Analysis of growth, development and yield in a spacing experiment with winter rye *(Secale cereale* L.*)*

J. BRUINSMA

Plant Physiological Research Centre, Wageningen, The Netherlands

Summary

From an experiment with Petkus winter rye sown at seven seed rates from 5 to 180 kg/ha, the following results were obtained.

- Crop analysis facilitated the interpretation of yield analysis, both by supplying information on factors occurring during the vegetation period and by indicating the nature of the relationship with the main factor under study.
- Crop analysis can be confined to the countings of plants at tillering, of ears during heading (also to establish developmental differences), and of florets per ear after anthesis; and to determinations of either dry weight or of nitrogen or chlorophyll contents per unit soil area, per plant or per organ.
- Tillering was able to compensate for lower plant densities until 1.5 dm^2 space per plant, i.e. 6 cm distance in the row or a seed rate of about 60 kg per ha.
- At decreasing seed rates the rate of development decreased, while the number of florets per ear, the fertility of the florets, and the rate and duration of grain filling increased.
- It was indicated that the number of florets per ear, their fertility, and grain filling, depended on the nutritive conditions during tillering and shooting, about anthesis, and during ripening, respectively.
- Close correlations occurred between the amount of nitrogen and of chlorophyll in the aerial parts, on the one hand, and the logarithm of plant or culm space, on the other hand, indicating that the relative space per plant or per culm rather than the absolute space per plant or per culm was the determining factor.
- Grain weight and total weight per culm, too, increased proportional to the logarithm of culm space and, hence, yield per unit area showed an optimum value at a culm density af about 2.7 × 10^6 culms per ha. This culm density was obtained at seed rates from 60 to 100 kg per ha.
- Dry matter distribution in the culms was largely independent of the size and the nutritive condition of the culms, grain weight always being about 30 % of total weight.

1. Introduction

In experiments on breeding and husbandry of cereal crops, analyses are frequently being made of the yield into its components of number of plants per unit area, number of ears per plant, and number and weight of grains per ear (ENGLEDOW, 1925; BROEKEMA, 1933; COÏC, 1959; NØRGAARD HOLM and PEDERSEN, 1962; WILSON and SWANSON, 1962). The limitation of this type of analysis is that the yield components themselves are the ultimate results of underlying growth and developmental processes falling out of the field of view, so that causal connections between the yield and

Received for publication: November 24, 1965.

factors occurring during the vegetation period may remain obscure. An analysis of growth and development may, therefore, substantially contribute to the comprehensibility and applicability of the yield analysis.

The value of such a crop analysis is estimated in this paper by attempting to relate the structure of the yield to the growth and development of a crop of winter rye in a spacing experiment. Although this experiment was originally initiated for another purpose (BRUINSMA, 1962), the wide range of its seed rates, from 5 to 180 kg per ha, renders it highly suitable for an analysis of the effects of plant and culm densities through the growth and development of the crop on the ultimate composition of the yield.

2. Methods

The experiment was laid out on a humous sandy soil with eight replicates per seed rate, the size of the individual plots was 9.5 × 4 m^2. After deduction of a margin of 0.5 m and a strip of 3 × 1 m^2 for crop analysis, a net yield area of 7 × 3 m^2 was left.

Petkus winter rye was sown with a row drill at 25 cm, adjusted to 180 kg/ha. The lower seed rates, 140, 100, 60, 30, 15, and 5 kg/ha, were obtained by thoroughly mixing the viable seed with known amounts of seed, previously steamed for 1 h at 120 °C and next dried back to its original weight. The homogeneity of the seed mixtures was checked by germination tests prior to sowing.

At the end of the winter, the plots were individually fertilized with 60 kg N/ha, while 100 kg P/ha and 140 kg K/ha were given over all. After removal of weeds by hand on 3rd May, the plots remained practically weed-free, even at the lowest seed rates. During ripening there was some hanging of the culms at the three highest seed rates but lodging did not occur up to harvest, on 9th August.

In the course of the vegetation period plant density, tillering and ear density were determined and samples were collected for the measurement of the development of the ear primordium (BRUINSMA and SWART, 1962) and for the periodic determination of fresh and dry weight production, total nitrogen uptake and chlorophyll content (BRUINSMA, 1963, 1965). Heading, anthesis, and ripening were followed by frequent determinations of percentages of visible ears and of flowering ears, and fresh and dry weights of samples of developing seeds, respectively.

One week after the dry weight of the grains had reached a constant level, five rows each of 1 m were gathered per plot for the yield analysis, except at the two lowest seed rates (5 and 15 kg/ha), the whole net yield areas of which served for this purpose. All the ears were counted, and the numbers of grains of 10 ears per plot and the weights of 5 samples of 100 grains each per plot were determined.

The net yield areas were cut, weighed and threshed per plot, the difference between sheaf and grain weights per plot being taken as a measure for gross straw yield. Grain and straw yields were afterwards corrected for the weights of the yield analysis samples.

3. Results

3.1. Growth and development

Plant density was proportional to the seed rate, 70 % of the viable seed having pro-

Table 1. Relations between seed rate, plant density, tillering, and culm production

Seed rate (kg/ha)	*Plant density (10^6/ha)*	*Plant space (dm^2/plant)*	*Lateral shoots per plant (17th March)*	*Culms per plant (harvest)*	*Culm space (cm^2/culm)*
5	0.131	7.63	3.6	8.97	85
15	0.356	2.81	3.8	4.89	57
30	0.713	1.40	3.8	3.05	46
60	1.35	0.741	3.4	1.89	39
100	2.35	0.425	2.9	1.16	37
140	3.23	0.310	2.3	1.02	30
180	4.08	0.245	2.0	0.97	25

duced an established plant at the end of the winter (Table 1). A similar percentage was mentioned by DOUGHTY and ENGLEDOW (1928) who stated that after winter the plant density remains constant. Table 1 further shows that at plant densities below an average plant space of about 1 dm², that is 4 cm in the row, the rate of tillering was reduced. At these higher seed rates only part of the lateral shoots, present on 17th March, succeeded in developing into a fertile culm. Practically no culms of the second order were formed at the two highest seed rates. At the two lowest seed rates, on the contrary, many tillers formed after the counting date, 17th March, must still have contributed to the ultimate culm density as appears from the numbers of culms per plant at harvest. Fig. 1 demonstrates that the ultimate number of culms per plant is proportional to the average space per plant at the higher seed rates and, as a result, ear density tended to level out (see also Fig. 5 A). At the two lowest seed rates, however, tillering could no longer fully compensate for the decrease in plant density.

