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Phytotron Cultivation of Early Barley Mutants

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Conclusions. The authors have tried to gather data which permit some information on the between and within locus reactions of induced early barley mutants to different photo- and thermoperiods. Eight mutant cases, showing rather drastic earliness in field cultivation and representing three different gene loci, were examined in phytotron experiments according to routine methods of cultivation. One of the mutants, *mat-a*^{8}, has been released as an original Swedish barley variety under the name of Svalöf's Mari. In a previous publication (DORMLING et al., 1966) this mutant was compared to its parent variety, Svalöf's Bonus, under 30 different climatic conditions. In the present investigation three photoperiods (24, 16 and 8 hours of artificial light) were combined with three suitable thermoperiods (20–15°, 20–10° and 15–10 °C).

The results indicate that photoperiodic insensitivity, with regard to ear formation and heading capacity, as well as kernel production, is of rather frequent occurrence in connection with drastically early mutants in barley. Four out of eight induced mutants give a more or less pronounced insensitivity. Three of the four insensitive mutants represent locus *a*, one belongs to locus *b*. Of the two *c*-mutants none was insensitive; both were on the contrary pronounced long-day types.

Photo- and thermoperiods interact in various ways. This is especially clear in the *c*-mutants just mentioned, which have a high generative productivity and efficiency at continuous light and high thermoperiods. They produce no grain but considerable vegetative matter at 8 hours of light, independently of thermoperiod, as well as at 16 hours of light with high temperatures. In fact, mutants of loci *a* and *c* differ strikingly with regard to their relations to the climatic conditions applied. The insensitive mutant b^{13} is remarkably similar to the mutant a^{12}, but its resemblance to the sensitive mutants b^7 and b^{10} of the same locus is evidenced by its high average internode number.

It ought to be pointed out here that the mutants of the three gene loci analysed in this study can be distinguished phenotypically with regard to morphological as well as physiological properties, in the field as well as in phytotron cultivation. The *c*-mutants are especially characteristic. However, there also seem to be clear differences in reaction between the allelic mutants of a locus. In fact, all eight mutants studied seem to react more or less differently.

The insensitive mutant a^8, which has been released into practice, is also widely used in recombination work, and successful segregates have been isolated. The characteristics of a^8, which make the mutant valuable in practice, are also found in phytotron experimentation, specially with regard to earliness, generative efficiency and yield. Also the semidwarf habit and the insensitivity to changes in photo- and thermoperiods readily show up.

Material for the study

It was shown in a paper by DORMLING *et al.* (1966) that Mari barley, arisen as an X-ray mutant of Bonus barley, has a changed photo- and thermoperiodic response compared to its parent variety. Mari was to a great extent "photoperiodically insensitive", since it was able to form seed at photoperiods of 24, as well as 16 and 8 hours. Bonus barley, on the other hand, gave a pronounced long-day reaction with no seed formation whatsoever at an 8 hour photoperiod. It is here denoted as "photoperiodically sensitive". Evidence was also presented that Mari reacted to high temperatures with a better seed setting than Bonus.

Mari barley is an early mutant, rather drastic in expression, previously denoted as early-a^8 or *ea*-a^8 (GUSTAFSSON *et al.*, 1960). According to a recent proposal of gene nomenclature in barley (GUSTAFSSON *et al.*, 1968) this denotion should be changed to *mat-a*^{8} (from "maturus", Latin for early). A series of mutant loci are involved in the drastic increase of earliness. Three of these gene loci are denoted as *mat-a*, *mat-b*, and *mat-c*, each locus possessing a series of alleles.

