

# Influence of temperature and light conditions on dry-matter distribution, development rate and yield in arable crops<sup>1</sup>

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## Summary

The distribution of dry matter over the various organs of a plant is not only important for the evaluation of the product finally harvested, but also for the growth rate and yield level. Differences in growth rate between species and even varieties are mainly due to the rate at which newly produced matter is converted to assimilating tissue and by the green area formed per unit of dry-matter weight. Shoot/root-ratio and moisture content in the plant show a certain correlation to growth rate, as can be established from the light response and temperature effects. As regards temperature, the final size of a plant is determined by mutually independent effects on growth rate and rate of development.

In temperate zone crops a warm climate (for instance 25° C) shortens the period of development without giving sufficient compensation by faster growth. As a result, the plants remain smaller than in a cool climate. In crops of subtropical origin (maize, beans) the growth rate is stimulated to such an extent under warm conditions that the plants grow larger despite the short growth period. This vigorous growth at high temperatures can be explained by a great increase in shoot/root-ratio, which is not shown by temperate zone plants (small cereals, peas and flax). The influence of phasic development on final yield is also demonstrated by photoperiodism. Optimal photoperiods give a fast development and too short a growing period. The best yields are obtained with suboptimal photoperiods.

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## 1. The distribution of material in a mature crop

The various parts of a crop plant are evaluated very differently and in practice the term "yield" is often limited to specific organs. The potato haulm is worthless and even a nuisance at the harvest. The seed of cereals is more highly esteemed than the straw. These examples show that the division of dry matter over different parts of the plant is as important as the total yield. An "increase in yield" resulting from the use of better varieties may be limited to a shift in the distribution of dry matter to more valuable organs without an increment in total yield. This is clearly the case in the sequence of wheat varieties in the Netherlands since 1900 (TABLE 1). Since it is difficult to raise total production without lengthening the life of a crop, it is doubtful whether it would have been possible to raise the kernel yield of wheat by breeding work without such a shift from vegetative organs to kernel.

<sup>1</sup> Lecture held at the course "Fundamentals of dry-matter production and distribution" organized by the Royal Netherlands Society for Agricultural Sciences, Wageningen, 10th January, 1962.

TABLE 1. Total yield and kernel/straw-ratio of leading winter-wheat varieties in the Netherlands; average from experimental fields in the province of Groningen

Variety	Period	Weight of straw + kernel (kg/ha)	Kernel/straw -ratio
Wilhelmina .....	1902—1932	12600	0,51
Juliana .....	1934—1947	12430	0,55
Staring .....	1948—1961	13900	0,59
Felix .....	1958—1961	12830	0,60
Heines VII .....	1953—1955	11860	0,66

Spring barley is equal to other cereals because of its high kernel/straw-ratio. The total yield is distinctly inferior, this being due to the relatively short growing period of this crop.

The final yield of specific organs is the result of production and distribution of matter in subsequent phases of plant development. Even when distribution under suitable conditions is a constant function of time per phase (as claimed by VAN DE SANDE BAKHUYZEN, 1937 and WITTENROOD, 1957), distribution in the final yield may be variable owing to the variable share of each phase in total production. Moreover, distribution within a phase depends on environmental factors.

## 2. The influence of the dry-matter distribution on plant growth

It is well known that the growth rate shows great specific differences and largely depends on climatic conditions. Generally speaking, however, it is impossible to explain this by differences in photosynthesis. According to HEATH and GREGORY (1938) several field crops do not differ substantially in assimilation rate. Although WATSON (1947) observed differences in assimilation rate between crops under field conditions, at present it is generally assumed that related species at least (for instance cereals) show no significant differences in the rate of photosynthesis per leaf unit (cf. for example for the genus *Triticum* BELKOV *et al.*, 1961).

According to GAASTRA (1959) photosynthesis is only slightly dependent on temperature when CO<sub>2</sub>-concentration or light intensity is the limiting factor in the process.

It may be assumed that specific and climatic fluctuations in growth rate are due to formative processes, especially the rate at which newly produced matter is converted to assimilating tissue. Plants may use newly formed matter either for organs involved in photosynthesis or for non-assimilating organs, for instance roots and parts of stems. It may also be stored in the form of carbohydrates.

When a certain quantity of dry matter is converted to assimilating tissue its efficiency still depends on cell elongation. The assimilating area per gram of dry matter is more or less inversely proportional to the dry-matter content of the tissue. At temperatures below 10° C in particular this content is high (TABLES 2 and 4) and it retards growth. At very low temperatures the dry-matter content is also affected by a sugar reserve which in young wheat plants may rise to 20 % in the dry matter (MILLER, 1939). As a result growth is kept at a low level. As to specific differences it is significant that at low temperatures wheat always has a higher dry-matter content and a slower growth rate than rye.

