

Development and Structure of Foliage in Wheat Stands of Different Density

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Abstract. The effect of sowing density (21, 85, 340 and 3400 plants per 1 m²) on the leaf area index (LAI), vertical arrangement of developing foliage and dry matter production was investigated in stands of wheat (*Triticum aestivum* L. cv. Niva).

1. With increasing sowing density.

- a) The LAI increased and the highest LAI = 9.6 was obtained with 3400 plants . m⁻². The largest development of foliage took place at ear emergence with 85, 340 and 3400 plants . m⁻², and in the flowering phase with 21 plants . m⁻².
- b) The overall leaf area duration was reduced, with a difference of 11 days between the lowest and the highest density.
- c) The number of leaves formed per one stem increased from 5 to 8.

2. An increase in the LAI affected the vertical distribution of leaf area and resulted in increased differences in relative light intensity between the top and bottom layers of the leaf canopy. Differences in LAI were linked with differences in leaf area duration and in the relative proportions of leaves of different age in the total number of leaves per 1 m².

3. a) Shoot dry matter production increased with increasing density; the maximum of 3811 g . m⁻² was obtained with 3400 plants . m⁻².

- b) The dependence of grain yield on sowing density had a parabolic character; the maximum yields of 470.1 g . m⁻² and 442.8 g . m⁻² were obtained with 340 and 85 plants . m⁻² respectively.

- c) The optimum LAI for the formation of grain yield was 2.3 to 3.2.

- d) The crop growth rate (C) increased with increasing density; the highest mean recorded C = 594 g . m⁻² . week⁻¹ corresponded to LAI = 9.6.

4. Thinning the stands of 3400, 340 and 85 plants . m⁻² in the phases of the 3rd leaf (22 days after sowing) and of tillering (30 days after sowing) to the next lower density resulted in a reduced LAI, leaf and tiller number, crop growth rate, shoot dry matter production and grain yield as compared with both the initial and standard densities.

The role of foliage with respect to both maximum dry matter production and maximum grain yield was defined by an optimum range of relations between the rate of foliage development, leaf area, vertical structure and distribution of light intensity within the stand operating as a self-controlling system.

The growth and development of foliage and its overall photosynthetic rate are the main factors directly affecting the production efficiency of a plant stand. The size of the foliage with respect to the processes of growth and yield formation is usually characterized by the leaf area index (LAI)

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which is defined as the total leaf area over a given ground area (WATSON 1947, 1956, NICHIPOROVICH, STROGONOVA, CHMORA and VLASOVA 1961, etc.). The LAI affects greatly other growth characteristics, and therefore regarded as an important criterion of the production efficiency of a stand. Maximum production is usually linked with the so-called optimum LAI (DAVIDSON and DONALD 1958, WATSON 1958, WATSON and FRENCH 1962, etc.) whose value varies with different species. For example, WATSON (1958), BLACK (1963) and NICHIPOROVICH (1963) quote LAI values of 3 to 5 being optimum for most crops under normal conditions; BROUGHAM (1956) has demonstrated that in grass stands the rates of dry matter production do not decrease up to the LAI values of 5 to 9. Higher values of the optimum LAI have been found e.g., in stands of *Celosia cristata* and *Zelkova serrata* (4 to 11) and of *Scilla hispanica* (13) by SAEKI (1960) and BLACKMAN (1962) respectively. The differences in the values of optimum LAI found in stands of different species have been explained by IWAKI (1958, 1959), SAEKI (1959, 1960, 1961), SAEKI and KUROIWA (1959), KUROIWA (1960), etc. as being due to differences in optical density and photosynthetic efficiency of the foliage. These authors stress the importance of the vertical gradients of irradiation density within the stand. These gradients depend, in turn, on the structure of the stand and of its foliage. This structure is characterized by the size and form of the leaves, by the vertical and horizontal distribution of total leaf area, by the height, shape and variation of plants forming the stand, etc. At optimum LAI, the irradiation density is evenly distributed in the foliage, being just above compensation point in the bottom layers of the leaf canopy.

Stand density, leaf canopy structure, and distribution of irradiation density are closely inter-dependent variables in their effect on photosynthetic production. These multiple correlations are taken into account in mathematical models of photosynthetic production in plant stands (e.g., DE WIT 1965, BUDAKOVSKY and ROSS 1966). The design of suitable and exactly fitting mathematical models depends, of course, on the supply of sufficient amounts of results of experimental work. In this respect, data are also needed on the changes of growth characteristics during the development of a plant stand.

This paper intends to contribute to the understanding of the effects of vertical stand structure on various production characteristics in wheat grown at different sowing densities. Attention is paid to morphological changes of the plants during the growing period, and to the relative proportions in the foliage of leaves of different age.

The following questions are being put:

1. What is the optimum LAI for attaining the maximum rate of shoot dry matter production and maximum grain yield respectively;
2. Under what conditions will the foliage have an optimum vertical structure;
3. What are the effects of sowing density and the resulting interference between plants on the growth of leaves and development of foliage as well as on the rates of dry matter production?

Material and Methods

Plants

In the field experiments, the spring wheat variety Niva (*Triticum aestivum* L. var. *erythrospermum* KÖRN. cv. Niva) was grown at 4 sowing densities of 21, 85, 340 and 3400 plants per square meter (1 m²), spaced evenly at 21.8 cm × 21.8 cm, 10.8 cm × 10.8 cm, 5.4 cm × 5.4 cm and 1.7 cm × 1.7 cm, respectively. The size of the experimental plots was 9 m². The density of 340 plants . m⁻² is the standard sowing density of wheat used in Central Bohemia.