The rate of leaf emergence on the main axis was hardly affected by the plant density. Mostly, 11 or 12 leaves were formed per culm, although above 100 kg/ha the percentage of culms with 12 leaves decreased in favour of those with 11 leaves (Table 2). This small decrease in leaf production may well be connected with an accelerated development of the ear primordium of more than one standard day unit on 29th March at these higher seed rates. Lack of space, nutrients or water (HUDSON, 1941 a) could have induced an earlier transition into the reproductive phase. Accord-

Table 2. Development of leaves and ear primordium on the main axis. Averages from countings of leaves of 50 plants per treatment, by ringing of their 4th, afterwards their 8th leaf; and from determinations of about 70 ear primordia per treatment, after Bruinsma and Swart (1962)

Seed rate (kg/ha)	*Number of leaves on culms of 1st order*	*Developmental stage of ear primordia on 29th March (standard day units)*
5	11.76	24.8
15	11.52	24.8
30	11.67	24.8
60	11.78	25.6
100	11.61	26.1
140	11.25	26.6
180	11.26	26.3

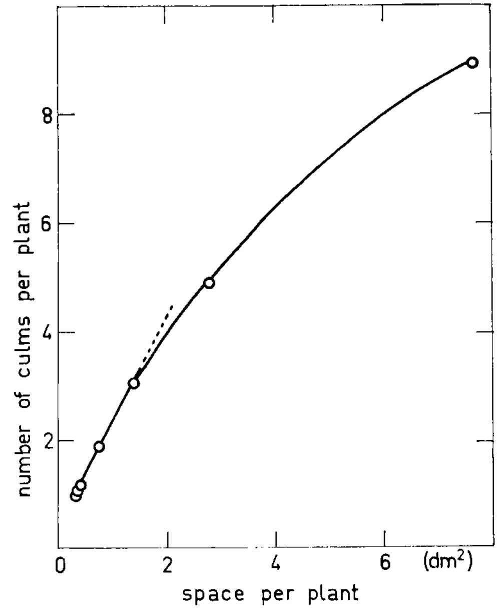

Fig. 1. Relation between average number of culms per plant and space per plant.

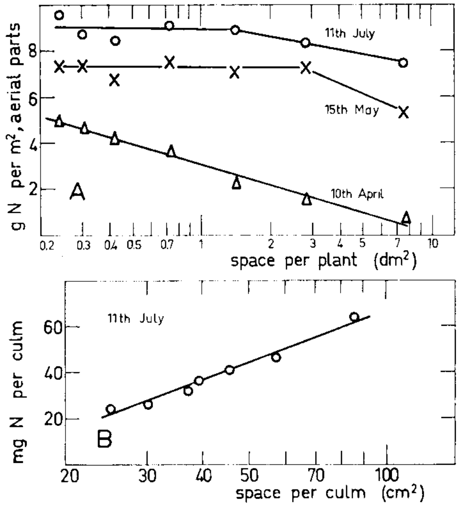

Fig. 2. The nitrogen content of aerial parts. Averages from determinations on eight samples of 0.5 m^2 aerial parts. A. N in aerial parts (per m^2) on 10th April, 15th May and 11th July. B. N per culm on 11th July.

ingly, marked differences were also observed in the rates of heading, as will be seen below (Fig. 3).

The nutritive condition at the different seed rates is also reflected in the dry weights and nitrogen contents of the aerial parts (Table 3). Before the leaf canopy closed the dry matter production per unit area considerably lagged behind at the lower seed rates and, below 60 kg/ha, it remained at a lower level although the differences diminished in the course of the vegetation period.

In the dry matter content two opposite tendencies could be distinguished. At the first sampling date, 10th April, the dry matter percentage was highest at the lowest seed rate and gradually dropped with increasing plant density. This may be due to the more abundant nutritive conditions prevailing at the lower seed rates as is also indicated by the higher nitrogen content data. However, at the later sampling dates the dry matter percentage varied in the reverse direction, the higher values showing up at the higher seed rates. This is a reflection of differences in developmental rates, the plants at the lower seed rates developing slower and, therefore, remained at lower dry matter values. The rapid increase of the dry matter content in the course of the vegetation period appears from the rise of the average values at the four sampling dates.

The higher nitrogen contents at the lower seed rates also point to a slower developmental rate, since the nitrogen content decreased in the course of the vegetation period. Fig. 2A shows that at the end of the tillering stage, on 10th April, the spacious growing plants at the lower seed rates absorbed less nitrogen per square meter from the soil, and that the more densily the plants grew and, therefore, penetrated the soil with their roots, the more nitrogen was found in their aerial parts per square meter. The logarithmic nature of the relationship will be discussed below. In the course of the development these differences tended to fade since considerable amounts of nitrogen were still taken up in the shooting stage at the lower seed rates. This is shown by the data of 15th May. Although an arrear remained up to the ripening stage, in July, because of the lower culm densities the amounts of nitrogen per culm were higher the lower the seed rate. In fact, as is shown in Fig. 2B, a logarithmic relationship existed again, at that time, between the amount of nitrogen per culm and the average soil area per culm.

Accordingly, the culms developed more abundantly at the lower culm densities. They were heavier, though not longer, and formed larger and broader leaves. As an example, weights of penultimate leaf blades are summarized in Table 4. At the lowest seed rate the amount of chlorophyll was about twice that at the highest seed rate. This is mainly due to the higher leaf weight, but next to that also to a somewhat larger chlorophyll content. This difference in foliage colour could be observed throughout the vegetation period and became even more pronounced during ripening, as will be seen below (Table 6).