From the ecological point of view this high dry-matter content and winter sugar reserve is important for increasing frost resistance and limiting growth, so that a

TABLE 2. Assimilation rate for plants sown January 8 and grown in a greenhouse (natural daylight) at several temperatures

A. Plants grown at 16° C 1 and transferred to temperatures of 0° C (average), 10° C and 16° C (constant) on February 21; harvest on March 6						
Tempera- ture (°C)	Species (variety)	Period Feb. 21—March 6		Daily increase of dry weight per g of fresh weight (mg)	Dry-matter % of shoot at harvest	
		average fresh weight of shoot (g)	increase of total dry weight (g)			
16	winter rye . . . . .	9,728	1,794	13,8	13,0	
	(Peikuser)					
10	winter wheat . . . . .	6,156	1,284	16,1	13,1	
	(Heines VII)					
0 2	winter rye . . . . .	6,074	0,836	10,0	14,5	
	winter wheat . . . . .	3,707	0,593	12,3	14,8	
	winter rye . . . . .	4,600	0,565	9,0	17,2	
	winter wheat . . . . .	2,381	0,246	8,0	18,0	

B. Plants grown initially at 6° C (later on at 10° C) and transferred to temperatures of 0° C (average), 10° C and 16° C (constant) on March 7; harvest on March 20						
Period March 7—20						
16	winter rye . . . . .	3,860	0,709	14,0	11,0	
	winter wheat . . . . .	2,500	0,488	15,0	11,6	
10	winter rye . . . . .	3,057	0,743	18,7	14,0	
	winter wheat . . . . .	1,714	0,460	21,8	14,8	
0	winter rye . . . . .	2,042	0,347	12,7	14,8	
	winter wheat . . . . .	1,042	0,183	13,5	17,9	

1 During this pre-treatment additional fluorescent light was applied during daytime.  
2 Damaged by frost.

compact rosette develops which is well adapted to cope with the perils of the cold season.

At normal temperatures the shoot/root-ratio is probably the most important factor regulating growth rate. There are indications that differences in growth between varieties can be explained by a different shoot/root-ratio and dry-matter content (TABLE 3). Related species (small cereals, for example) also show a correlation between shoot/root-ratio and growth rate. It is well known that rye grows faster than barley and wheat. These crops show a decreasing shoot/root-ratio in this sequence. TABLE 4 gives some figures for winter rye and winter wheat (the influence of temperature on shoot/root-ratio will be discussed later).

TABLE 3. Fresh weight, dry weight and shoot/root-ratio of 3 winter-wheat selections showing differences in vegetative growth in early spring. Date April 12

Selection	Fresh weight of shoots (g)	Dry-matter content (%)	Dry weight of shoots (g)	Shoot/root-ratio
MGH ....	6,4	16,2	1,04	1,4
GB .....	5,6	18,0	0,99	1,3
HC .....	4,9	17,1	0,84	1,2

TABLE 4. Shoot/root-ratio of winter wheat and winter rye sown January 8 in a greenhouse at different temperatures and complete nutrition

Temperature (°C)	Species (variety)	Age (days)	Leaf number	Total dry matter (mg/plant)	Dry matter of tops (%)	Shoot/root-ratio
6—10*	winter rye ( <i>Petkuser</i> )	58	4,4	167	15,7	2,2
	winter wheat ( <i>Heines VII</i> )	58	3,7	105	16,2	2,0
	winter rye	71	5,8	667	—	2,4
	winter wheat	71	5,3	350	17,0	2,1
16	winter rye	36	5,4	490	9,5	4,4
	winter wheat	36	4,0	311	9,6	3,1
	winter rye	49	7,0	2284	13,0	6,7
	winter wheat	49	6,6	1595	13,1	3,7

\* Seedling growth initially at 6° C, later on at 10° C.

In order to compare the assimilation rates of the two species at various temperatures rye and wheat plants were grown as seedlings in a greenhouse. The plants were then divided into 3 groups and grown at temperatures of 16° C, 10° C and about 0° C. After 13 days the increases in dry weight were divided by the average fresh weight in the same period so as to obtain a growth rate per unit of assimilating tissue (TABLE 2). Rye shows a somewhat lower assimilation rate than wheat, possibly as a result of more mutual shading of leaves<sup>1</sup>, but it is obvious that the faster growth of rye is not caused by higher assimilation. This supports the theory

<sup>1</sup> Table 2 does not enable any conclusions to be drawn on the influence of temperature on assimilation. The highest figures were obtained in cases in which there was no change in temperature (a: 16° C, b: 10° C), indicating that transfer caused a shock.

that the main reason for this phenomenon is to be sought in the distribution of material over the plant parts.  
In the following sections special attention will be given to the influence of light and temperature on growth rate and it will be shown that dry-matter distribution and especially shoot/root-ratio again have a decisive influence. The data on growth and shoot/root-ratio were obtained by periodical sampling of plants grown at constant temperatures but under natural light.