Measurements taken

Number of shoots formed per 1 m², total leaf number and relative proportions of leaves of different age, the total leaf area index (LAI) and its distribution into different layers of foliage, the assimilating surface of stems and leaf sheaths, shoots dry weight and total dry weight, grain yield per 1 m² and relative light intensity at different heights in the leaf canopy. In one part of the experiment, the densities of 3400, 340 and 85 plants . m⁻² were thinned to the next lower densities in the phases of the 3rd leaf (22 days after sowing) and tillering (30 days after sowing), and the subsequent changes of LAI, leaf and tiller number per 1 m² and of shoot dry weight and grain yield per 1 m² were recorded.

From the measurements of total (shoot + root) dry weight and leaf area, the mean values for the growing period of the following growth characteristics were calculated using the formulas given, e.g., by ŠESTÁK, ČATSKÝ, et. al. (1966): crop growth rate (C), defined as the weekly rate of total dry matter production per 1 m², relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR). As the relation between LAI and total dry weight was approximately linear, NAR was calculated using the formula of WILLIAMS (1946), i.e.:

$$\text{NAR} = \frac{(W_2 - W_1) \cdot (\ln A_2 - \ln A_1)}{(A_2 - A_1) \cdot (t_2 - t_1)},$$

in which W_1 , W_2 are the dry weight values and A_1 , A_2 are those of leaf area recorded in two subsequent harvests taken at times t_1 , t_2 .

The harvests were taken at the following phases of development: that of the 3rd leaf, tillering, shooting, ear emergence, flowering, milky ripeness, waxy ripeness, i.e. 22, 30, 43, 55, 65, 76 and 96 to 107 days after sowing respectively. At each harvest in each density, 3 parallel samples were taken, each from an area of 0.5 m² in the central part of the plot, leaving out 0.5 m wide margins as guard rows. All values were calculated for a ground area of 1 m².

Measurement of leaf area

The area of each leaf was calculated as the product of leaf length times maximum leaf width multiplied by a correction coefficient, according to NICHIPOROVICH et al. (1961) — see also tab. 1 — and the leaf area index was calculated from these values. For the calculation of the correction

coefficients, all leaf area was measured — with a hand planimeter — of 50 plants taken at random from each sowing density treatment at each phase of development.

Table 1

Correction coefficients for calculating leaf area from the product of the length times maximum width of the leaf blade

Number of days after sowing	Number of plants per 1 m ²			
	21	85	340	3400
	$\bar{x} \pm s_{\bar{x}}$	$\bar{x} \pm s_{\bar{x}}$	$\bar{x} \pm s_{\bar{x}}$	$\bar{x} \pm s_{\bar{x}}$
22	0.69 $\pm$ 0.001	0.69 $\pm$ 0.002	0.68 $\pm$ 0.001	0.81 $\pm$ 0.003
43	0.69 $\pm$ 0.001	0.68 $\pm$ 0.001	0.68 $\pm$ 0.001	0.80 $\pm$ 0.001
55	0.68 $\pm$ 0.002	0.67 $\pm$ 0.001	0.66 $\pm$ 0.002	0.77 $\pm$ 0.002
76	0.67 $\pm$ 0.001	0.66 $\pm$ 0.001	0.65 $\pm$ 0.001	0.70 $\pm$ 0.002

The area of leaves attached to each 10 cm section of culm was measured separately and the foliage was thus divided into portions, each consisting of leaf blades attached to one section. The mean surface area of the culms and leaf sheaths per 1 m² was calculated from the culm lengths (from coleoptile to ear base) and from the diameters of the lowest and uppermost internodes of both the main culm and the tiller ones.

Estimation of dry matter production

The shoots growing on the sampling area were cut off just above the coleoptile, dried at 105° C and weighed after 24 hours of drying. Grain yield per 1 m² of ground area was estimated at the end of the growing period. Roots were collected to the depth of 50 cm from the same area, washed, dried and weighed in the same way. In view of the difficulties the sampling of roots presented under field conditions, the samples certainly did not comprise the whole root systems and the resulting values of root dry weight are only approximate.

Light intensity

Light intensity was measured on clear days at 11 a.m. with a selenium barrier layer photocell with a neutral reduction filter. Measurements were taken in the open and within the foliage at ground level and at the heights of 5, 15, 25, 35, 45, 55, and 65 cm above the ground. As a result, values were obtained of relative light intensity within the leaf canopy.

Results and Discussion

The sowing density of the wheat stands affected the leaf area index (LAI), the shoot and leaf number per 1 m², and the characteristics of shoot growth (Fig. 1 — A, B, C, D, E). With increasing stand density, both the LAI and leaf area duration were increased (Fig. 1—A). At the time of maximum

Fig. 1.