Heading took place in the course of May. The delay in ear emergence at the lower seed rates, mentioned before, is shown in Fig. 3. As a modified time axis, the hourly measured temperatures over 0 °C were added from the beginning of the heading period until its completion. The culms at 180, 140, and 100 kg/ha headed simultaneously and started very early already, apparently within the minimum time required for ear emergence. At the lower seed rates heading occurred later, the more so as the spacing was wider: at 50 % heading with the high seed rates, less than 20 % had only emerged at 15 and 5 kg/ha. This is a matter of a general delay in ear emergence at the lower seed rates rather than a reflection of any irregular heading owing to the numerous culms of high order at these seed rates, because the heading process at these seed rates is completed within a shorter period of time. With an average hourly temperature of 11.7 °C, during the heading period, the delay in heading with e.g. 5 kg/ha was 193 standard hours at 20 % heading, 165 hours at 50 %, and only 140 hours at 80 % emergence. Hence, the later start cannot be ascribed to irregularities of dis-

Table 3. Dry matter production and nitrogen content of aerial parts. Average values of 8 determinations on 2 m rows of plants each. Developmental stages: 10th April, beginning of shooting; 15th May: heading; 14th June: end of flowering; 11th July: milk-ripe grains

Seed rate (kg/ha)	*Dry weight (g/m² area)*				*Dry matter content (% fresh weight)*				*N content (% dry weight)*			
	10th April	*15th May*	*14th June*	*11th July*	*10th April*	*15th May*	*14th June*	*11th July*	*10th April*	*15th May*	*14th June*	*11th July*
5	12	263	732	885	16.7	16.8	29.0	37.8	4.9	2.0	0.89	0.85
15	32	516	908	1,095	15.9	17.5	31.1	38.2	4.7	1.4	0.71	0.76
30	51	566	914	1,201	15.8	17.9	32.0	38.8	4.4	1.2	0.66	0.74
60	91	658	1,055	1,254	14.9	18.6	33.0	39.0	4.0	1.2	0.66	0.73
100	119	651	907	1,198	14.4	19.7	33.1	39.4	3.7	1.0	0.63	0.71
140	141	712	1,028	1,211	14.4	19.3	32.5	39.2	3.7	1.0	0.63	0.73
180	136	728	984	1,284	14.9	20.0	32.2	39.1	3.5	1.0	0.66	0.74
			Average value		*15.2*	*18.5*	*31.8*	*38.7*	*4.1*	*1.2*	*0.69*	*0.75*

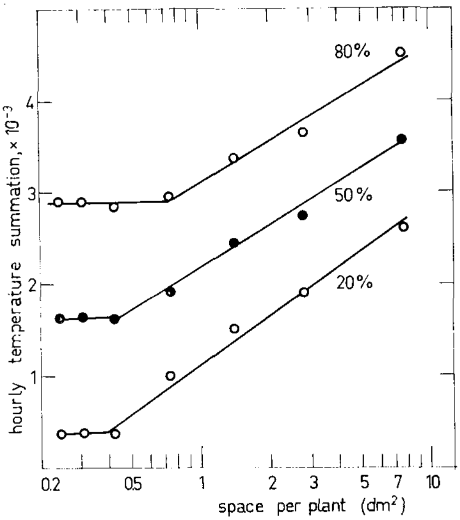

Fig. 3. Rates of heading at different seed rates. The heat sum over 0 °C from 5th May, 1 p.m., is given for 20, 50 and 80 % of emerged ears, obtained by interpolations from daily countings until complete emergence.

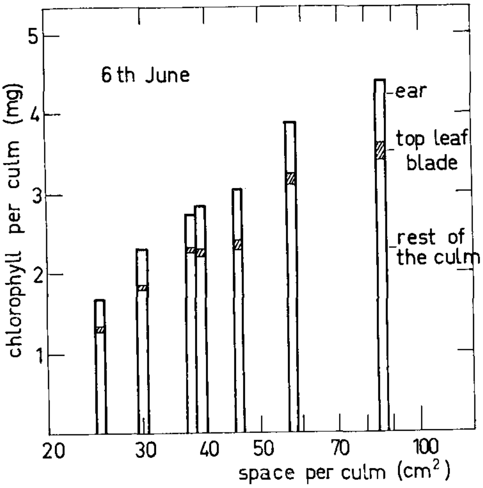

Fig. 4. Chlorophyll content of culms at the end of anthesis. Averages from duplicate determinations of ears, top leaf blades, and remainder, of 40 culms per sample.

Table 4. Weight and chlorophyll content of the penultimate leaf blade. Mean values of two determinations on 30 blades, sampled on 28th April

Seed rate (kg/ha)	*Fresh weight (mg/leaf)*	*mg chlorophyll*	
		per leaf	*per g fresh weight*
5	702	1.43	2.04
15	676	1.34	1.98
30	667	1.27	1.90
60	538	0.98	1.82
100	448	0.82	1.83
140	425	0.76	1.78
180	379	0.67	1.77

Table 5. The course of anthesis. Mean values of eight estimations each

Seed rate (kg/ha)	*Percentage of flowering ears*			
	29th May	*1st June*	*5th June*	*9th June*
5	0	12	62	98
15	6	28	88	100
30	12	42	90	100
60	46	74	100	—
100	58	86	100	—
140	72	92	100	—
180	68	94	100	—

similar culms but is a symptom of the delayed development because of the ampler nutritive conditions.

Although anthesis is always more weather-dependent and, therefore, had to be estimated rather roughly, it showed a similar retardation as observed with ear emergence. The more space available per culm the later anthesis occurred (Table 5). The culm populations at the lower seed rates consisted predominantly of culms of higher order but, nevertheless, their ears were considerably larger, on an average, than those of the monocultures of primary culms at the higher seed rates. Average spikelet numbers per ear increased from 30 at 180 kg/ha up to 38 at 5 kg/ha (cf. Table 8).

Shortly after anthesis, when starch accumulation in the seeds was about to start, the chlorophyll content of the culms was determined again (Fig. 4). The chlorophyll contents of the ear, the top leaf blade, and the remainder of the culm — mainly the upper four leaf sheaths — increased about proportional with the logarithm of culm space from 1.7 mg per culm at 180 kg/ha to 4.4 mg at 5 kg/ha. In so far as the amount of chlorophyll of a plant organ is related to its photosynthetic capacity (cf. BROUGHAM, 1960; BRUINSMA, 1965), these data point to considerable differences in dry matter production at the outset of grain filling. In the course of ripening, these differences only became more and more pronounced because yellowing was delayed at the lower seed rates.