### 3. Determination of shoot/root-ratio and growth rate during vegetative growth

Shoot-root-ratio and growth rate change during development. In most annual plants the following pattern can be observed *under optimal conditions*. During germination root growth first dominates to such an extent that the shoot/root-ratio is low. In the seedling stage the shoot overtakes the root and the distribution established at the end of this stage remains almost constant during subsequent vegetative development (FIG. 1). During the transition to the generative stage the shoot/root-ratio shows a sharp increase as a symptom of a new distribution pattern more favourable for the tops. In each phase of development the points obtained when the shoot and root figures are plotted together form approximately straight lines, showing that there is no substantial change in the distribution within a phase.

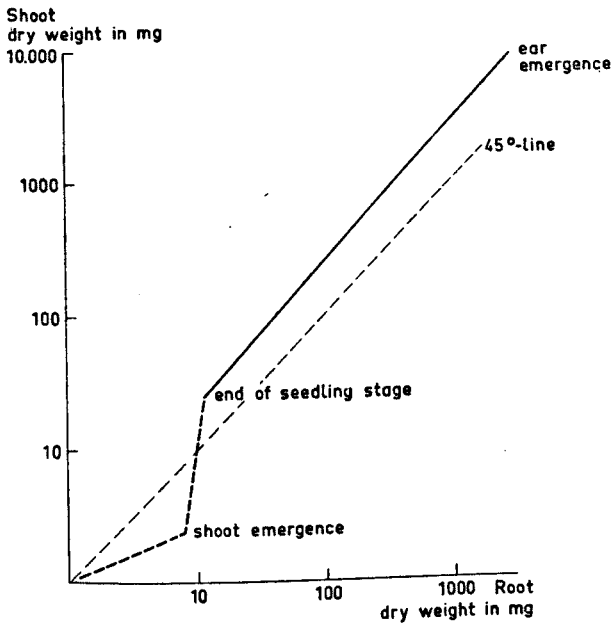


FIG. 1.  
Shoot/root-ratio in a rye plant grown under optimal conditions in daylight at a constant temperature of 10° C. Logarithmic scale; i.e. all observations with the same shoot/root-ratio lie on 45°-lines

The shoot/root-ratio figures from TABLES 3—6 correspond to a point of reference in the middle of the post-seedling vegetative stage. The growth-rate figures (TABLES 7 and 9) were taken from the same stage. The increase in weight for free-standing plants is exponential and therefore gives straight lines when plotted logarithmically

against time (FIG. 2). It shows that for peas and other crops with large seeds seedling growth is relatively more vigorous than growth in the subsequent vegetative stage. In the case of cereals this is only true for the high temperatures.

The growth rate figures (TABLE 7) refer to the gradients of the lines representing the post-seedling stage. They indicate the number of days in which dry weight increases tenfold. The figures thus obtained are inversely proportional to growth rate. It should be emphasised here that this rate only applies to a certain period of development and is not the only factor determining the ultimate yield. In the generative phase growth rate is considerably slowed down owing to the formation of non-assimilating tissue. The figures in TABLE 7 and 9 can be used, however, to demonstrate the specific differences and the influence of environmental factors.

