

Limitations for Finding a Linear Relationship Between Chlorophyll Content and Photosynthetic Activity

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Abstract. In experiments with fodder cabbage and sugar beet the influences were tested which restrict the finding of a uniform linear dependence between the chlorophyll content and photosynthetic rate. The main factor is most probably the irradiation during the growth of plants and the measuring of photosynthetic rate. Changes in the density and length of irradiation with the proceeding spring season are reflected in the decrease of unit chlorophyll activity in all leaves of the plant. Such differences were not observed in plants grown in winter months at a low greenhouse irradiation density. High irradiation density during the measurement of photosynthesis ensures the finding of high correlation of photosynthetic rate with the chlorophyll amount per unit area of leaf. With a low irradiation density, or in thick leaves, the lower layers of chloroplasts are not saturated with radiation, and hence a higher correlation coefficient is found by relating photosynthetic rate to the percentage of chlorophyll in dry weight than to the quantity of chlorophyll per unit area of leaf blade. In some experiments higher activity of chlorophylls was found in young leaves before they have reached the state of "photosynthetic maturity" than after this turning point. This difference diminished by relating the photosynthetic rate to chlorophyll *a* content instead of the total amount of chlorophylls ($a + b$). High activity of chlorophylls in very young leaves and great individual variability within the experimental plant groups caused by uneven cultivation conditions are the basis of apparent sigmoid character of average curves for the chlorophyll-photosynthesis relation.

The determination of the relation between the amount of chloroplast pigments, most frequently chlorophylls, and the photosynthetic rate has already been the subject of a great number of publications (see ŠESTÁK and ČATSKÝ 1966). Despite differences in their results, the predominant opinion is that there is no relationship between the chlorophyll content and the photosynthetic rate or that the amount of chlorophyll has an effect under weak light only ("Chlorophyll als Schwachlichtfaktor" — GABRIELSEN 1948, 1960). Many of the older studies have basic shortcomings, such as measuring photosynthesis under unsuitable conditions (mainly at low irradiation density), not taking into consideration the ontogenetic age of the leaves or stressing extreme

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leaf types (mutants or plants cultivated under abnormal nutrition, the photosynthetic system of which works entirely differently).

Our experiments, too (ŠESTÁK and ČATSKÝ 1962, ŠESTÁK and BARTOŠ 1962, 1963, AVRATOVŠČUKOVÁ, BARTOŠ and ŠESTÁK 1962, ŠESTÁK 1963a, 1963b, ŠESTÁK and VÁCLAVÍK 1965) do not as yet make it possible to draw final conclusions, even though they clearly prove that there is a relationship between the chlorophyll content and the photosynthetic rate. Its linear expression, however, is limited by the inherent properties of the plants, as well as by the selection of experimental procedure. Let us demonstrate on the example of our further experiments with fodder cabbage and sugar beet some of the main reasons which make it difficult to find the direct relationship between the chlorophyll content and the photosynthetic rate.

Materials and Methods

Plants: Fodder cabbage [*Brassica oleracea* L. convar. *acephala* (DC.) ALEF. var. *medullosa* THELL.] was cultivated throughout the year in pots in a greenhouse. Sugar beet was grown in field plots under normal agrotechnical conditions.

Photosynthetic rate was determined from the increase in dry weight in disks cut out from the leaves (method of BARTOŠ, KUBÍN and ŠETLÍK 1960). The disks were exposed for 6 hours under constant conditions in holes in foamy polyurethane plates, revolving on a turntable in a special apparatus (AVRATOVŠČUKOVÁ and ŠESTÁK 1966). The following experimental conditions were maintained: continuous water saturation of the tissue, 0.03% or 4% CO₂ in the air (200 l. hour⁻¹), temperature 25° ± 0.2° C, equal irradiation for all 45 exposed samples (each constituted by 12 disks) in two levels: full irradiation (20 Tungfram Krypton Superba 100 W/220 V lamps above the turntable, density of photosynthetically active radiation 2 · 10⁵ erg · cm⁻² · s⁻¹) or half irradiation (10 lamps above the turntable). The dried disks were weighed on a torsion balance with an accuracy of ± 0.02 mg.