This is shown in Table 6 for the later stage of ripening in which the upper internode was the only part of the culm left green. The table demonstrates that chlorophyll breakdown occurred more rapidly as the culms stood more densily. At the lower seed rates, therefore, grain filling could be expected to proceed not only at a higher speed but also during a longer period of time.

Table 6. The chlorophyll content during ripening. Duplicate determinations of 80 upper internodes per treatment

Seed rate (kg/ha)	*mg chlorophyll per internode*	
	11th July	*20th July*
5	1.37	0.50
15	0.75	0.27
30	0.52	0.15
60	0.39	0.09
100	0.36	0.07
140	0.27	0.08
180	0.26	0.06

This was found, indeed, from weekly determinations of the dry weight of seeds in the course of ripening, summarized in Table 7. It can be seen that, at the lower seed rates, after an initial arrear because of the delayed anthesis, dry matter accumulation was both accelerated and prolonged in comparison with the higher seed rates. Hence, at harvest the dry weight of the grains was found to be highest at the lowest seed rate and gradually dropped as the seed rate increased.

Notwithstanding the higher dry weight of the grains at the lower seed rates, ripening remained delayed up to harvest. Table 7 shows that the drying out of the grains proceeded slower as the seed rate was lower. At 5 kg/ha the dry matter percentage

Table 7. The course of the filling and the ripening of the grains. Average values from determinations on eight samples of seeds from ten ears each

Seed rate (kg/ha)	*Dry weight of 100 grains (in g). In brackets the dry matter percentage of the grains*				
	5th July	*13th July*	*20th July*	*27th July*	*2nd August*
5	2.5 (*39*)	3.3 (*46*)	4.0 (*50*)	4.8 (*55*)	4.8 (*68*)
15	2.8 (*42*)	3.5 (*47*)	4.3 (*52*)	4.5 (*58*)	4.5 (*73*)
30	2.8 (*43*)	3.5 (*49*)	3.9 (*53*)	4.1 (*61*)	4.3 (*79*)
60	2.8 (*44*)	3.6 (*51*)	4.0 (*54*)	4.1 (*61*)	4.0 (*80*)
100	2.9 (*45*)	3.5 (*51*)	3.9 (*54*)	4.0 (*63*)	3.9 (*80*)
140	2.9 (*46*)	3.5 (*52*)	3.7 (*54*)	3.8 (*67*)	3.8 (*79*)
180	2.8 (*46*)	3.4 (*52*)	3.7 (*54*)	3.7 (*66*)	3.8 (*79*)

Table 8. Numbers of florets and grains per ear. The numbers of florets are mean values from 100 ears per seed rate, counted on 20th June; the percentages of fertilization were calculated from these data and from the numbers of grains per ear in the yield samples

Seed rate (kg/ha)	*Number of florets per ear*	*Percentage of fertile florets*	*Number of grains per ear*
5	76	74	56
15	72	72	52
30	72	66	48
60	68	65	44
100	65	63	41
140	63	58	36
180	59	51	30

lagged a week behind that at the highest seed rates, and even at harvest there was a definitely higher water content. ENGLEDOW (1925) found a delay of 8 days at very low seed rates.

The culms at the lower seed rates not only produced more dry weight per grain, they also had to fill more grains per ear. It can be seen from Table 8 that the number of florets per ear increased with space per ear. Moreover the percentage of fertilization of these florets increased in much the same manner, from about half to three quarters of all florets present at anthesis. As a result, the ultimate numbers of grains per ear ranged from 30 with narrow-spaced ears to nearly twice this number at 5 kg/ha.

3.2. Yield and its achievement

According to the formulation of ENGLEDOW (1925), yield:

$$y = peng$$

in which p = plant number per unit area, e = ear number per plant, n = number of grains per ear, and g = grain weight. For the present experiment this yield analysis is given in Fig. 5.

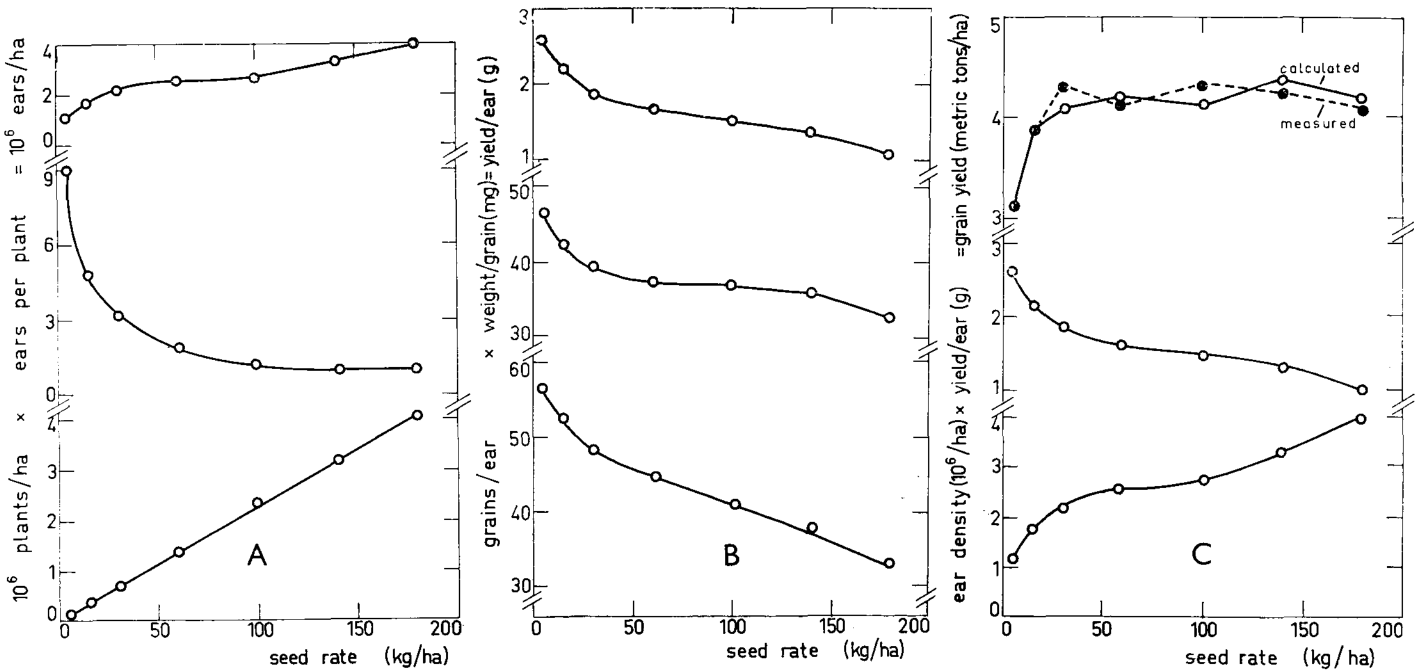

Fig. 5. Ear density = plant number per unit area × ear number per plant (A); yield per ear = grain number per ear × weight per grain (B); grain yield = ear density × yield per ear (C).