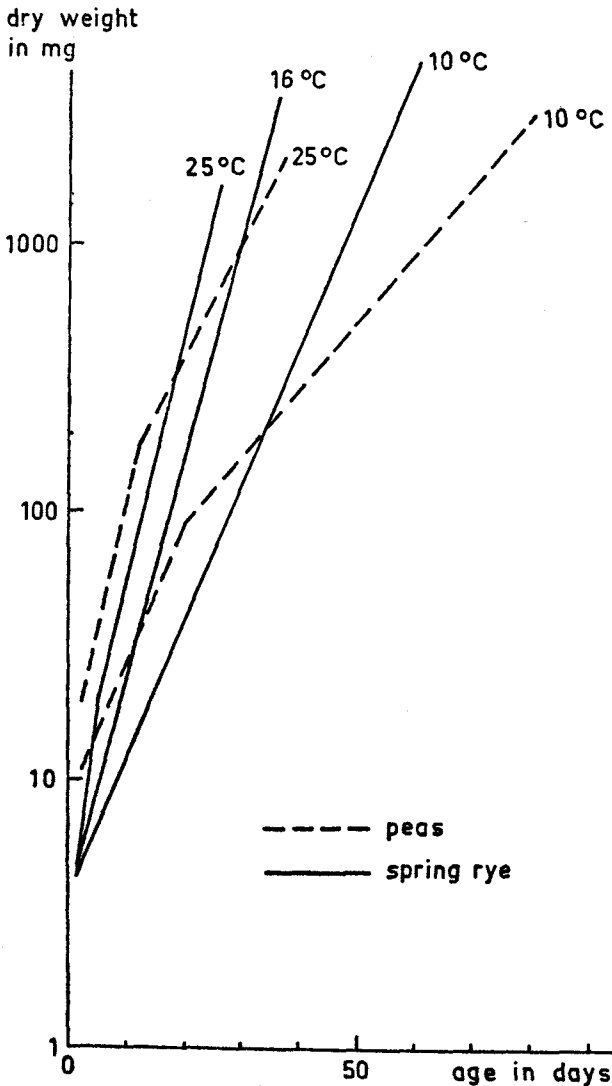


FIG. 2.

Increase in dry weight of pea and spring rye plants grown under optimal conditions at several temperatures. Logarithmic scale for ordinate. Seedling and vegetative post-seedling stage

4. The influence of light on distribution of material in the plant

Light intensity and light-colour influence the distribution of dry matter in the plant. Many light responses can be understood in this way. In etiolated shoots stem growth is maximal but leaf development is suppressed. When the shoots are illuminated relationships are presumably inverted by a different distribution of matter among the stem and leaves.

The vigorous growth of shoots in the absence of light corresponds to a high shoot/root-ratio. Apparently the material available is used as far as possible for stem growth and this, combined with a maximum cell elongation, gives the shoot a better chance to reach full daylight.

It is well known that light colour has a formative influence on plants. DOWNS, HENDRICKS and BORTHWICK (1957) have shown that "far red" radiation given in the dark period may elongate shoots and leaves. The results of our own experiments indicate that shoot elongations of this kind can be connected with an increased shoot/root-ratio (TABLE 5). Both incandescent filament lamps and low-pressure mercury lamps emit a great deal of "far red". Under these lamps plants develop relatively long and weak leavves. Shoot yield is above and root yield below the yield

TABLE 5. Influence of additional irradiation on yield and shoot/root-ratio of young plants of *Petkuser* winter rye sown January 16 in a greenhouse at 16° C and harvested February 12

Lamp type	Daily irradiation (p.m.—a.m.)	Dry weight (mg/plant)		Dry matter of tops (%)	Shoot/root-ratio
		tops	roots		
— (controls) . . . . .	—	87,0	27,0	9,8	3,2
Incandescent lamp 25 W . .	0—24	98,4	16,5	8,5	5,9
Low pressure mercury lamp 250 W	7—19	116,3	20,0	9,4	5,8
8 fluorescent tubes 60 W . . (Philips No. 33)	7—19	166,0	52,2	10,6	3,2

of controls, so that the shoot/root-ratio is considerably higher. When these plants are allowed to continue growing they gain an advantage over the controls in total yield which is readily explained by the larger leaf area. The low figures for dry-matter content indicate that "far red" radiation also stimulates the cell elongation that contributes to the formation of a large assimilating area. A fairly strong additional illumination with fluorescent tubes (without much far red) increases the yield considerably by high light intensity but does not influence the shoot/root-ratio.

Apparently the influence of light colour is especially important when the basic illumination is weak, for instance daylight in winter (in our own experiments) or a short daily illumination (DOWNS *et al.*, 1957).

The effect is also specific. In peas an elongation of the stem can be obtained with "far red", but the shoot/root-ratio is not affected.

5. The influence of temperature on the distribution of material in the plant

It can be concluded from the results presented in TABLES 4 and 6 that the shoot/root-ratio generally increases with temperature. This has also been observed by KHALIL (1956). At temperatures just above zero cereals and peas show ratios between 1 and 2. In the range 10—16° C much higher values are reached with great specific

TABLE 6. Shoot/root-ratio for plants grown in sandy soil with optimal mineral and water supply in greenhouses at several temperatures; sowing dates: Feb. 1 (10° C), Feb. 28 (16° C) and March 16 (25° C)

Temperature (°C)	Spring rye ( <i>Petkuser</i> )	Spring wheat ( <i>Peko</i> )	Spring barley ( <i>Herta</i> )	Oats ( <i>Marne</i> )	Peas ( <i>Rondo</i> )	Flax ( <i>Wiera</i> )	Maize ( <i>Pioneer m.</i> )	Beans ( <i>Beka</i> )
10	2,5	1,5	1,7	2,2	2,0	3,5	—	—
16	6,0	3,0	3,0	4,0	3,0	6,0	3,0	4,5
25	6,0	4,2	3,0	4,0	3,5	7,0	5,0	8,0

Note. To satisfy daylength requirements for long-day species extra light hours were supplied by single fluorescent tubes (Philips No. 33).

differences. Between 16° and 25° C several species seem to show a maximum or at least no further increase. The same applies to growth rate (TABLE 7). There are distinct differences between temperate zone crops and such subtropical crops as maize and beans. The latter only start growing at about 10° C. At higher temperatures the shoot/root-ratio and growth rate increase without reaching an optimum value within the range of our investigations.