Chlorophyll content was measured in an 80% acetone extract on a Pulfrich photometer with Elpho photocell attachment (total chlorophyll) or by a two-wavelength spectrophotometric method on Optica Milano CF 4 or Beckman DB, using a nomogram (ŠESTÁK 1966) calculated on the basis of the Mackinney-Arnon equations (ARNON 1949).

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Results and Discussion

1. The effect of the advancing vegetation season and the ageing of plants

In experiments with leaves of different age of the same plant or with the homogeneous plant population in the vegetative stage we usually find a linear relationship between the chlorophyll content and the photosynthetic rate. If we start with the leaf which is at the stage of "photosynthetic maturity" (usually reached before the leaf acquires maximum area and even before

reaching maximum areal chlorophyll content), further ageing of the leaf is displayed in a gradual decrease in chlorophyll content and in a still greater fall in photosynthetic rate. Finally, at a certain chlorophyll amount (0.5 to 2.5 mg . dm⁻²) we find zero apparent photosynthesis. We denote this amount, at which the photosynthetic activity of the tissue stops, as the "chlorophyll compensation point" (c_0). For one plant or very homogeneous plant population, the relationship between the total chlorophyll amount and the photosynthetic rate under optimum external conditions can thus be approximately expressed by the simple linear equation

$$P = (c_t - c_0) a_c, \quad (1)$$

where P means photosynthetic rate, c_t total chlorophyll content and a_c the trend of the line which determines the relationship.

With the ageing of the plant, c_0 increases slightly and a_c falls markedly. Thus, with the ageing of the leaf and the entire plant, the photosynthetic activity of a unit amount of chlorophyll is decreased and the tissue containing the same amount of chlorophylls forms a smaller amount of assimilates. This is shown in Fig. 1 representing three succeeding measurement series made in May or June on a group of fodder cabbage plants sown in February. The respective regression coefficients indicate a fall in the photosynthetic activity of the chlorophylls on ageing of the plant. Similar differences were found by

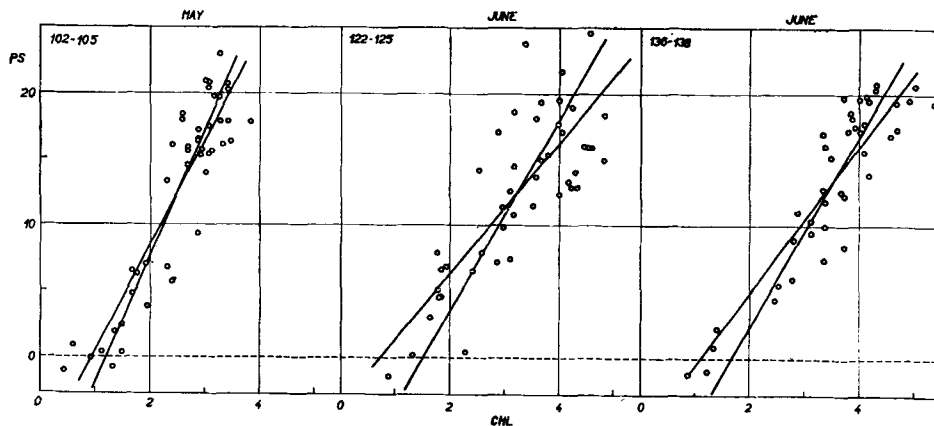


Fig. 1. The dependence of photosynthetic rate on chlorophyll content in leaves of different age from fodder cabbage plants sown in February and analysed in May (left — plants 102- to 105-days-old) or June (middle — plants 122- to 125-days-old; right — plants 136- to 138-days-old). Abscissa — chlorophylls ($a + b$) in mg . dm⁻²; ordinate — photosynthesis in mg dry weight dm⁻² . h⁻¹. The straight lines represent the regression coefficients.