At increasing plant density the number of ears per plant sharply dropped so that ear density shifted only gradually towards a level between 2 and 3 millions of ears per ha at moderate seed rates (Fig. 5 A). The plants had then formed 1–2 ears. At the highest seed rates, 140 and 180 kg/ha, plant density continued to increase lineally and, because each plant tended to produce at least one ear, ear density too increased proportionally again giving the impression that some optimum level is broken through.

At increasing seed rates both the number of grains per ear and the weight per grain decreased and, hence, grain yield per ear fell off (Fig. 5 B). A rather constant grain weight appears to be obtained at moderate seed rates but, again, at the two highest seed rates this level was passed and grain weight dropped below it.

Since ear density and grain yield per ear rather reflect each other because of mutual compensation, their multiplication into the yield per unit area gives a curve running about horizontally (Fig. 5 C). Except for the two lowest seed rates, where tillering was unable to compensate for the low plant density, a rather constant grain yield was obtained. The yield data calculated from the samples for yield analysis (open dots) reasonably agree with the yields actually obtained from the net yield areas (black dots), so that the analysis given above can fairly be relied upon. This picture of a yield analysis in a spacing experiment is the one generally found (e.g. Nørgaard Holm and Pedersen, 1962; Wilson and Swanson, 1962).

Gross straw and total yields are shown in Fig. 6. Again, at the two lowest seed rates tillering failed to make up for the wider plant stand. There appears to be an optimum with the heavy culms at the moderate seed rates, the yield tending to decrease with the lighter culms at the highest densities, but because of the deviation at 60 kg/ha this tendency is not significant.

It will now be considered as to how far the data obtained from the crop analysis

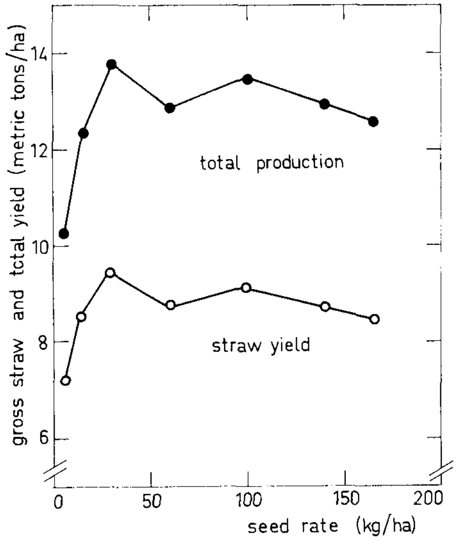

Fig. 6. Gross straw yield and total production of aerial parts.

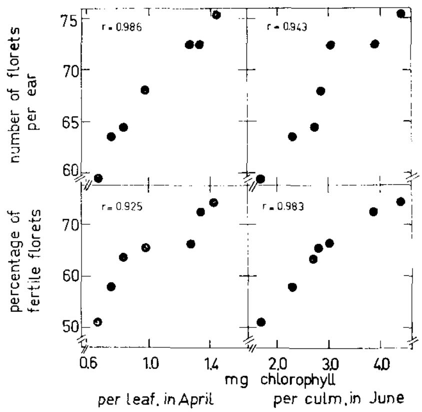

Fig. 7. Relation between, on the one hand, floret number per ear and fertility of florets and, on the other hand, chlorophyll contents in April and June.

can be used for a further comprehension of the yield analysis, i.e. how the yield can be understood as the final result of the growth and development of the crop.

Most of the data on growth and development turn out to be closely correlated already. For instance, the amount of chlorophyll per plant, per culm, or per leaf, nicely corresponds with the amount of nitrogen taken up at that time, the correlation coefficient, *r*, mostly being about 0.97. The nitrogen uptake at any time, in turn, is correlated with the logarithm of plant or culm space and, these entities being constant throughout the vegetation period, data from different sampling dates are also correlated. This existence of a systematic set of growth and development data, on the one hand, restricts the reduction of yield data to them and, thereby, limits their value for the present approach. On the other hand, these spurious correlations enable the crop analysis to be confined to only a few of all the factors determined in the present experiment, which will be discussed below.

Yet, although no significant differences in correlation coefficients occurred, a value of $r = 0.98$ reflects a much nicer graphical correspondence than a value of, e.g., $r = 0.92$. In Fig. 7, for example, the number of florets per ear corresponds better with the chlorophyll content in April than with that in June, whereas the reverse holds for the fertility of these florets. This agrees with the expectation that the floret number is determined during tillering and shooting, and the transition into a grain about anthesis. Likewise, the weight per grain agrees best with crop analysis data from July, during ripening, of which Fig. 8 is an example.

These three factors composing yield per ear: number of florets, floret fertility and grain filling, all increase at decreasing seed rates. The delay of transition into the reproductive phase at the lower seed rates (Table 2) need not reduce the number of florets. KLEINENDORST and SONNEVELD (1965, 1966) showed that the larger the number of ridges on the vegetative growing point at the moment of transition, the larger the ultimate size of the ear of perennial rye grass (*Lolium perenne* L.). Moreover, the further differentation of spikelet primordia on the growing point proceeds upwards and downwards during the shooting period until about heading. The delay in heading observed at the lower seed rates (Fig. 3) may, therefore, also have contributed to the increased number of florets per ear. FRIEND (1965) found that the length of wheat ears is greater both as the size of the vegetative apex is larger at the transition stage and as the interval between this stage and anthesis increases. HÄNSEL (1951) demonstrated for Petkus winter rye that a delay in heading, induced by short days, resulted in the formation of more spikelets, and that ears are larger because of more spikelets being formed rather than less being degenerated.