It was considered important to study the photo- and thermoperiodic reactions of some early mutants with common ancestry but belonging to different gene loci. We chose for examination the following eight mutants arisen from Bonus barley (cf. GUSTAFSSON *et al.*, 1960, p. 676):

mat-a^8,	isolated 1950, induced by 20000 r of X-rays
a^{11},	isolated 1953, induced by chronic gamma irradiation
a^{12},	isolated 1954, induced by fast protons
mat-b^7,	isolated 1950, induced by 5500 r of X-rays
b^{10},	isolated 1952, induced by 10000 r of X-rays
b^{13},	isolated 1954, induced by 540 rep of neutrons
mat-c^{16},	isolated 1955, induced by 960 rep of neutrons
c^{19},	isolated 1956, induced by 400 rep of neutrons

The mutants have special phenotypical characteristics according to their locus derivation. Locus *b*-mutants are generally more productive in the field than the *a*-mutants but, on the other hand, less lodging resistant, partially owing to another culm and internode structure. Locus *c*-mutants differ strikingly in morphological respects, especially with regard to ear length and spikelet number. To the trained eye there is no great difficulty in recognizing the chief gene loci involved in the strongly increased earliness of mutants from Bonus barley. Allelic mutants are to some extent distinguishable; they differ with regard to degree of earliness, productivity, internode structure, and often in general appearance. Mutant b^{10} deviates from the other *b*-mutants in having a reciprocal chromosome translocation in addition to the mutated *b*-locus.

Cultivation methods

Experience from phytotron cultivation has indicated that the optimal temperatures for growth and seed setting of Swedish barley varieties are 15 °C continuously, or 15—10° (DORMLING *et al.*, 1966, as well as unpublished data) under a photoperiod of 16 to 24 hours of light. On the other hand, temperatures of 25° continuously or in different combinations with lower night temperatures, are generally unsuitable for barley cultivation. This is valid with regard to Bonus but also, although not so pronounced, to Mari. The following nine climatic conditions were chosen in this study:

24 hours of light — temperatures 20—15 °C
temperatures 20—10°
temperatures 15—10°

16 hours of light — temperatures 20—15°
temperatures 20—10°
temperatures 15—10°

8 hours of light — temperatures 20—15°
temperatures 20—10°
temperatures 15—10°

(For day and night temperatures, *cf.* DORMLING *et al.*, l.c., p. 222.)

Relative humidity was controlled at the 75—80% level. Light intensity amounted to circa 20000 lux (2000 foot candles) at seedling level. Seven plants per mutant case and condition were cultivated in pots on wheeled trucks according to methods outlined in the paper by DORMLING *et al.* (l.c.) and continuously standardized for the barley work by D. VON WETTSTEIN, GUSTAFSSON and others. The Hoagland solution was used throughout as a suitable nutrient in barley cultivation. For general information on the Stockholm phytotron and methods applied, *v.* also the papers by GUSTAFSSON (1965) and WETTSTEIN (1967).

In the following analysis special attention is paid to the end stage of development, i.e. the time of plant maturity and harvest. Some notes are added, however, concerning earlier developmental stages. Juvenile growth varies with the gene loci involved and is sometimes quite characteristic also of the individual alleles within a locus.

Vegetative versus generative growth

In Table 1 data are gathered with regard to vegetative and generative development at harvest time. The table presents the *total* number of shoots comprising three kinds: vegetative shoots without ear formation, generative ones with ear formation but without ears heading, and generative ones with ears heading. In the last three columns the number of heading tillers, with awns clearly protruding, is given. Since not heading tillers were left undissected with regard to ear formation, the second group is not separately tabled. Dissection data are however included in Table 4, dealing with dry weights of vegetative and generative parts.

Photo- and thermoperiods exert a striking influence on the total number of shoots developed. They also interact in a definite way.

With 24 hours of continuous light shoot number is very high at 20—15°, mostly intermediate at 20—10°, and decidedly reduced at 15—10°. This is evident in all mutant cases irrespective of gene locus. A similar relationship is found with regard to the number of heading tillers.