MURATA, OSADA, IYAMA and YAMADA (1957) in rice sown in 4 periods — early till late in the season: plant sown late in the season did not attain the same photosynthetic activity of unit chlorophyll amount in any stage of their development as the plants sown early. The reason for these changes are doubtlessly external conditions during cultivation, particularly factors of light,

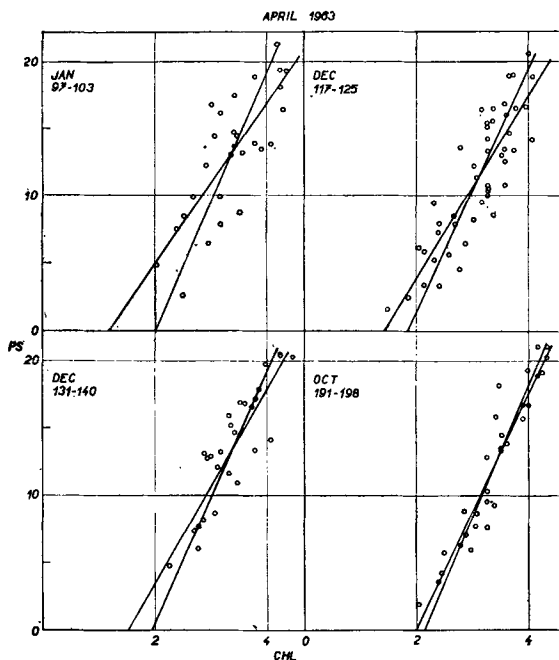


Fig. 2. The dependence of photosynthetic rate on chlorophyll content in leaves of different age from fodder cabbage plants analysed together in April 1963, but sown in January (at the day of analysis 93- to 103-days-old), December (117- to 125-days-old or 131- to 140-days-old) or October (191- to 198-days-old). Abscissa — chlorophylls ($a + b$) in $\text{mg} \cdot \text{dm}^{-2}$; ordinate — photosynthesis in $\text{mg dry weight} \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$.

which cause changes in the photosynthetic system of the plant, possibly also in conjunction with photoperiodicity. Apparently for this reason we find no expressive differences in experiments carried out in winter on plants of different age, which grew under unfavourable irradiation conditions. We have verified this on plants of fodder cabbage, sown in different months (October till January) and analysed together in April (Fig. 2). The photosynthetic rates in young leaves, most important for the plant, were essentially the same and the dependence of the photosynthetic rate on the chlorophyll content was not significantly different.

2. The effect of the individual variability of plants

The correlation and regression coefficients determining the relationship between the chlorophyll content and the photosynthetic rate calculated per leaf area unit are usually high and statistically confirmed. The fields limited by the multiple of experimental points, however, are far from an ideal comprehension. If we, however, wish to replace the individual experimental points by an average curve and thus calculate for the various intervals of the chlorophyll content mean values of photosynthetic rate, we do not have to obtain a straight line corresponding to the equation (1) but rather a curve of a sigmoid nature — see Fig. 3: The first and second curves summate the first and last

series of measurements presented in Fig. 1. The last two curves summate results for fodder cabbage plants sown in November and January and analysed at the same time in May.

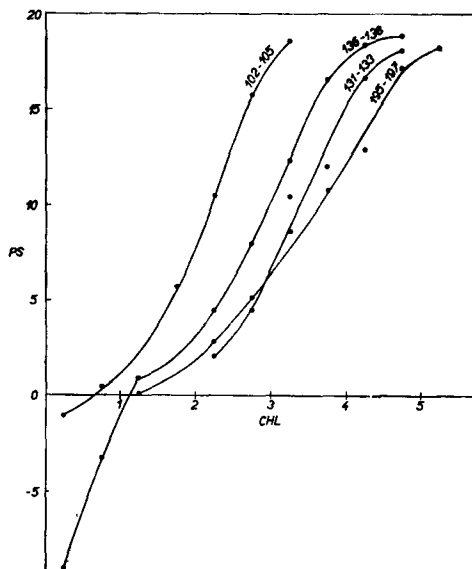


Fig. 3. Mean values for chlorophyll content [abscissa — chlorophylls ($a + b$) in $\text{mg} \cdot \text{dm}^{-2}$] and photosynthetic rate (ordinate — dry weight increase in $\text{mg} \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$) in leaves from fodder cabbage plants. The 1st and 2nd curve from the left represent the 1st and 3rd series of measurement from Fig. 1, the last two curves represent the experiments from Fig. 4. The numbers express the age of plants in days.