Table 8 shows that number of florets, percentage of fertile florets, and the result of the two (the ultimate number of grains per ear) all follow the same course at increasing seed rates. Their drop is related to decreases in culm space, nitrogen intake, and amount of chlorophyll. This agrees with the conclusion of BREMNER and INGHAM (1960) for winter wheat, viz. that the size of the ears is influenced by the level of nitrogen fertilization through its effect upon leaf size. Similar results were obtained by DÉZSI et al. (1960).

The number of grains being determined at the onset of grain filling, the weight of the grains depends both on the capacity (Fig. 4) and on the rate of decay (Table 6) of the photosynthetic apparatus during ripening. At moderate culm densities, the number of grains gradually dropped at increasing seed rates, so that grain weight could be maintained at a rather constant level of about 37 mg (Fig. 5B). At the two highest seed rates only, notwithstanding a further reduction of grain number, grain

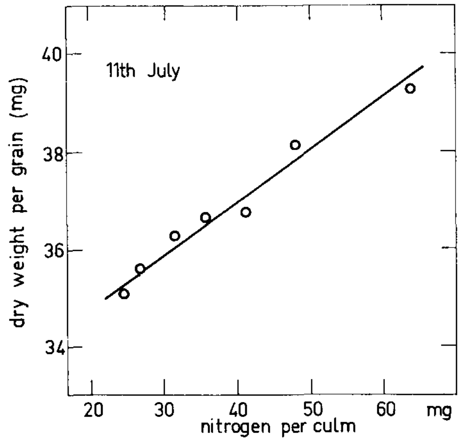

Fig. 8. Relation between grain weight and nitrogen content of the culm in July.

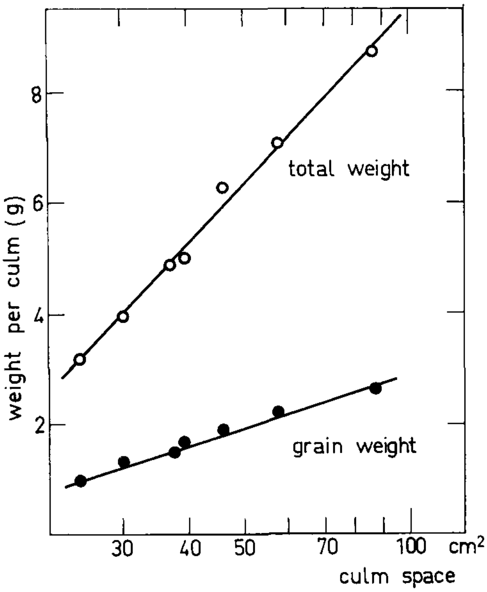

Fig. 9. Relation of culm and ear weights with culm space.

weight diminished, too. Although it seems from the yield analysis data (Fig. 5A, B) that at 140 and 180 kg/ha culm density and grain weight were pushed through optimum levels, yet both grain weight per culm and total culm weight were strictly proportional with the logarithm of culm space throughout the range of culm space (Fig. 9). An important conclusion to be drawn from Fig. 9 is that the dry matter distribution in the culms must have been largely independent from the size and the nutritive condition of the culms: although Fig. 2A showed remarkable differences in the rate of nitrogen uptake, at all culm densities grain weight took 30 % of the total culm weight. This agrees with the findings of DE WIT (1958), who computed that in different experiments with various wheat varieties, giving dry matter productions from 50 to 300 g per plant, the seed production invariably was about 36 % of the total yield.

If the straight lines of total and grain weights in Fig. 9 were extended towards lower values of culm space without deflection, they should intersect at the abscissa at 12.5 cm^2, i.e. at 8 million culms per ha no production should be left. Extrapolation towards higher values of culm space must eventually lead to bending of the curves into horizontal lines. However, because plants grown from the same seed in the same year under the same field conditions at 50 × 50 cm^2, i.e. corresponding to a seed rate of 1.7 kg/ha, produced 27 ears per plant, on an average, with up to 94 grains per ear, the culm and grain weights at 5 kg/ha may still be considered to be determined by the available space per culm.

The relation between yield per ha and culm density, calculated from Fig. 9, is shown in Fig. 10, the part extrapolated at higher densities than the experimentally used ones being given as a broken line. The curves resemble the parabolic ones found by HUDSON (1941b) and by HOLLIDAY 1953, 1960a b) for yields of seed crops, but they are no parabolas since they are asymmetrical. The position of the optimum yield closely approaches that mentioned by HOLLIDAY (1960b) for winter wheat, viz. 3 × 10^6 culms per ha. On a seed rate basis, HOLLIDAY (1960a) found the optimum at 125 kg/ha. Transformation of Fig. 10 into seed rate curves, with the aid of the data on ear density from Fig. 5C, and with the assumption that at higher seed rates than 180 kg/ha the plants are still able to produce one ear each (DÉZSI et al., 1960), renders Fig. 11. The experimentally found yield values are inserted, those from the yield analysis samples fit better. Grain yield is rather independent from the seed rate over a large range, while the reduction in total yield, insignificantly noticeable in Fig. 6 already, shows up above 120 kg/ha. If the plants at higher seed rates form less than one ear, on an average, then the yield depression becomes perceptable at higher seed rates than in Fig. 11, but then part of the seed is wasted. It can be concluded, that if the logarithmic relationship found for the grain and total weight per culm between 5 and 180 kg/ha may be generalized, yield per unit area shows an optimum at moderate seed rates.