With 16 hours of light there are striking differences in total shoot number between 20—15°, on the one hand, and the lower temperatures of 20—10° and 15—10°, on the other, and this rule holds true with regard to most mutants of loci *a* and *b* (cf. Plate 1b and e). In the case of the *c*-mutants, and also b^7, the highest two temperatures are definitely superior to the lowest temperature as to shoot formation. The number of heading tillers seems to behave in a similar way.

With 8 hours of light the phenotypical reactions profoundly change. At this photoperiod the highest number of shoots appears at a temperature of 15—10°, the number of shoots decreases at 20—10° and gives a low value at 20—15°. All gene loci and alleles show the same reaction. With regard to the number of heading spikes four mutants behave as photoperiodically insensitive, four as photoperiodically sensitive. In the former group we find the mutants a^8, a^{11}, a^{12} and b^{13}, in the latter group b^7, b^{10}, c^{16} and c^{19}. The insensitive *a*-mutants give similar reactions with regard to heading tillers and total number of shoots, i.e. the higher the temperature conditions the lower the number of heading tillers. The insensitive mutant b^{13} has its maximum of heading tillers at the medium temperature condition. The sensitive mutants produce some heading tillers at low temperature (15—10°), none or almost none at the thermoperiod 20—15°.

The genotype interactions with climatic conditions are obvious. As compared to the *a*- und *b*-mutants the *total number of shoots* is throughout superior in the case of *c*-mutants at all photoperiods and temperatures, and especially conspicuous at 16 hours of light. The *a*-mutants are superior to the sensitive *b*-mutants at 24 hours of light and at high tempera-

Table 1. *Total number of shoots and heading tillers in early mutants of Bonus barley*

	Total No. of shoots/plant[1]			Number of heading tillers/plant[1]		
	20—15°	20—10°	15—10°	20—15°	20—10°	15—10°
24 hours of light						
a^8	40.6	35.4	15.6	31.0	23.8	14.2
a^{11}	33.4	24.2	11.2	23.0	15.6	10.6
a^{12}	33.4	33.4	23.2	23.2	19.8	18.2
b^7	23.4	17.6	12.2	15.2	12.0	10.6
b^{10}	22.6	18.2	12.0	15.2	13.2	10.6
b^{13}	36.0	31.4	21.8	25.8	17.4	17.2
c^{16}	41.0	40.6	23.2	33.6	29.8	21.8
c^{19}	42.4	36.8	29.6	32.4	27.6	24.2
Harvest; No. of days after sowing	91	92	112	91	92	112
16 hours of light						
a^8	32.0	24.2	21.4	24.0	18.2	17.2
a^{11}	34.4	23.4	21.2	22.2	18.2	17.0
a^{12}	39.2	21.2	21.4	23.0	17.6	15.8
b^7	32.0	25.2	12.4	24.4	15.2	12.0
b^{10}	34.4	17.2	17.2	21.6	14.8	15.4
b^{13}	36.8	21.0	21.4	21.0	14.8	15.4
c^{16}	66.6	52.0	31.4	43.4	39.2	24.8
c^{19}	53.4	49.4	33.8	37.8	34.0	25.6
Harvest; No. of days after sowing	97	99	120	97	99	120
8 hours of light						
a^8	11.8	18.8	33.2	11.4	14.0	22.6
a^{11}	16.4	19.8	36.2	12.6	14.2	22.6
a^{12}	17.8	32.4	42.4	15.0	21.6	25.2
b^7	18.4	20.8	32.8	0	1.6	0.8
b^{10}	18.4	19.8	34.2	0	0.6	0.8
b^{13}	16.6	34.8	39.4	13.4	23.4	19.0
c^{16}	19.0	42.0	48.4	1.0	4.8	4.0
c^{19}	22.4	43.8	51.8	0	2.2	2.4
Harvest; No. of days after sowing	112	142	153	112	142	153

[1] Average of five plants per mutant case and condition.

tures. The insensitive b^{13} deviates from the two other alleles of the locus. With 16 hours of light the six *a*- and *b*-mutants are almost equal at high temperatures, but at 15—10° the *a*-mutants are superior to b^7 and b^{10}. With 8 hours of light the six *a*- and *b*-mutants are all equal, independent of the thermoperiod.