Fig. 4 shows the numeric basis of these last two curves — the undistinguished experimental points on the right, and on the left lines connecting the experimental points for different leaves of each plant separately. We see that the studied relationships for the individual experimental plants is very close to linearity. But in the whole plant population not cultivated under standard phytotronic conditions the rate of development and ageing of various plants and individual leaves varies greatly. For example, in some plants in the population we find a low chlorophyll content and unusually low photosynthetic rates. Such plants evidently influence the situation near the chlorophyll compensation point, partially also because they show increased respiration.

3. The different activity of chlorophyll in very young leaves

The bend in the region of high chlorophyll contents in Fig. 3 is caused by summing up the data for young leaves and leaves that have already reached their photosynthetic maturity. In some plants (*Nicotiana sanderae* — see ŠESTÁK and ČATSKÝ 1962) the activity of chlorophylls in the youngest leaves differs only slightly from that in the mature leaves and, therefore, in summation this curve-bend is not found. On the contrary, in the case of maize (ŠESTÁK and VÁCLAVÍK 1965) and sugar beet the activity of chlorophylls in

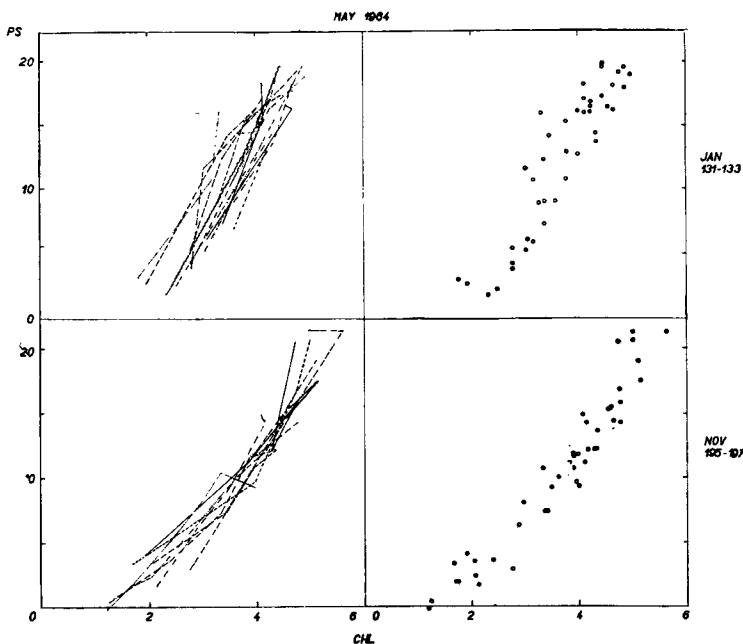


Fig. 4. The relationship of chlorophyll content and photosynthetic rate expressed as experimental points undistinguished for all the analysed groups of plants (right) or shown as lines of different form, which connect values for different leaves of each individual plant (left). Plants of fodder cabbage sown in January (131- to 133-days-old) and November (195- to 197-days-old) were analysed in May. Abscissa — chlorophylls ($a + b$) in $\text{mg} \cdot \text{dm}^{-2}$; ordinate — photosynthesis in $\text{mg dry weight} \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$.

the young leaves was higher than in the older leaves. An example of this different chlorophyll activity in the leaves of one plant of sugar beet is indicated in Fig. 5.

The turning point in the chlorophyll activity apparently takes place in the period of "photosynthetic maturity". It seems that the photosynthetic activity of chlorophylls would for many plants have to be solved separately for the leaves before and after reaching their photosynthetic maturity.

4. The importance of chlorophyll a

In every experimental series higher correlation coefficients were found when relating photosynthetic rate to chlorophyll a content than to the total chlorophyll amount. One explanation could be the higher accuracy of chlorophyll a than chlorophyll b estimation by using the two-wave-length spectrophotometric method. But the chlorophyll b forms only about 25 to 30% of the total chlorophyll quantity and hence the higher experimental error for the estimation of total chlorophyll could not be the main argument. Better explanation extends the leading role of chlorophyll a forms *in vivo* in photosynthetic reactions (see, e.g. WITT et al. 1965). The quantity of chlorophyll a by itself is doubtlessly a more exact characteristic of the photosynthetic activity, as

the experiments with natural algae associations (ODUM, McCONNELL and ABBOTT 1958), with barley mutations (HIGHKIN and FRENKEL 1962) etc. have shown.