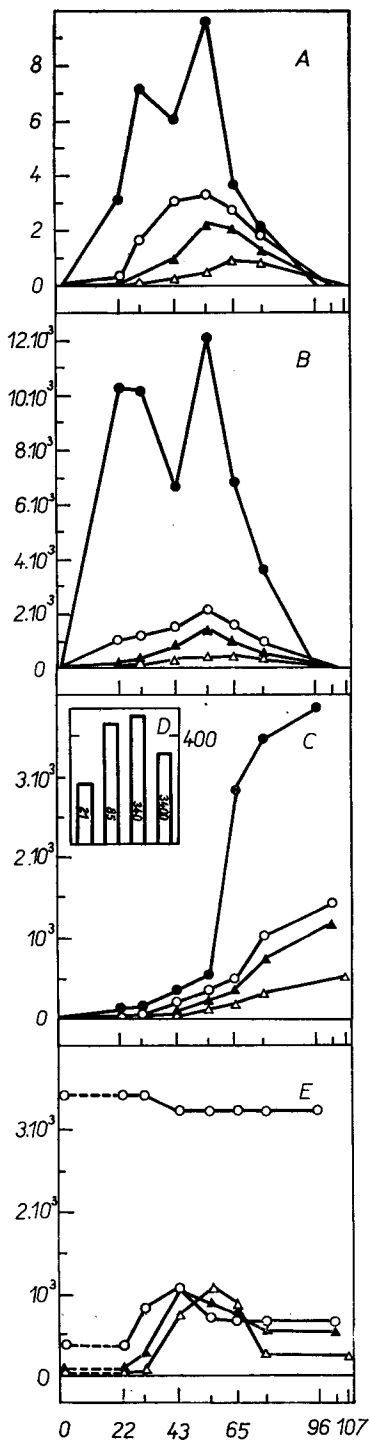


Fig. 1. Leaf area index (LAI), number of leaves, number of tillers, shoot dry matter production and grain yield in stands of different density.

Abscissa: number of days after sowing;

Ordinate: LAI — $\text{m}^2 \cdot \text{m}^{-2}$ (A), number of leaves per 1 m^2 (B), shoot dry matter production — $\text{g} \cdot \text{m}^{-2}$ (C), grain yield — $\text{g} \cdot \text{m}^{-2}$ (D) and number of tillers per 1 m^2 (E).

Densities: $\triangle - \triangle$ — 21 plants $\cdot \text{m}^{-2}$; $\blacktriangle - \blacktriangle$ — 85 plants $\cdot \text{m}^{-2}$; $\circ - \circ$ — 340 plants $\cdot \text{m}^{-2}$; $\bullet - \bullet$ — 3400 plants $\cdot \text{m}^{-2}$.

Fig. 2. Vertical distribution of leaf area, culm area and that of leaf sheaths and the vertical light profiles in stands of different density.

Abscissa-bottom: leaf area (—), culm and leaf-sheath area (---) — both m^2 ; top: relative light intensity in different canopy layers expressed as percentage of light intensity in the open ($\bullet - \bullet$);

Ordinate: height of canopy layers in centimeters measured from ground level. Densities: 21, 85, 340, 3400 (plants $\cdot \text{m}^{-2}$), A — 43 days, B — 55 days, C — 66 days, D — 76 days after sowing.

Fig. 3. Changes of the number of leaves of different age during the vegetation period in stands of different density.

Abscissa: number of days after sowing;

Ordinate: number of leaves per 1 m^2 . 1, 2, 3, 4, 5, 6, 7, 8 — order of leaves from the oldest to the youngest ones.

Fig. 4. Average values of LAR, NAR, RGR and C (crop growth rate) for the whole vegetation period in unthinned ($\bullet - \bullet$) stands and in those thinned in the phase of the 3rd leaf ($\bullet - \dots - \bullet$) or in that of tillering ($\bullet - \dots - \bullet$).

Abscissa: logarithm of stand density = number of plants $\cdot \text{m}^{-2}$;

Ordinate: LAR — $\text{dm}^2 \cdot \text{g}^{-1}$, NAR — $\text{g} \cdot \text{dm}^{-2} \cdot \text{week}^{-1}$, RGR — $\text{g} \cdot \text{g}^{-1} \cdot \text{week}^{-1}$ and C — $\text{g} \cdot \text{m}^{-2} \cdot \text{week}^{-1}$.

Fig. 2.