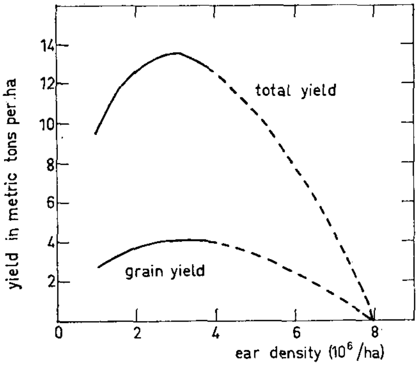

Fig. 10. Relation between yield per ha and ear density. (Calculated from Fig. 9)

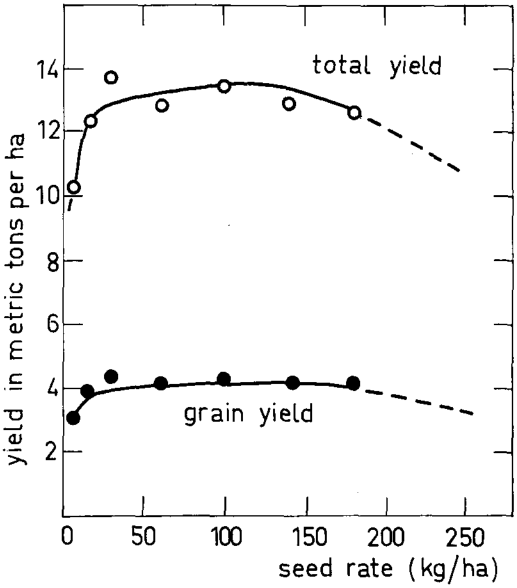

Fig. 11. Relation between yield per ha and seed rate. (Calculated from Fig. 5A and 10)

4. Discussion

The discussion will be confined to three questions.

1. How far can a crop analysis contribute to a comprehension of a yield analysis?
2. What is the nature of the logarithmic relationship of crop and yield data with plant and culm space?
3. Which conclusions can be drawn from the present experiment for the growth, development and yield of winter rye?

Ad *1*.
The main limitation of the usefulness of crop analysis data for an understanding of the achievement of the yield lies in the spurious correlation between many of these data, so that indications rather than evidences about relationships are obtained. This is demonstrated in the foregoing part for the composition of the yield per ear out of floret number, fertility and grain filling. However, the correlations also allow for a restriction of the crop analysis to only a few factors. It would be enough to count plant numbers once in the tillering stage and ear numbers about daily during heading, the latter determination giving also the sharpest establishment of differences in developmental rates. After anthesis floret numbers may be counted. Growth as mass production is correlated with dry weight, or amount of nitrogen or chlorophyll per unit area or per plant or organ.
Apart from supplying the actual data, crop analysis can also be useful for yield analysis in that it indicates the nature of the relationship with the main factor under study, in this case the logarithmic relationship with the seed rate. This will be discussed in the following paragraph.

Ad *2*.
The yield of cereal crops is mostly related not to the seed rate but to the plant or culm density (BLEASDALE and NELDER, 1960; CAMPBELL, 1962; HOLLIDAY, 1960a) or its reverse, plant or culm space (DE WIT and ENNIK, 1959; DE WIT, 1960). Whether plant or culm space is taken as the variable depends on whether the population is still composed of plants as the individual entities or consists of individual culms already, the transition taking place in the course of the shooting period.
Most of the crop analysis data of the present experiment were, indeed, a function of plant or culm space, although generally not a linear one:

$$y = ax + b \tag{1}$$

but rather a logarithmic one:

$$y = a \log x + b \tag{2}$$

in which y = growth, amount, or yield, per plant or per culm, and x = plant or culm space.

According to eq. 1:

$$\mathrm{d}y = a \,.\, \mathrm{d}x \tag{3}$$

while after eq. 2:

$$\mathrm{d}y = a \,.\, \frac{\mathrm{d}x}{x} \tag{4}$$

Eq. 4 expresses that it is the relative space rather than the absolute space which determines the growth or yield of the individuals: the effect of an increase in space depends on the space already occupied. This can be interpreted in terms of extension of root growth in dependence of the size of the root system already present. An alternative explanation could be that the more space becomes available the more the plant or culm approaches its optimum conditions and, therefore, the smaller the effect of space enlargement. Fig. 9 shows that for the yield data, too, the logarithmic relation gives the lines of the best fit.

If in the equation:

$$dy = a \cdot \frac{dx}{x^n} \qquad (5)$$

for the power n of x any other value than unity is substituted, the proportional relation is lost. Although for a range of moderate densities, where x varies only little so that a/x^n becomes relatively constant, eq. 1 and 3 (as well as any equation of type 5) seem to be applicable, particularly at the highest space values eq. 2 and 4 turn out to be the appropriate ones.

Eq. 2 and 4 cannot be easily related to the equation given by De Wit (1960), the latter describing the linear relation between space per plant and space per total yield, because plant density is a component of both his variables. The consequences of the two sets of equations are different, since eq. 2 describes an optimum curve (Fig. 10), whereas that of de Wit gives a curve reaching a stable maximum with increasing plant density. Conflicting data occur in the literature on the question whether the yield of cereals per unit area decreases at increasing seed rates or remains constant (Dézsi et al., 1960; Doughty and Engledow, 1928; Engledow, 1928; Fawcett, 1964; Holliday, 1953, 1960 a, b; Hudson, 1941; Kanda and Sato, 1963; Plhàk, 1959). The statement by Holliday (1960 a), that the relationship between yield per unit area and plant density shows an optimum at a definite seed rate in the cases where yield is a function of reproductive growth, and reaches a stable maximum where yield results from vegetative growth, can no longer be generalized, as has been demonstrated by Bleasdale and Nelder (1960). These authors (see also Campbell, 1962) proposed the pliable equation:

$$\frac{1}{y^p} = a \cdot \frac{1}{x^q} + b \qquad (6)$$

in which the powers, p and q, are positive quantities usually less than unity. In cases that the ratio p/q is unity, the yield per area is about constant above a certain plant density. If the ratio is greater than unity the yield per area continues to increase with plant density, whereas if the ratio is smaller than unity the yield per unit area passes through an optimum value at a certain finite density.

The last situation is about equivalent with that described by eq. 2, the power of y being unity, while the logarithm of x gave better fitting results with the data of both crop and yield analysis than any tested value of the power of x smaller than unity.

It is recommended for future examinations of yield/density relationships, to include crop analysis data as indications of the relation between the population entity which produces the yield and its space. And, moreover, to vary the spacing widely, not only downwards where crowding may facilitate the occurrence of lodging and diseases which may confuse the results, but particularly upwards, too, where the extreme values enable to determine the power of x in one of the equations, 5 or 6, as well.

Ad *3*.