Fig. 5. shows how the dispersal of experimental points narrows down when bringing the photosynthetic rate into dependence with only chlorophyll *a* quantity instead of the entire chlorophyll (*a* + *b*) content.

An even better characteristic would be obtained by determining the quantity of different forms of chlorophyll *a* in vivo, which would probably also explain the existence of non-active chlorophyll *c*₀; for such an analysis, however, there is still no expeditious method. Naturally, further research is requested to show whether more linear relationship cannot be found by relating the photosynthetic activity of leaves to the quantity of some important substance in the photosynthetic electron transfer chain, for example, of ferredoxin or plastoquinone or some important enzyme [SMILLIE (1962) observed interesting changes in the activities of ribulose-1,5-diphosphate carboxylase, photosynthetic pyridine nucleotide reductase, and transketolase with increasing leaf age].

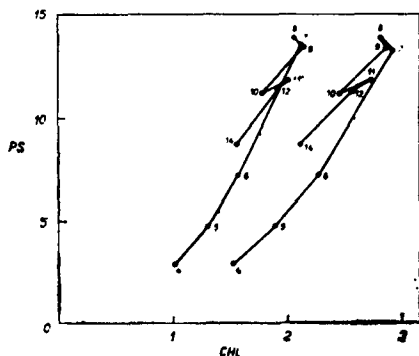


Fig. 5. Photosynthetic rate (ordinate — $\text{mg dry weight} \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$) is more directly related to chlorophyll *a* $\cdot \text{dm}^{-2}$ content (left curve) than to chlorophylls (*a* + *b*) content (right curve). Values for leaves of different age (numbered from the oldest leaf) on one plant of sugar beet (105-days-old).

5. The influence of leaf thickness and exposure conditions in measuring the photosynthetic rate

The linear dependence between the chlorophyll content and photosynthetic rate can obviously be found only under optimum conditions of exposure, where the entire chlorophyll system of the tissue can be included into the photosynthetic process. Although sufficient water supply and plentiful access of CO_2 into the assimilating tissue are very essential experimental conditions for obtaining reliable results, the most important exposure factor is the density of irradiation. We have already shown (ŠESTÁK 1963b, ŠESTÁK and BARTOŠ 1963) that the effect of the amount of chlorophylls per unit area of leaf becomes more expressive with greater irradiation than with low radiation densities. Fig. 6 illustrates the differences in the dependence of photosynthetic rate on the chlorophyll *a* content in sugar beet plants which assimilated in the atmosphere with 4% CO_2 under a density of irradiation of $2 \cdot 10^5 \text{ erg} \cdot \text{cm}^{-2} \cdot \text{s}^{-1}$ (left) or with half a dosage of radiation energy (right).

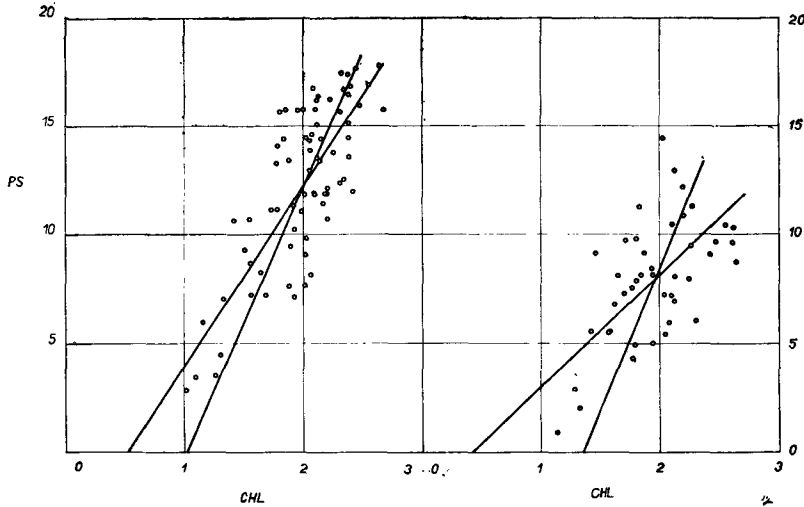


Fig. 6. The relationship of chlorophyll *a* content (abscissa — mg . dm⁻²) and photosynthetic rate (ordinate — mg dry weight . dm⁻² . h⁻¹) determined under different experimental conditions: left 4% CO₂, full irradiation (correlation coefficient *r* = 0.829); right — 4% CO₂, 1/2 irradiation (correlation coefficient *r* = 0.613). The straight lines represent the regression coefficients. — Leaves of different age from sugar beet plants ca. 100-days-old.