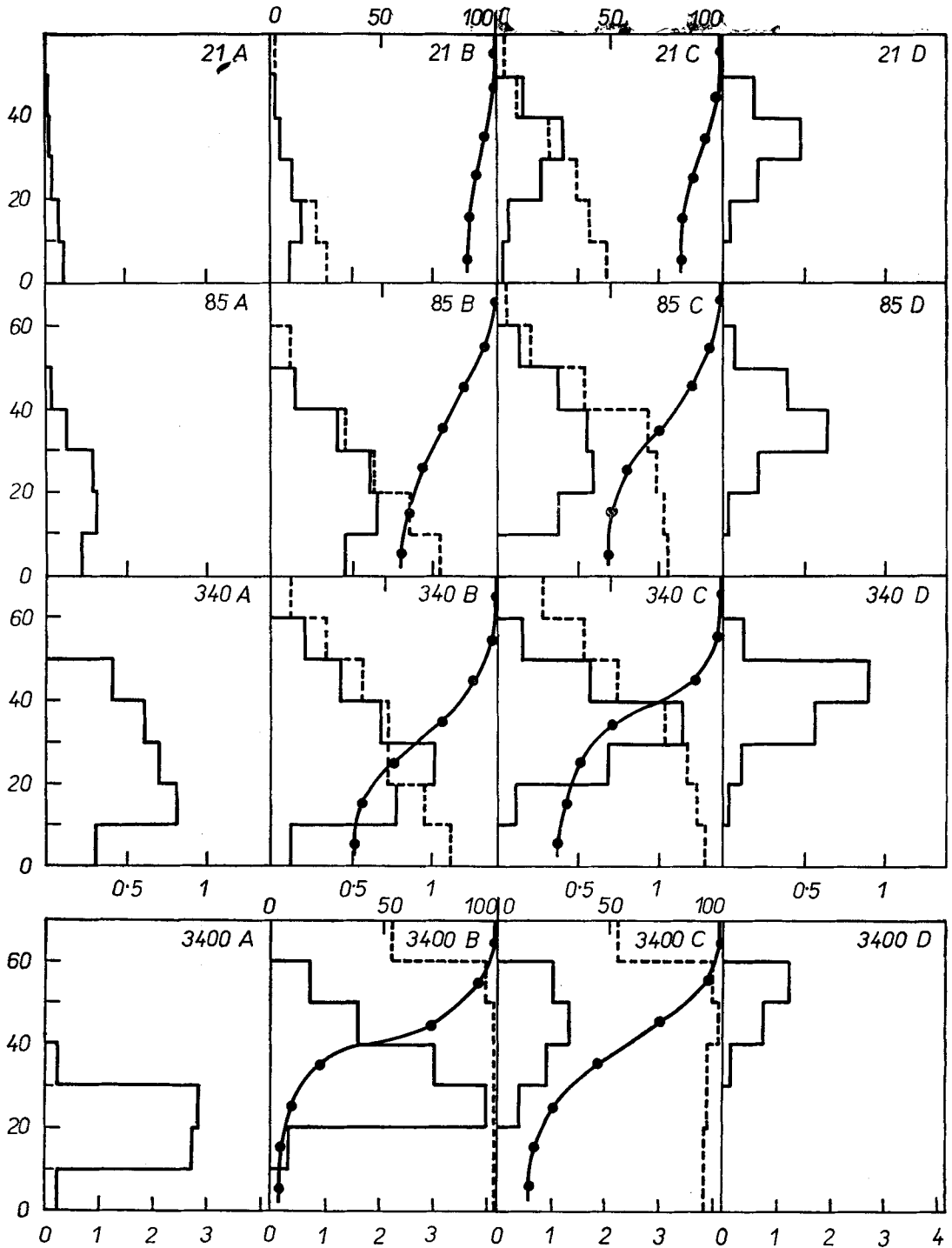


Fig. 3.

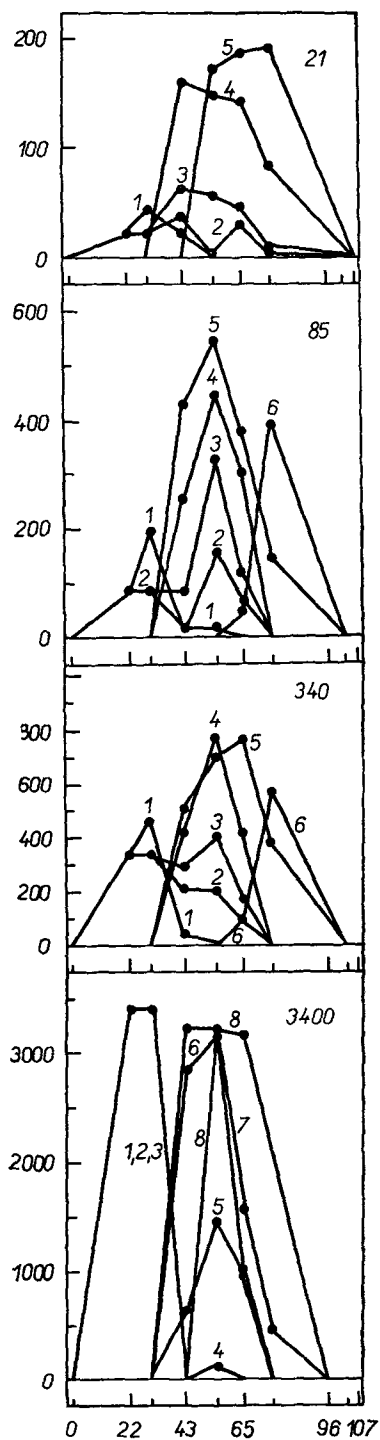
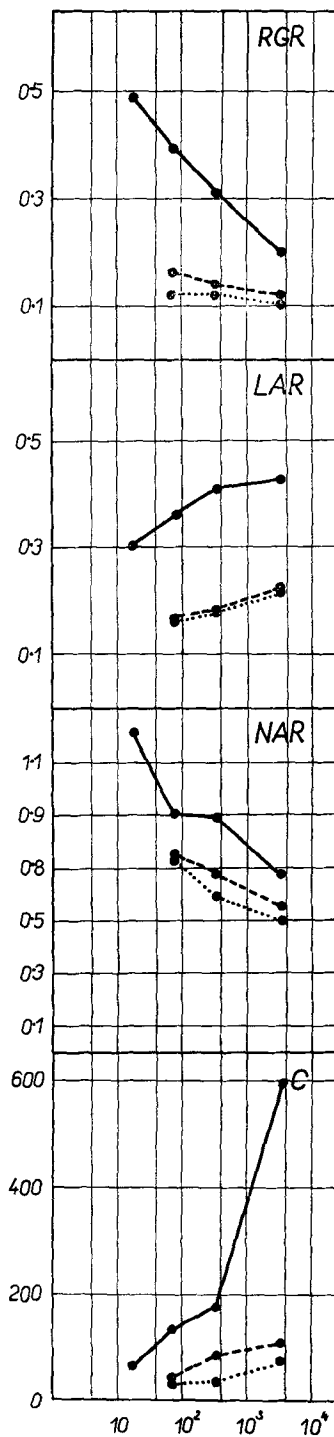


Fig. 4.



development at ear emergence and flowering, the LAI values were 0.9, 2.3, 3.2, and 9.6 with the sowing densities of 21, 85, 340 and 3400 plants m^{-2} respectively. The greatest differences in LAI values were observed in the first half of the growing period, this being due to the differences in the rates of foliage development. With increasing density, the rate of foliage development increased whereas the duration of maximum leaf area was reduced, and the decrease of LAI values after reaching the maximum was more rapid. The highest LAI was reached just before flowering (55 days after sowing) with 85, 340 and 3400 plants m^{-2} ; with 21 plants m^{-2} , the maximum was reached 10 days later. The figure 1-A also shows that with increased LAI the time of active life of the foliage was shorter: the difference between the lowest and highest densities was 11 days. With 3400 plants m^{-2} , the curve of changes of LAI during the growing period had two peaks and its character corresponded with the changes in leaf number per 1 m^2 , in the same way as with the other densities (Figs. 1-B and 3).