TABLE 7. Number of days in which the dry weight of juvenile plants increased tenfold under optimal conditions; the figures are inversely proportional to the growth rate

Temperature (°C)	Spring rye	Spring wheat	Spring barley	Oats	Peas	Flax	Maize	Beans
10	22	32	20	23	42	27	—	—
16	14	22	12	20	27	23	19	33
25	13	20	11	18	23	20	9	15

Comparison of TABLES 6 and 7 shows a clear agreement in temperature response between shoot/root-ratio and growth rate. This is strong evidence that the response of growth to temperature is mainly governed by shifts in the shoot/root-ratio.

## 6. The influence of temperature on growth, development and the final plant weight

The yield is determined by both the growth rate and the length of the growth period. This period depends on the rhythm of development. The effect of the temperature on the length of the period from emergence to flowering is independent of the effect of temperature on growth. The mutual independence of growth and development has been emphasized in Russian work on phasic development, especially that done by LYSENKO. This concept seems to provide a good explanation of the influence of temperature on the final crop yield.

When the temperature is raised from 16° to 25° C vegetative growth in small cereals and peas is distinctly accelerated in the seedling, but only slightly in the following stage<sup>1</sup> (TABLE 7), whereas development is speeded up considerably (TABLE 8). As a result the plants remain smaller at 25° C as compared to 16° C (FIG. 3 and 5).

<sup>1</sup> In this connection it should be observed that seedling growth mainly depends on kernel reserves; this may explain its higher temperature optimum.



Figures 3-7

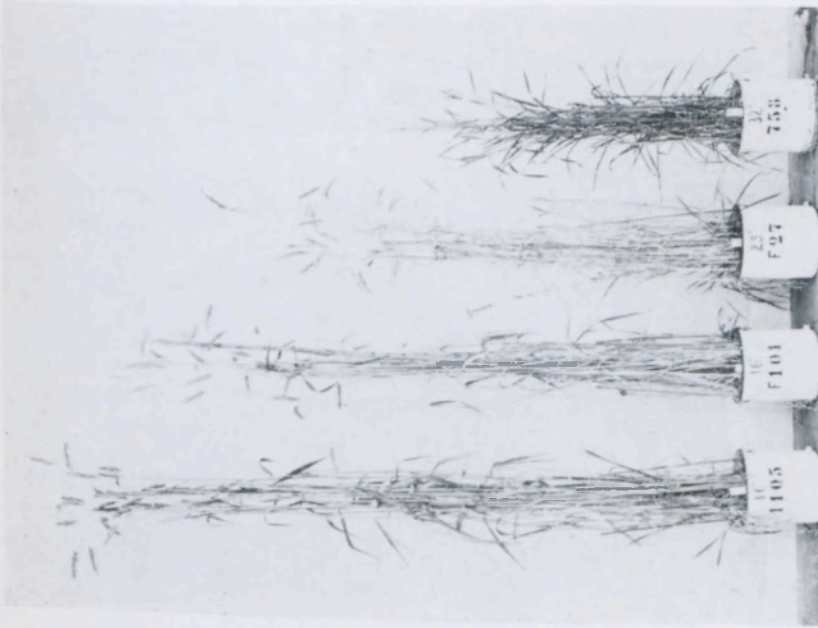


FIG. 3. *Petkus* spring rye, from left to right grown at 10 - 16 - 25 - 32° C respectively. The plants have reached their ultimate height