In the present experiment, tillering was unable to compensate for the low plant densities below the seed rate of 60 kg/ha, and the yields at these densities were, therefore, obviously reduced. From 60 kg/ha onwards, maximum dry matter productions were obtained in the present experiment (Table 3), although the somewhat delayed closure of the leaf canopy at 60 kg/ha may be a disadvantage when appreciable weed contaminations occur (COLWELL, 1963). At seed rates over 100 kg/ha, the optimum culm density shown in Fig. 10 is surpassed and grain weight per ear decreases more than ear density increases. The optimum seed rate, therefore, turns out to be between 60 and 100 kg/ha, the higher as the risk of freezing out or of weed infestation is greater.

ACKNOWLEDGEMENTS

The author gratefully acknowledges the technical assistance of Mr. J. Swart and Miss E. Gerritsen and the cooperation of members of the staff of the Institute for Biological and Chemical Research on Field Crops and Herbage, Wageningen. He thanks Professor J. H. A. Ferguson and Mr. M. Keuls for helpful discussions.

REFERENCES

Bleasdale, J. K. A. and Nelder, J. A. 1960 Plant population and crop yield. *Nature 188,* 342.

Bremner, P. M. and Ingham, A. P. 1960 Some aspects of ear development in winter wheat. *Univ. Nottingham, School Agric. Rept. 1960,* 1–4.

Broekema, C. 1933 Oogstanalytische vergelijking van tarwerassen. *Landbouwk. Tijdschr. 45,* 921–937.

Brougham, R. W. 1960 The relationship between the critical leaf area, total chlorophyll content and maximum growth rate of some pasture and crop plants. *Ann. Botan. N.S. 24,* 463–474.

Bruinsma, J. 1962 The effect of a spray with 4,6-dinitro-o-cresol (DNOC) on growth, development and yield of winter rye (*Secale cereale* L.). *Weed Res. 2,* 73–89.

Bruinsma, J. 1963 The quantitative analysis of chlorophylls a and b in plant extracts. *Photochem. Photobiol. 2,* 241–249.

Bruinsma, J. 1965 Effects of pesticidal treatments on the chlorophyll content of plant parts. *Residue Rev. 10,* 1–39.

Bruinsma, J. and Swart, J. 1962 The development of the rye spike until emergence. *Acta Botan. Neerl. 11,* 411–417.

Campbell, R. C. 1962 The relationship between population, yield and yield components. Statistical appendix. *J. Agric. Sci. 59,* 63–66.

Coïc, Y. 1959 Recherches sur le meilleur équilibre entre densité de plantes et fertilisation azotée du blé d'hiver. *Ann. Physiol. Végétale 1,* 53–58.

Colwell, J. D. 1963 The effect of sowing rate on the yield and composition of wheat grown on soils of high fertility in southern New South Wales. *Australian J. Expt. Agric. Animal Husbandry 3,* 114–118.

Dézsi, L. Dévai, M., Nagy, Z. and Pálfi, G. 1960 Correlations between plant density, mineral uptake and yield in winter wheat. *Növénytermelés 9,* 299–308.

Doughty, L. R. and Engledow, F. L. 1928 Investigations on yield in the cereals. V. A study of four wheat fields: the limiting effect of population density on yield and an analytical comparison of yields. *J. Agric. Sci. 18,* 317–345.

Engledow, F. L. 1925 Investigations on yield in the cereals. II. A spacing experiment with wheat. *J. Agric. Sci. 15,* 125–146.

Engledow, F. L. 1928 Investigations on yield in the cereals. IV. The action of the seed drill. *J. Agric. Sci. 18,* 1–40.

Fawcett, R. G. 1964 Effect of certain conditions on yield of crop plants. *Nature 204,* 858–860.

Friend, D. J. C. 1965 Ear length and spikelet number of wheat grown at different temperatures and light intensities. *Can. J. Botan. 43,* 345–353.

Hänsel, H. 1951 Über die Wirkung des Kurztages auf Zeit des Ährenschiebens und auf Ärchenzahl pro Ähre bei Petkus Winterroggen. *Bodenkultur 5,* 305–312.

Holliday, R. 1953 Agronomic research in grassland husbandry problems. *Agric Progr. 28,* 109–123.

Holliday, R. 1960a Plant population and crop yield. *Nature 186,* 22–24.

Holliday, R. 1960b Plant population and crop yield. *Field Crop Abstr. 13,* 159–167.

Hudson, H. G. 1941a Population studies with wheat. II. Propinquity. *J. Agric. Sci. 31,* 116–137.

Hudson, H. G. 1941b Population studies with wheat. III. Seed rates in nursery trials and field plots. *J. Agric. Sci. 31,* 138–144.

Kanda, M. and Sato, F. 1963 On the relationship between leaf area index and population growth of rice plants. *Sci. Rept. RITU, D 14,* 57–73.

Kleinendorst, A. and Sonneveld, A. 1966 Influence of vernalization period and light intensity on shooting and composition of the inflorescence of perennial rye grass (*Lolium perenne* L.). Jaarboek I.B.S. 1965, Wageningen, 49–55.

Kleinendorst, A. and Sonneveld, A. 1967 Influence of light intensity and temperature before and after reaching the reproductive phase on the behaviour of perennial rye grass (*Lolium perenne* L.). Jaarboek I.B.S. 1966, Wageningen. (in press)

Nørgaard Holm, S. and Pedersen, A. 1962 The yield structure of grain crops as influenced by nitrogen application and the seed rate. *Årsskrift Kong. Vet. Landbohøjskole Køb. 1962,* 62–93.

Plhàk, F. 1959 Der Einfluss der Dichte des Pflanzenbestandes auf Wachstum, Wasser-, Chlorophyll- und Phosphorgehalt in Weizen und Korn. *Biol. Plantarum 1,* 248–257.

Wilson, J. A. and Swanson, A. F. 1962 Effect of plant spacing on the development of winter wheat. *Agron. J. 54,* 327–328.

Wit, C. T. de 1958 Transpiration and crop yields. *Versl. Landbouwk. Onderz. 64* 1–88.

Wit, C. T. de 1960 On competition. *Versl. Landbouwk. Onderz. 66,* 1–82.

Wit, C. T. de en Ennik, G. C. 1959 Over concurrentie. Jaarboek I.B.S. 1958, Wageningen, 59–73.