Both the rate of foliage development and the duration of its physiological activity are important controlling mechanisms within the stand. The production efficiency of the foliage depends not only on the magnitude of LAI but also on its changes during the growing period. The importance of the time factor has been stressed by WATSON (1956): In wheat stands, the LAI values are smaller than 1 over more than one half of the growing season; the control of LAI and of its time changes plays therefore an important role in increasing the yield. According to NICHIPOROVICH (1964), a formation of foliage which goes on either too rapidly or too slowly, results in decrease of production because of the unfavourable changes it brings about in the direction and rate of assimilate translocation. Different species thus appear to have different requirements with respect to both the rate of formation and duration of active life of the foliage. In cereals, for instance, where the aim is to obtain the highest possible grain yield, the foliage should develop relatively slowly and the maximum LAI values should not be very high, but the leaves should die off rapidly at the end of the growing period. The situation is quite reverse in crops which should give the highest possible yield of vegetative parts.

Figure 1-E shows the changes of LAI which were closely linked with the rates of both tiller and shoot formation in the first half of the growing period. Plants grown at the density of 3400 plants m^{-2} did not form any tillers and the total number of shoots per 1 m^2 was reduced by 6 per cent by the end of the growing period. Apart from the differences in tillering between the densities of 340, 85 and 21 plants m^{-2} , the shoot number per 1 m^2 was highest in the phases of shooting and ear emergence, with the maximum values differing only little from one another. Similar changes were observed by THORNE (1962) in stands of barley. According to this author, the dying off of shoots results mainly from severe competition with other ones on the plant. In our experiments comparison between individual densities show that with increasing tiller formation the dying off of tillers was also enhanced. Not only did the rate of tillering increase with increasing stand density but also the waxy ripeness set on later and the leaf area duration was extended. According to NANDA et al. (1959), the retardation

of the development of wheat plants, connected with an increase in tillering rate, is brought about by changes in phosphorus metabolism.

The changes of LAI found in the experiments referred to in this paper have confirmed NICHIPOROVICH's (1966) conclusion on the differences in foliage development existing between stands of optimum, supra-optimum and sub-optimum densities as affecting both dry matter production (biological yield) and grain production (economic yield). While increased density brought about an increase in shoot production (the maximum of $3811 \text{ g} \cdot \text{m}^{-2}$ was obtained with 3400 plants $\cdot \text{m}^{-2}$, fig. 1-C), the relation between density and grain yield had a parabolic character with maximum values ($471.1 \text{ g} \cdot \text{m}^{-2}$) obtained with 340 plants $\cdot \text{m}^{-2}$ (fig. 1-D). The corresponding LAI was 3.2, which is near the lower limit of the range of LAI values regarded by NICHIPOROVICH (1963) as optimum for wheat, i.e. $\text{LAI} = 3$ to 4. On the other hand, a decrease in LAI by about $1/3$ — with 85 plants $\cdot \text{m}^{-2}$ the LAI was 2.3 — resulted in an only slightly and insignificantly lower grain yield ($442.8 \text{ g} \cdot \text{m}^{-2}$). It seems therefore that a rather wide range of LAI values may be regarded as optimum for seed production, even under one set of environmental conditions. According to LUDVIG, SAEKI and EVANS (1965), wide ranges of the optimal LAI are conditioned by similar values of net photosynthesis. This similarity results, mainly from the balance of different photosynthetic and respiration rates in lower and upper layers of foliage.

The differences in rates of production depending on differences in sowing density and LAI can be explained — apart from other factors — also by the differences in leaf arrangement. This was followed between shooting and milky ripeness (fig. 2 — A, B, C, D). During this period, changes took place in the number, height and size of individual leaf layers. The denser the stand the more rapidly died off the basal leaves. In the densest stand (3400 plants $\cdot \text{m}^{-2}$), the lowest leaves died off already in the shooting phase and only 3 out of 6 leaf layers were left in the phase of milky ripeness whereas with 21, 85 and 340 plants $\cdot \text{m}^{-2}$, the lowest leaf layers began to die off only in the phase of ear emergence. With all densities, the areas of individual leaf layers underwent marked changes: at the ear emergence and flowering phases, when the foliage was fully developed, the leaf layer between 20 and 30 cm had the largest area with 3400 and 340 plants $\cdot \text{m}^{-2}$ whereas with 85 and 21 plants $\cdot \text{m}^{-2}$, it was the leaf layer between 10 and 20 cm that had the largest area. The density-induced different rates of leaf dying-off changed also the relative positions of the largest leaf layers. At the phases of flowering and milky ripeness, the leaf layers having the largest leaf area were situated at 50 to 60 and 40 to 50 cm with 3400 and 340 plants $\cdot \text{m}^{-2}$ respectively, and were at 30 to 40 cm with the other two densities of 85 and 21 plants $\cdot \text{m}^{-2}$. The figure 2-B, C shows the distribution of the assimilatory surface of leaves and leaf sheaths in the stands, and the relative light intensities in different leaf layers at the time of the highest LAI. Measurements of relative light intensities have shown that the experimental stands intercepted 12 to 96 per cent of total incident light energy, the relative interception depending on stand density. With increasing density and height of the stand, the mean relative intensity of the light falling on one leaf layer was reduced and greater differences were found in relative light in-