Heading tillers are more frequent in the insensitive mutants than in the two sensitive *b*-mutants with 24 hours of light at 20—15° and 20—10°, but equal in number at 15—10°. With 16 hours of light the differences almost disappear. With 8 hours of light the number of heading tillers is equal in the three *a*-mutants and in the insensitive b^{13}.

This analysis indicates genotype-climate interactions both of gene loci and alleles. The high tillering ability of the *c*-mutants in the case of high temperatures with 24 or 16 hours of light and at low temperatures with 8 hours of light is especially striking.

The analysis of *kernel production* illustrates in the same manner locus and allele differences, as well as genotype-climate interactions (Table 2). The figures given are means of 25 spikes and 5 plants per condition. No evident differences have been found between the analysed spikes of a plant as to kernel number. The data indicate that in the case of insensitive mutants kernel number per spike greatly increases to a maximum at the thermoperiod of 15—10° independent of light constellation. The same is true of the sensitive mutants with 24 and 16 hours of light. This is in agreement with the phytotron experience gathered. (Note here that, according to Table 3 in DORMLING *et al.*, l.c., p. 227, the kernel number is highest at a constant temperature of 10°, which, however, unduly prolongs the growth period.)

The *a*-mutants give a fairly good kernel production at all three thermoperiods, also at extreme short-days (8 hours of light). Mutant b^{13} closely approaches the *a*-mutants in its behaviour to photo- and thermoperiods. Mutants b^7 and b^{10} almost entirely lack kernels at 8 hours of light, indicating an exclusively vegetative growth. At 16 hours of light the interaction with temperature is obvious. In spite of the high capacity

Table 2. *Number of kernels at the time of maturity (average of 5 plants and 25 spikes per allele and condition)*

Light, hours	24			16			8		
Temperature °C	20—15	20—10	15—10	20—15	20—10	15—10	20—15	20—10	15—10
locus a^8	15.8	15.5	24.0	12.0	18.1	23.4	8.0	14.3	18.6
a^{11}	14.0	13.6	22.6	10.1	14.6	21.7	8.8	15.5	17.3
a^{12}	14.9	20.6	23.0	9.3	19.8	21.1	4.5	12.6	10.5
b^7	16.5	16.8	20.4	1.8	4.3	24.9	0	0	0
b^{10}	15.2	14.8	21.1	0.7	3.0	24.6	0	0.1	0
b^{13}	12.8	15.7	24.0	11.6	20.0	22.5	5.1	12.1	11.4
c^{16}	10.3	11.9	17.0	0.6	2.2	18.2	0	0.6	0.9
c^{19}	10.0	11.3	15.4	1.1	2.9	17.9	0	1.0	0.3

Table 3. *Spike fertility (the number of kernels in per cent of the total number of spikelets per spike) in photoperiodically insensitive mutants (a^8, a^{11}, a^{12}, b^{13}) and photoperiodically sensitive mutants (b^7, b^{10}, c^{16}, c^{19})*

Light, hours	24			16			8		
Temperature °C	20—15	20—10	15—10	20—15	20—10	15—10	20—15	20—10	15—10
Insensitive mutants	61	78	87	49	77	96	38	74	71
Sensitive mutants	84	84	90	5	15	92	—	—	—

Table 4. *Relative productivity at maturity (dry weight, highest and lowest values: grams/plant): order of performance*

