yield indicate trends of variations corresponding to variations in yield. Ranking of morphological characters according to the absolute value of their loading in a yield factor may indicate their relative importance for yield. In factor analysis such rankings are obtained from the whole correlations matrix; therefore the whole pattern of interrelationships between characters is taken into account. This is not the case with the other methods

TABLE 3
Loading of yield in first four factors

Year	Factor			
1975	1	2	3	4
yield/m^2	0.197	−0.215	−0.665	−0.228
yield per ear	−0.098	−0.070	−0.797	−0.169
1976				
yield/m^2	0.286	0.045	−0.286	0.106
yield per ear	0.294	−0.897	−0.083	0.051

In 1975 two factors (factors 3 and 6) showed high loadings for yield per ear (culm yield) and therefore may be described as culm yield factors. One of those factors (factor 3) appears at the same time to be a yield per unit area factor. In 1976 there was only one culm yield factor. No factor could

TABLE 4
Yield factors extracted from the correlation matrix

	Loadings		
	Year		
	1975		1976
	Factor n°		
Characters studied[1]	3	6	2
1) Yield, yield components and ear characters			
Yield/m^2	−0.665 4[2]	—	—
Yield per ear	−0.797 2	0.421 7	−0.897 2
GN	−0.954 1	—	−0.953 1
N	—	—	−0.780 3
NEp_1	—	—	−0.646 7
GNEp	−0.715 3	—	−0.706 6
G_1W	—	0.620 4	—
2) Leaf characters			
A_2	—	0.366 9	—
L_1	—	0.390 8	—
L_2	—	0.748 2	−0.372 11
L_3	—	0.604 5	—
W_1	−0.381 5	—	−0.456 9
W_2	—	—	−0.403 10
SLW_2	—	—	−0.513 8
3) Other vegetative characters			
G_1	—	0.781 1	−0.728 5
G_1L	—	0.633 3	—
DG	—	0.511 6	−0.739 4

[1] Only characters with loadings ≥ 0.36 (in absolute value) are presented; see Table 1 for symbols.
[2] The second number is the rank (according to absolute value of loading).

be recognized as yield per unit area factor. The loadings of yield in the four first factors are given in Table 3. The loadings (ranked by absolute value) in the yield factors (factors 3 and 6 in 1975, and factor 2 in 1976) are given in Table 4.

Consideration of these indicates the importance of grain number, sheath characters and dry weights of the lower of the uppermost leaves for culm yield. We reach the same conclusion as in the correlation studies.

Other factors were less typical and more variable. They will not be discussed in detail. We will only note the existence in both years of leaf area factors, and of one stomata factor. Those showed low loading for all other morphological characters.

Regression Analysis

Multiple regressions or stepwise regressions did not add any further information, therefore they will not be discussed in detail. When culm yield was related to the areas of each of the three upper leaves, only the third one showed a significant relationship to yield in 1976; in 1975, the relationships were not significant, but the second leaf was better related to yield per ear than the other leaves (partial correlation and partial regression coefficients, in absolute value, were greater).

When the dry weights of the flag sheath and of each of those leaves are the independent variables in the equations, only the sheath was significantly related with culm yield *etc.* . . . In 1976, the relationships were generally not significant, but as in 1975, the sheath was better related to culm yield than any other characters. In both years the relationship between culm yield and the flag leaf was negative. In stepwise regression only one or two characters were usually selected by the process (level of entrance in the equation $P = 0.05$). When yield components are included as potential independent variables, no vegetative character is selected.

Despite some differences between 1975 and 1976, there are also common trends. Only the latter will be discussed. It is likely that most of the differences are due to the exceptionally dry and hot weather in 1976.

Although statistical analyses do not necessarily show cause to effect relationships, the trends indicate that at least in some cases the importance of the flag leaf in determining differences in culm yield (yield per shoot) may have been overemphasized. Experiments with defoliation treatments seem to confirm this point of view (LEDENT 1977c). Here the main culm yield component appeared to be grain number (a result also found by HSU and WALTON 1971). This component is determined to a great extent during the period of spike development preceding ear emergence and even flag leaf emergence. Thus the poor relationship between flag leaf and culm yield can be explained. The results indicate that in our conditions grain filling and the plant parts responsible for it do not account for much of the differences in culm yield. Despite minor differences we reach the same conclusions as in the world collection studies (LEDENT 1977b) or the within variety studies (LEDENT 1974, 1977a). WILLIAMS and HAYES (1977) working on barley also found similar results. The relationship between the different plant parts during the period of spike development preceding ear emergence seems more likely to account for the relationships observed. A study of those should yield more valuable information to the plant breeder than just the consideration of characters related to grain filling, as suggested by LUPTON (1973).

Results indicating a close relationship of yield per ear with the flag sheath might also be interpreted in the same manner. The flag sheath indeed develops after the corresponding lamina, during the period of rapid spike development, preceding ear emergence. In within genotypes studies, it can be verified that ear size at anthesis is more closely related to the flag sheath size than to the flag leaf lamina (LEDENT, in preparation).

Yield per unit area was much less closely related to morphological characters than yield per ear. The results obtained were much less consistent and no clear conclusions could be drawn.

It is clear that the results reported here apply to variations of yield within year and location. This type of results would not necessarily apply to variations of yields from year to year or from location to location. Moreover the results were obtained in relatively good conditions: plots with normal density, healthy crops, with grain yields of 5 to 6 tons of dry grains/ha.

The experiments were also conducted for only two years. However the drastic differences between 1975 and 1976 (the latter year was abnormally hot and dry) confers some generality to the results. So does the similarity of the results reported here to those of the first series of experiments mentioned in the introduction.

It is beyond the scope of this particular study to infer what possible application these results might have with respect to breeding or agrotechnical treatments. It seems clear however that any treatment favorably influencing plant growth during the preanthesis period when spike size, grain number, size of the penultimate or antepenultimate leaf are determined, should improve yield. This period corresponds roughly to the period of rapid stem elongation, which is definitely a critical period for grain yield during which any stress should be avoided. Avoidance of water stress or mineral nutrient stress (the latter for instance by split nitrogen dressing with a high fraction at the beginning of rapid stem elongation) is certainly important. As far as plant breeding is concerned, a better knowledge of the behaviour of different genotypes during that period would be highly valuable. Moreover when simple characters possibly related to yield are considered to characterize genotypes, considerations of dry weight or width seem better than areas, and flag sheath or second or third uppermost leaf lamina better than flag leaf lamina.

The importance of plant morphology for understanding physiology of yield seems to be related more to the physiology of spike development and growth before anthesis during the period of rapid stem elongation than to the physiology of grain filling.

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