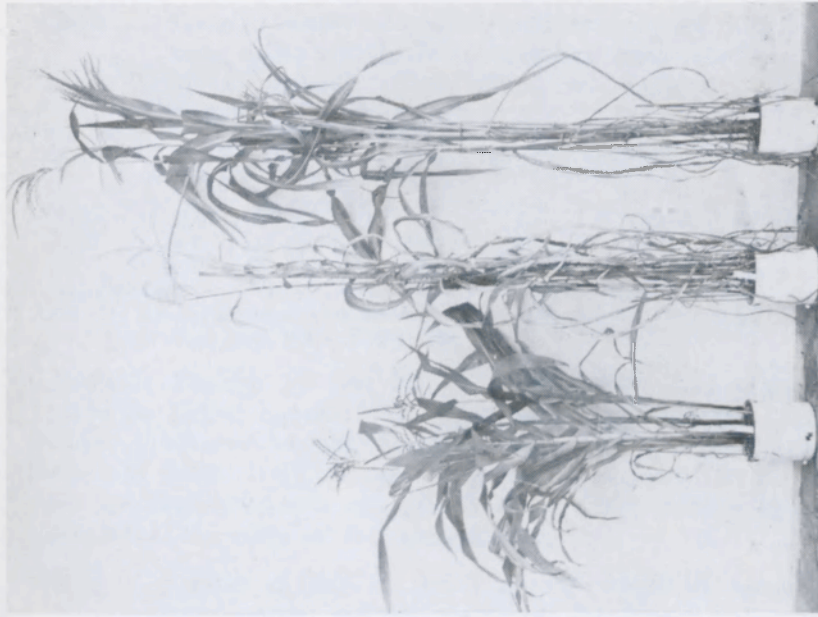


FIG. 4. *C.I.V.* 2-maize, from left to right grown at 16 - 25 - 32° C respectively; photographed after emergence of male inflorescence

FIG. 5. *Rondo* peas grown at 16° C (left) and 25° C (right); photographed at the beginning of flowering



FIG. 6. *Beka* beans grown at 16° C (left) and 25° C (right); photographed at the beginning of flowering



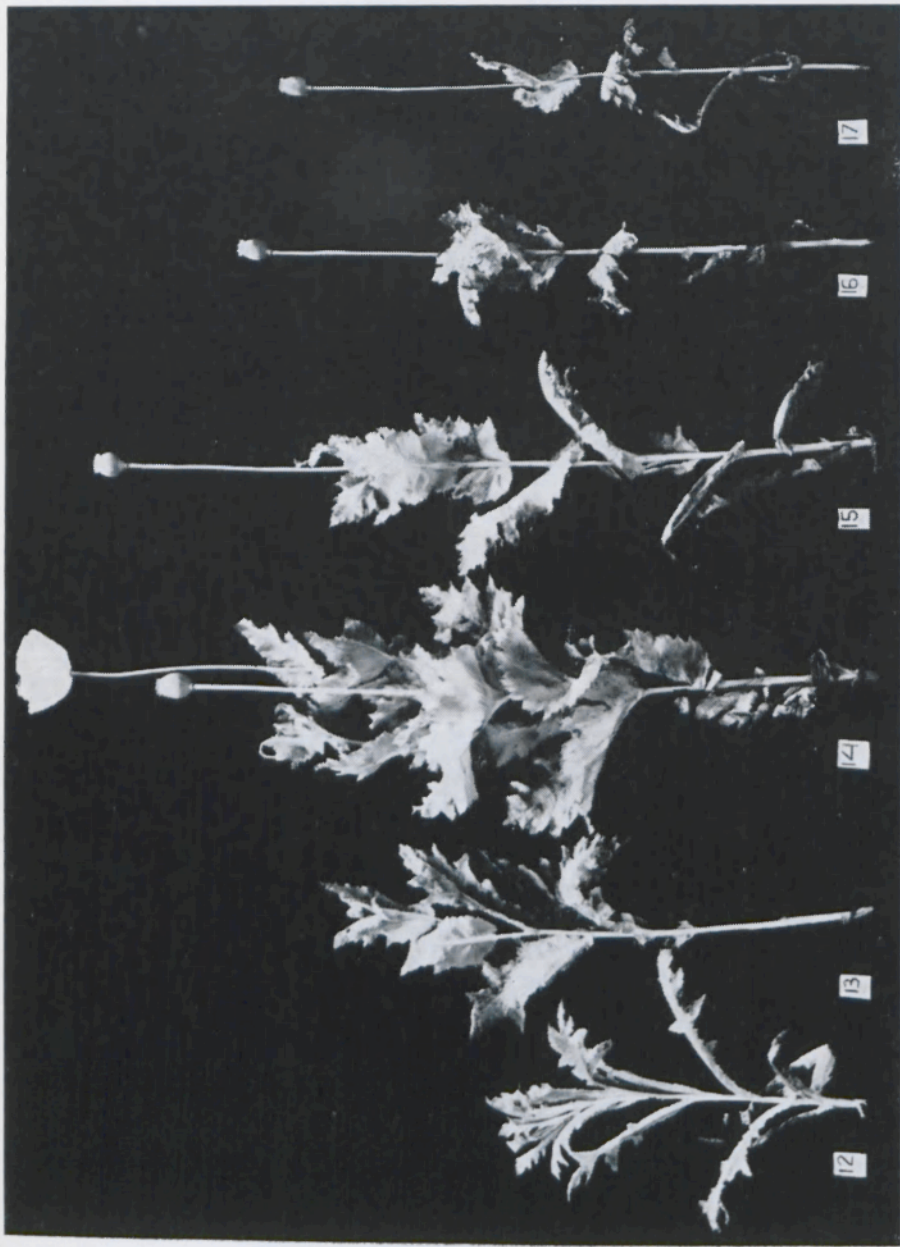


FIG. 7. A poppy variety of the temperate zone grown in full daylight during 12 hrs and afterwards exposed to artificial weak light to a total daylight of (from left to right) 12 - 13 - 14 - 15 - 16 - 17 hrs