tensity between the top and bottom leaf layers. The differences in the vertical distribution of relative light intensity along the light profiles demonstrate that the differences in optical density, found between the stands, were, among other factors, due to the differences in vertical leaf distribution. The exponential character of the relation between relative light intensity and the number, area, transmission and height of individual leaf layers demonstrates that the densest stands intercepted most of the incoming light in the top layers (the lowest 3 layers received only 6 to 10 per cent of full illumination) whereas with the other three densities the light was more or less evenly distributed throughout the foliage. The changes in the position and size of leaf layers and in the relative amounts of light they received may be explained in accordance with the results and conclusions of SÆKI (1960, 1961). The reduction of light intensity to values below the compensation point and the resulting unfavourable balance between respiration and photosynthesis bring about a more rapid dying off of the bottom leaf layers and interfere, especially in annual plants, with the translocation of assimilates to generative organs. For this reason, it is justified to consider the dependence of the economic yield on the size and structure of the foliage although the direct participation of ear photosynthesis in grain formation must be taken into account. It is evident that the formation of the optimum size and structure of foliage in wheat was linked with the potential interception of 51 to 74 per cent of the incoming light energy.

For the understanding of the role foliage plays in determining the production rate of a stand, the "qualitative" side of the foliage structure is also important. This includes the assessment of the numbers and relative proportions in the foliage of leaves of different age (fig. 3). The total number of leaves produced per a individual shoot was different with each density: 5, 6, 6 and 8 leaves were formed with densities of 21, 85, 340 and 3400 plants $\cdot m^{-2}$ respectively. The greatest heterogeneity in the foliage, expressed in terms of the age difference between the relatively oldest and youngest leaves in the foliage, was found in the period between shooting and flowering. The duration of the period for which each leaf is physiologically active is of great importance from the point of view of yield formation. With increasing density, the leaf area duration was extended, especially in old leaves. It seems a reasonable assumption that the more rapid dying off of the leaves at the highest density was responsible for the change in the rate and direction of assimilate transport which, in turn, had an unfavourable effect on plants' growth and development and the formation of generative organs.

In drawing comparisons of the numbers of leaves of different age in stands of different density, it should not be forgotten that qualitative differences exist between leaves on the main culms and those on the tiller ones. This difference was found in wheat, e.g. by KRAVTSOVA (1957).

Changes in the environment within the stand resulting from thinning the stands of 3400, 340 and 85 plants $\cdot m^{-2}$ to the next lower density in the phases of the 3rd leaf and tillering, were reflected in a decreased LAI, leaf and tiller number per 1 m^2 , mean crop growth rate, and grain yield in comparison with both the initial densities and with the unaltered ones used as standards (tab. 2); the relative proportion between the densities, however,

Table 2
LAI, number of leaves, number of tillers, shoot dry matter production and grain yield in the thinned stands

Growth characteristic	Number of days after sowing	Thinning in the phase of the 3rd leaf				Thinning in the phase of tillering			
		Number of plants per 1 m ²				Number of plants per 1 m ²			
		3400 → 340	340 → 85	85 → 21		3400 → 340	340 → 85	85 → 21	
		$\bar{x} \pm s_{\bar{x}}$	$\bar{x} \pm s_{\bar{x}}$	$\bar{x} \pm s_{\bar{x}}$		$\bar{x} \pm s_{\bar{x}}$	$\bar{x} \pm s_{\bar{x}}$	$\bar{x} \pm s_{\bar{x}}$	
LAI m ² · m ⁻²	30	0.53	0.50	0.09		—	—	—	—
	43	0.78	0.62	0.13		0.47	0.49	0.13	
	55	0.69	0.58	0.23		0.55	0.44	0.22	
	65	0.71	0.42	0.21		0.49	0.36	0.19	
Number of leaves per 1 m ² ground area	30	724.3 ± 17.2	177.3 ± 6.3	87.4 ± 3.8		—	—	—	
	43	790.2 ± 10.3	197.5 ± 10.7	94.9 ± 2.4		489.3 ± 11.6	176.6 ± 12.7	99.5 ± 4.1	
	55	805.5 ± 8.9	205.6 ± 6.8	109.8 ± 1.2		569.2 ± 10.3	198.9 ± 7.6	110.4 ± 6.5	
	65	612.1 ± 6.5	168.2 ± 3.2	113.1 ± 0.4		398.5 ± 6.5	159.1 ± 9.1	96.3 ± 5.7	
	76	524.3 ± 12.3	161.7 ± 7.1	121.1 ± 3.1		318.1 ± 6.3	124.2 ± 7.1	89.4 ± 2.7	
Number of tillers per 1 m ² ground area	30	273.6 ± 8.2	149.4 ± 2.2	133.6 ± 8.5		—	—	—	
	43	205.3 ± 1.9	176.4 ± 1.3	161.8 ± 2.7		98.2 ± 2.3	39.6 ± 3.2	24.1 ± 1.1	
	55	186.8 ± 3.4	133.7 ± 1.0	121.8 ± 1.3		126.2 ± 1.8	51.3 ± 2.8	29.3 ± 2.2	
	65	171.1 ± 1.8	128.3 ± 2.7	113.1 ± 1.3		113.7 ± 8.4	43.1 ± 4.3	35.2 ± 1.6	
	76	158.2 ± 3.9	123.3 ± 1.6	112.5 ± 2.1		90.9 ± 3.2	30.5 ± 1.7	27.8 ± 1.3	
Shoot dry matter production (in g) per 1 m ² ground area	30	42.6 ± 1.2	12.5 ± 0.4	2.7 ± 0.1		—	—	—	
	43	123.7 ± 3.4	36.9 ± 3.8	11.3 ± 0.3		31.8 ± 1.4	23.5 ± 1.1	10.6 ± 1.2	
	55	263.8 ± 2.8	99.4 ± 3.1	42.8 ± 1.9		67.3 ± 1.8	47.7 ± 2.4	21.0 ± 2.1	
	65	360.2 ± 2.1	234.2 ± 12.4	76.1 ± 1.2		112.6 ± 10.3	98.1 ± 2.8	73.6 ± 6.3	
	76	459.9 ± 1.9	330.4 ± 7.6	183.5 ± 4.1		203.3 ± 6.9	151.0 ± 7.6	148.7 ± 13.1	
	96—106	981.4 ± 13.8	803.6 ± 2.8	429.9 ± 7.6		434.5 ± 17.3	275.7 ± 7.3	220.4 ± 9.2	
Grain yield (in g) per 1 m ² ground area	96—106	276.4 ± 2.4	216.8 ± 10.5	122.1 ± 7.8		276.3 ± 2.4	216.9 ± 10.5	122.6 ± 7.8	