A comparison of rank correlation coefficients for sugar beet leaves in Tab. 1 displays the concurrent influence of irradiation density during the determination of photosynthesis and of the thickness of leaves [expressed as dry weight

Table 1

Rank correlation coefficients *r_d* for experimental series with sugar beet leaf disks assimilating at 0.03 or 4% CO₂ and full (2 . 10⁸ erg . cm⁻² . s⁻¹) or half irradiation density

CO ₂ concentration, %	Relative irradiation density	Characteristics of material used in each series of experiments				Rank correlation coefficients <i>r_d</i> for photosynthetic rate with		
		Photosynthetic rate mg dry weight . dm ⁻² . h ⁻¹	Chlorophyll <i>a</i> content, mg . dm ⁻²	Dry weight of tissue unit, mg . dm ⁻²	No. of experimental values	chlorophyll <i>a</i>		dry weight per leaf area unit
						per leaf area unit	as per cent dry weight	
0.03	50	7.14	2.02	291.1	43	0.373*	0.661**	-0.337*
0.03	100	11.82	2.19	311.1	35	0.917**	0.603**	0.037
4.00	50	7.92	1.96	274.2	43	0.545**	0.680**	-0.287
4.00	100	13.59	2.15	288.9	45	0.683**	0.475**	-0.229
4.00	100 ¹⁾	17.12	2.59	444.2	43	0.423**	0.783**	-0.537**

¹⁾ Analysed from October 6 to 13; other series analysed in the second half of July and first week of August.

** P = 0.01; * P = 0.05.

per leaf area unit — see also “density thickness” of McCLENDON (1962)] on the importance of chlorophyll factor. In thinner leaves and at high irradiation density photosynthesis is saturated with radiation practically in all the tissue layers and, therefore, we find a higher correlation of photosynthetic rate with chlorophyll amount per leaf area unit than with the percentage of chlorophyll *a* in dry weight (“chlorophyll concentration”). Inverse situation is found in similar leaves at half irradiation density or at full irradiation in half as thick leaves: photosynthesis is then correlated better with chlorophyll percentage in dry weight. At the same time, negative correlation of photosynthetic rate with the dry weight per unit leaf area is much more expressive and significant. From the comparison of these values with the correlation coefficients in Tab. 2 representing some of the fodder cabbage experimental series illustrated in Fig. 1 to 4, the following conclusion may be drawn: At irradiation densities saturating the whole tissue profile, when certain positive correlation of photo-

Table 2

Rank correlation coefficients r_d for experimental series with fodder cabbage leaf disks assimilating at 0.03% CO₂ and 2 · 10⁵ erg · cm⁻² · s⁻¹

Date of analysis	Age of plants, days	Characteristics of material used in each series of experiments				Rank correlation coefficients r_d for photosynthetic rate with		
		Photosynthetic rate, mg dry weight · dm ⁻² · h ⁻¹	Chlorophyll (a + b) content, mg · dm ⁻²	Dry weight of tissue unit, mg · dm ⁻²	No. of experimental values	chlorophyll (a + b)		dry weight per leaf area unit
						per leaf area unit	as per cent dry weight	
April 1963	93—103	13.47	3.44	208.5	35	0.825**	0.542**	0.379*
May 14 to 17, 1963	102—105	12.51	2.52	385.3	45	0.829**	0.675**	0.609**
May 14 to 16, 1964	131—133	10.55	3.63	259.0	44	0.961**	0.826**	0.566**
May 20 to 22, 1964	195—197	12.39	3.70	256.4	42	0.912**	0.762**	0.478**

** P = 0.01; * P = 0.05.

synthesis and leaf thickness exists, photosynthetic rate is in best correlation with chlorophyll amount per leaf area unit, which sums up both chlorophyll concentration and leaf thickness. If some tissue layers are undersaturated with radiation and consequently photosynthetic rate is in a significant negative correlation with leaf thickness, only the validity of chlorophyll concentration in tissue volume unit is clearly expressed.