TABLE 8. Number of days from emergence until heading (cereals) or flowering

Temperature (°C)	Spring rye	Spring wheat	Spring barley	Oats	Peas	Flax	Maize	Beans
10	82	129	99	115	86	100	—	—
16	51	70	63	68	52	65	87	46
25	37	57	52	50	37	50	50	24

At our institute BROUWER (1959) demonstrated this temperature effect for the first time with peas. The relation between temperature and final plant weight has been discussed by LUNDEGARDH (1954) who observed that the temperature optimum for the final size of rye is much lower than for seedling growth. His explanation that the growth optimum of rye decreases during development is not satisfactory. The temperature determines the ultimate size as the result of a mutually independent influence of temperature on growth (daily increment in weight) and development (length of the growth period). For small cereals and peas the time available for production is reduced by a rise in temperature without being sufficiently compensated by more vigorous growth, so that the plants remain smaller when the temperature is higher.

When the temperature is raised from 10 to 16° C the rates of growth and development are accelerated stronger than in the range 16—25° C but in this case the rate of development also shows the highest figures (TABLE 9). As a result the plant size is expected to decrease at about the same rate as in the range 16—25° C.

In the case of our present experiment the drop in final plant weight, however, was much greater than expected (TABLE 10). The reason may be that the plants at 10° C

TABLE 9. Acceleration of the rates of growth<sup>1</sup> and development<sup>2</sup> at a rise in temperature

Rise in temperature	Spring rye	Spring wheat	Spring barley	Oats	Peas	Flax	Maize	Beans
10—16° C								
Rate of growth . . .	1,4	1,4	1,7	1,2	1,6	1,2	—	—
Rate of development	1,6	1,8	1,6	1,7	1,6	1,5	—	—
16—25° C								
Rate of growth . . .	1,1	1,0	1,1	1,1	1,1	1,2	2,1	2,2
Rate of development	1,5	1,3	1,2	1,3	1,4	1,3	1,7	1,9

<sup>1</sup> Number of days in which the dry weight increased tenfold at 10° C (16° C) divided by the same value at 16° C (25° C).

<sup>2</sup> Number of days from emergence to flowering at 10° C (16° C) divided by the same value at 16° C (25° C).

TABLE 10. Dry weight (mg) of plants (tops) at the moment of heading (cereals) or first flowering attained at several constant temperatures

Temperature (°C)	Spring rye	Spring wheat	Spring barley	Oats	Peas	Flax	Maize	Beans
10	8780	16240	12000	16210	4880	3160	—	—
16	4560	11100	6790	9750	3220	2160	13660	3650
25	4050	7250	5400	7350	1970	1700	35150	4860

finished their growth in much stronger daylight. They were harvested in June whereas the plants at 16° C and 25° C were harvested almost simultaneously in the beginning of May.

It is sure, however, that even under constant light conditions there is a general tendency for temperate zone crops (small cereals, peas, flax) to reach large proportions in cooler climates and this is the main reason why even the day-neutral varieties of these crops (for instance canning peas) are unable to give high yields when sown late in spring.

For maize and beans reverse relations prevail. When the temperature rises from 16° to 25° C growth is accelerated relatively more than development (TABLE 9), so that the plants finally become larger (FIG. 4 and 6, TABLE 10). Hence maize and beans have the faculty of compensating and even overcompensating the acceleration of development at higher temperatures by a relatively still greater increase in daily growth rate. This faculty is probably typical of species originating from warm climates. Without it, annuals in tropical regions would never reach large proportions.

As TABLE 9 shows, the specific differences in temperature response are greater for growth rate than for development, and since growth rate is apparently mainly governed by the shoot/root-ratio it may be suggested that the distribution of material in the plant is the key to the important problem of the influence of temperature on plant production.