remained unchanged. It may be therefore assumed that the specificity of the self-controlling relations operating within the stands had been established in the earliest phases of development. A comparison of the stands' reaction to thinning indicates that changing the stand environment in the later phases of development markedly affected the values of the growth and production characteristics. According to WATSON (1958), IWAKI (1958), NICHIPOROVICH (1964) and HIROI and MONSI (1966), smaller values of the characteristics may be ascribed to the changes in the relation between LAI and NAR. In our experiments with wheat, the mean value of NAR decreased with increasing LAI (fig. 4) in both thinned and unthinned stands. According to NICHIPOROVICH (1964), the optimum relation between LAI and NAR is achieved, in theory, when the NAR acquires values which are about one half of the highest NAR possible under a given set of conditions. In the experiments with wheat, referred to in this paper, the mean NAR was $0.68 \text{ g. dm}^{-2} \cdot \text{week}^{-1}$ with $3400 \text{ plants} \cdot \text{m}^{-2}$. This is approximately one half of the value obtained with $21 \text{ plants} \cdot \text{m}^{-2}$, i.e. $1.21 \text{ g. dm}^{-2} \cdot \text{week}^{-1}$. On the other hand the NAR mean values corresponding to the LAI which was optimum for grain production were relatively low, 0.89 to $0.90 \text{ g. dm}^{-2} \cdot \text{week}^{-1}$. This demonstrates that both the size and structure of foliage required for attaining a high economic yield of wheat were different from those resulting in a high biological yield. Moreover, the reduction of mutual shading of the leaves following thinning the stands did not result in mean higher values of NAR and of crop growth rate as compared with the standards. WATSON and FRENCH (1962) found in kale that crop growth could be increased by reducing the LAI to its optimum value. In our experiments with wheat, the LAI did not reach the values needed for attaining maximum production in any of the thinned stands. Although the order of densities was preserved, thinning appeared to be a rather drastic treatment bringing about changes in the soil and microclimatic conditions which had an unfavourable effect on the morphogenetic development of the plants. HUGHES and EVANS (1962) observed an increase in the values of NAR and RGR after transferring the plants of *Impatiens parviflora* from a lower light intensity to a higher one. The reaction of our wheat stands, however, was in agreement with the conclusions of BJÖRKMAN and HOLMGREN (1963), drawn from experiments with *Soildago virgaurea*. According to these authors, an increase in light intensity brings about a decrease of photosynthetic activity in leaves of plants that were grown under low light intensities. In these leaves, both the photochemical capacity and the photosynthetic rate at light saturation seem to have been affected. The reaction of the thinned stands of wheat shows clearly that development of a given stand in a given environment is determined from its very early phases. This is in agreement with NICHIPOROVICH's (1966) theory of the self-controlling character of a stand's development.

Conclusions

The results of the experiments carried out with wheat stands of different density have demonstrated that:

1. The correlations between LAI and dry matter production were different from those between LAI and grain yield: The highest dry matter production was obtained with $LAI = 9.6$ whereas the highest grain yield was obtained in stands with $LAI = 2.3$ to 3.2 . Increased stand density resulted in decreased NAR and RGR mean values. The highest dry matter production was attained with a mean $NAR = 0.68 \text{ g} \cdot \text{dm}^{-2} \cdot \text{week}^{-1}$ but the yield was highest with $NAR = 0.89$ to $0.90 \text{ g} \cdot \text{dm}^{-2} \cdot \text{week}^{-1}$.
2. The vertical structure of the foliage could be regarded as optimum when the leaf area was evenly distributed in the stand and 51 to 74 per cent of incoming light energy were intercepted by the leaf canopy.
3. The development of the foliage was determined in the very early phases of the plants' development by the specificity of self-controlling reactions within the stands: decreasing the density and LAI of the developing stands by thinning had a negative effect on their growth and production characteristics.