These results clearly show that comparable results can be obtained only at saturating irradiation density for each type of leaves. From this point of view many data in the literature should be revised, e.g. GABRIELSEN'S (1948) results obtained with low irradiation densities (up to 9000 lx). Density of irradiation also designates whether or not photosynthetic rate is in correlation with the thickness of leaf (McCLENDON 1962) or its mesophyll (PIETERS 1960).

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V pokusech s krmnou kapustou a cukrovkou byly sledovány vlivy, které omezují nálezni jednotné lineární závislosti mezi obsahem chlorofylu a intenzitou fotosyntézy. Hlavním činitelem je pravděpodobně ozáření během pěstování rostlin i při měření intenzity fotosyntézy. Změny v hustotě a délce ozáření s postupujícím jarem se odrážejí v poklesu jednotkové aktivity chlorofylu ve všech listech na rostlině. Takový pokles byl pozorován u rostlin vypěstovaných v zimě při nízké hustotě skleníkového ozáření. Vysoká hustota záření během měření fotosyntézy zaručuje stanovení vysoké korelace mezi intenzitou fotosyntézy a množstvím chlorofylu na plošnou jednotku listu. Při nízké hustotě ozáření nebyly v tlustých listech nejsou spodní vrstvy chloroplastů zářením nasyceny. V těchto případech nalezneme vyšší korelační koeficient při vztažení intenzity fotosyntézy k procentu chlorofylu v sušině než k množství chlorofylu na plošnou jednotku listové čepule. V některých pokusech byla nalezena vyšší aktivita chlorofylů v mladých listech před dosažením jejich „fotosyntetické dospělosti“ než po tomto stavu. Tento rozdíl se snížil vztažením intenzity fotosyntézy k obsahu pouze chlorofylu a místo k celkovému množství chlorofylů ($a + b$). Vysoká aktivita chlorofylů ve velmi mladých listech a velká individuální variabilita uvnitř souborů pokusných rostlin, způsobená nejednotnými kultivačními podmínkami, jsou podkladem zdánlivě sigmoidního charakteru průměrových křivek pro danou závislost.

З. Шестак, Отделение физиологии растений, Институт экспериментальной ботаники ЧСАН, Прага: Факторы ограничивающие линейную зависимость между содержанием хлорофилла и фотосинтетической активностью. — *Biol. Plant.* 8 : 336—346, 1966.

Изучались влияния ограничивающие обнаружение линейной зависимости между содержанием хлорофилла и интенсивностью фотосинтеза у растений кормовой капусты и сахарной свеклы. Вероятно, основным фактором влияющим на эту зависимость является интенсивность освещения во время выращивания растений и во время измерений фотосинтеза. Изменения в интенсивности и длительности освещения в зависимости от времени года отражаются в понижении единичной активности хлорофилла у всех листьев растения. Такая закономерность не была обнаружена у растений выращиваемых в теплице при низкой зимней интенсивности освещения. Высокая интенсивность освещения во время измерений фотосинтеза обеспечивает получение высоких значений коэффициента корреляции между интенсивностью фотосинтеза и количеством хлорофилла в расчете на единицу поверхности листа. При низкой интенсивности освещения или у листьев с толстой листовой пластинкой нижние слои хлоропластов не насыщены светом. Более высокий коэффициент корреляции был тогда обнаружен в случае пересчета интенсивности фотосинтеза на процентное содержание хлорофилла в сухом весе чем на единицу листовой поверхности. В некоторых опытах была обнаружена более высокая активность хлорофилла у молодых листьев до начала достижения их «фотосинтетической зрелости» чем после этого. Разница уменьшалась в случае отношения интенсивности фотосинтеза только к хлорофиллу a вместо к общему содержанию хлорофиллов ($a + b$). Высокая активность хлорофиллов у очень молодых листьев и большая индивидуальная изменчивость растений, вызванные неодинаковыми условиями выращивания, являются основой для получения кажущегося сигмоидного характера средних кривых у данной зависимости.