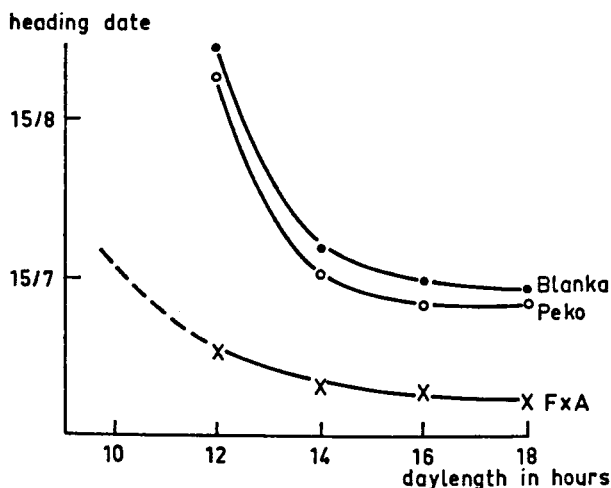


FIG. 8.

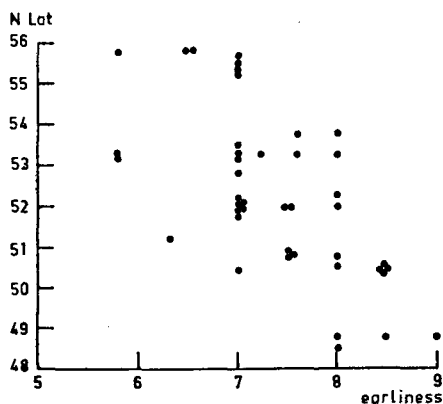
Influence of daylength on heading date of three spring-wheat varieties: *Blanka* (Swedish), *Peko* (German) and *Florence* × *Aurore* (Australian, grown in the Mediterranean region)

## 7. The impact of photoperiodicity on yield

The final yield of a crop is largely determined by its longevity. For instance, it is well known that a late potato variety can produce more than an early one. Longevity, however, depends on phasic development, and this in turn is influenced by climatic factors. Consequently temperature and light conditions have both an indirect and direct impact on yield. The influence of temperature on development has already been demonstrated in the preceeding section. The role of daylength will now be discussed.

The length of the juvenile stage largely determines the size a plant reaches at flower-





where they are grown. For Western Europe the same has been demonstrated for wheat (FEEKES, 1941).

FIG. 8 gives an example from own experiments. The spring wheat variety *Peko* shows approximately the same daylength response as the poppy variety from FIG. 7. From an agricultural point of view developmental rhythm for this variety is optimal in a daylength of 14 hours. This daylength prevails in the Netherlands at the time when the young plants become sensitive to photoperiod (April). This is of decisive importance for the good results obtained with this variety. In the experiment recorded in FIG. 8 the treatment with a daylength of 14 hours headed on July 15. The Scandinavian-bred variety *Blanka* has the same heading date (and therefore a good developmental rhythm) in the daylength of about 16 hours which prevails in Southern Scandinavia when spring wheat emerges. In our experiment the Australian variety *Florence*  $\times$  *Aurore*, which is widely grown in the Mediterranean region as a winter crop, headed on July 15 in a daylength of about 11 hours (by extrapolation). This is exactly the photoperiod it receives in the field in February when the young plants are in the sensitive stage.

The well-known experience that wheat varieties from the north grown in the Netherlands are "late", whereas French varieties are "early" can also be explained by daylength response. For northern forms our daylength is "short", for French varieties "long". It could be shown that figures for "earliness" given to winter wheat varieties in the Netherlands "List of Varieties" are correlated to the latitude where they are bred (FIG. 9). This implies that a universal variety of a crop with a clear daylength response is an impossibility. A relationship of the kind shown in FIG. 9 could not be established for spring barley. Barley, although a long-day plant, has a far weaker response than wheat, oats and rye. This is also the reason why it is acceptable as a catch crop. When sown late in spring (in long days) it maintains a reasonable growth period.

Difficulties with maize in northern regions are connected with its short-day habit. For this crop in particular the breeding of day-neutral forms is imperative. It could be shown that such forms are quite common in collections of land varieties. From the agricultural point of view daylength response is as important for potatoes as for seed crops (BODLAENDER, 1958). All varieties grown in the Netherlands are accelerated in tuber formation by short day. In 12—13 hours light plants have a short juvenile phase. This means that tuber growth begins early. As a result the haulm remains limited in size, does not flower and ripens early. High yields are only obtained in long days when tuber initiation is retarded, enabling the haulm to reach a large size and a long growth period. It was shown by BODLAENDER (personal communication) that potatoes planted in March for early consumption are accelerated in tuber formation by the relative short days during emergence in April. This is of practical significance for this type of crop where earliness is more important than yield.

In mountainous tropical and subtropical regions with their shorter days Dutch potato varieties develop too rapidly and are unable to obtain the yield of the temperate zone, but they may be esteemed owing to their freedom from diseases. According to unpublished results obtained by BODLAENDER the important export variety *Alpha* shows a weaker response to daylength than other Dutch varieties and this may contribute to its good performance in southern regions.



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