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D. HODÁŇOVÁ, Ústav experimentální botaniky ČSAV, Praha: Vývoj a struktura zápoje listoví v různě hustých porostech pšenice. — Biol. Plant. **9** : 424—438, 1967.

Bylo studováno prostorové členění vyvíjejícího se zápoje listoví pšenice (*Triticum aestivum* L. cv. Niva) a závislost produktivity porostu, nadzemní produkce sušiny a výnosu zrna na rozdílné hustotě porostu (21, 85, 340 a 3400 rostlin na m²) a změnách pokryvnosti listoví.

1. a) Se zvyšováním hustoty porostu
 - a) se zvyšovala pokryvnost listoví (maximální LAI = 9,6 byl dosažen u varianty 3400): největšího rozvoje povrchu listoví v průběhu vegetace dosáhly varianty 85, 340 a 3400 ve fázi metání a varianta 21 ve fázi kvetení;
 - b) zkracovala se úhrnná délka života zápoje listoví (rozpětí mezi krajními variantami činilo 11 dní);
 - c) zvětšil se počet listů vytvořených na jednom stéble z 5 na 8.
2. Se zvětšením LAI se zmenšilo rozpětí zastoupení listové plochy v jednotlivých patrech porostu a zvětšil se rozdíl mezi relativní hustotou ozáření spodních a horních pater listů.

Změna velikosti LAI byla spojena s rozdílnou integrální listovou plochou a rozdílnou dynamikou četnosti listů na m^2 podle jejich stáří.

3. a) Se zvyšováním hustoty vzrůstala produkce nadzemní sušiny: maximální produkci sušiny vytvořila varianta 3400 ($3811 \text{ g} \cdot m^{-2}$);
- b) závislost hospodářského výnosu na hustotě porostu měla parabolický charakter s maximálním výnosem zrna u varianty 85 a 340 ($442,8 - 470,1 \text{ g} \cdot m^{-2}$);
- c) optimální velikost LAI v daných experimentálních podmínkách byla s ohledem na výnos zrna $= 2,3 - 3,2$;
- d) se zvyšováním hustoty se zvětšila průměrná produktivita porostu: maximální produktivita ($C = 594 \text{ g} \cdot m^{-2}/\text{týden}$) odpovídal LAI $= 9,6$.
4. Protrhání variant 3400, 340 a 85 v období fáze 3. listu (22. den po výsevu) a odnožování (30. den po výsevu) na nejbližší nižší hustotu mělo za následek zmenšení LAI, počtu listů a odnoží, nadzemní produkce sušiny a výnosu zrna jak ve vztahu ke kontrolním tak i výchozím hustotám.

Funkce zápoje listoví pšenice s ohledem na maximální produkci sušiny a výnos zrna byla vymezena optimálním rozpětím autoregulačních vztahů mezi intenzitou vytváření povrchu listoví, jeho velikostí, prostorovou strukturou a distribucí záření uvnitř porostu jako celistvého systému.

Д. Годаньова, Институт экспериментальной ботаники ЧСАН, Прага: Развитие и распределение площади листьев пшеницы в посевах различной плотности. — Biol. Plant. 9 : 424—438, 1967.

Изучались динамика развития и пространственное распределение площади листьев пшеницы (*Triticum aestivum* L. cv. Niva) и зависимость продуктивности посева, надземной продукции сухого вещества и урожая зерна от различной плотности стояния растений (21, 85, 340 и 3400 растений на m^2) и изменений относительной площади листьев.

1. Увеличение густоты стояния растений вызывало:
 - a) увеличение листового индекса (максимального значения $LI = 9,6$ было достигнуто в густоте 3400): самое интенсивное развитие площади листьев было приурочено к фазам колошения (густоты 85, 340 и 3400) и цветения (густота 21);
 - b) укорочение общей длины жизни листьев (разница между крайними густотами составляла 11 дней);
 - v) увеличение числа листьев, образованных на одном стебле с 5 на 8.
2. С увеличением листового индекса уменьшалось вертикальное распределение площади листьев в посевах и увеличивалась разница между относительной интенсивностью освещения нижних и верхних ярусов листьев. Изменение относительной площади листьев было связано с изменением фотосинтетической мощности посева и с различной возрастной динамикой числа листьев на единицу площади.
3. a) Увеличение густоты посева вызывало увеличение надземной продукции сухого вещества: максимальная продукция $= 3811 \text{ г}/m^2$ была достигнута в густоте 3400;
- b) зависимость урожая зерна от густоты посева носила параболический характер с максимальными значениями в густотах 85 и 340 ($442,8 - 470,1 \text{ г}/m^2$);
- v) оптимальная величина LI по отношению к максимальному урожаю зерна в данных экспериментальных условиях была равна $2,3 - 3,2$.
- г) с увеличением густоты увеличилась средняя продуктивность посева: максимальной продуктивности ($C = 594 \text{ г}/m^2/\text{неделя}$) отвечал $LI = 9,6$.
4. Изреживание посевов в фазе 3. листа (22. день вегетации) и купения (30. день вегетации) по направлению к ближайшей нижней густоте вызывало уменьшение показателей LI , числа листьев и боковых побегов, продуктивности посева и урожая зерна как по отношению к исходным так и контрольным густотам.

Оптимальная функция площади листьев при формировании биологического и хозяйственного урожая была определена авторегуляционными взаимоотношениями между интенсивностью образования площади листьев, ее пространственной структурой, величиной листового индекса и оптической плотностью посева как целостной системы.