	24 hours			16 hours			8 hours		
	20—15°	20—10°	15—10°	20—15°	20—10°	15—10°	20—15°	20—10°	15—10°
Vegetative parts	b^{13}	a^8	b^{13}	b^7	b^{10}	b^{10}	b^{10}	b^{10}	b^{10}
	a^{12}	b^{13}	a^{12}	b^{10}	b^7	c^{16}	c^{19}	b^7	b^7
	a^{11}	a^{11}	c^{16}	c^{16}	c^{16}	b^7	c^{16}	c^{16}	c^{19}
	a^8	a^{12}	a^8	c^{19}	c^{19}	c^{19}	b^7	c^{19}	c^{16}
	b^7	c^{16}	c^{19}	a^{12}	a^{11}	a^{11}	a^{12}	a^{12}	a^{12}
	c^{16}	b^7	a^{11}	b^{13}	b^{13}	a^{12}	b^{13}	b^{13}	b^{13}
	b^{10}	b^{10}	b^7	a^{11}	a^{12}	a^8	a^{11}	a^{11}	a^{11}
	c^{19}	c^{19}	b^{10}	a^8	a^8	b^{13}	a^8	a^8	a^8
Highest value, g	8.00	7.40	12.32	11.78	12.26	13.10	8.98	15.72	22.16
Lowest value, g	5.22	5.68	8.50	5.58	5.06	8.18	2.06	3.44	6.48
Generative parts	b^7	c^{16}	a^{12}	a^8	a^8	c^{19}	a^{11}	a^{11}	a^8
	c^{19}	a^8	b^{13}	a^{11}	b^{13}	c^{16}	b^{13}	b^{13}	a^{11}
	c^{16}	c^{19}	a^8	b^{13}	a^{11}	a^8	a^{12}	a^{12}	a^{12}
	a^8	b^7	c^{16}	a^{12}	b^7	b^{10}	a^8	a^8	b^{13}
	a^{11}	a^{12}	c^{19}	b^7	a^{12}	a^{11}	b^{10} [1]	c^{16} [1]	c^{16} [1]
	b^{10}	a^{11}	b^7	b^{10}	b^{10}	b^{13}	c^{16}	c^{19}	c^{19}
	a^{12}	b^{10}	a^{11}	c^{16}	c^{16}	a^{12}	b^7	b^7	b^7
	b^{13}	b^{13}	b^{10}	c^{19}	c^{19}	b^7	c^{19}	b^{10}	b^{10}
Highest value, g	9.42	10.44	15.64	6.44	7.90	14.66	2.20	4.08	6.42
Lowest value, g	6 24	7.98	10.20	1.68	2.66	11.50	0.04	0.30	0.16

[1] Below 1 g/plant.

of ear formation the kernel number is very low in b^7 and b^{10} at the thermoperiods of 20—15° and 20—10°, but normal at 15—10°. At 8 hours of light b^{13} has a high number of heading tillers and a kernel number almost equal to that of the a-mutants. Mutants b^7 and b^{10} give few or no heading tillers, and the heading ones produce no kernels. On the whole, the two c-mutants react as the two sensitive b-mutants.

The calculation of the actual *spike fertility* (ratio of number of kernels to total number of spikelets per spike, Table 3) further indicates that the thermoperiod 15—10° leads to the best generative results, in fact to an almost complete fertility. This is specially the case applying 16 hours of light.

At 24 hours of light the sensitive mutants show high fertility in all three thermoperiods. Consequently at continuous light the photoperiodically sensitive mutants are "*thermoperiodically insensitive*". At 16 hours of light the fertility has a maximum at 15—10° both in the insensitive and the sensitive mutants. At higher temperatures the fertility is good in the insensitive mutants but very low in the sensitive ones. At 8 hours of light mutants a^8 and a^{11} are highly fertile. Here mutants a^{12} and b^{13} react less well. b^7 and b^{10} are completely sterile. In c^{16} and c^{19} a few kernels are formed at low temperatures.

Plate 2 shows spikes from three mutants under favorable conditions (15—10° with 24 and 16 hours of light). *Continuous light* gives rise to stiff, well-developed ears. The *c*-mutants have very short ears, here illustrated by c^{16}; mean length without awns being 72.6 mm *versus* 93.6 mm in a^8 and 86.9 mm in b^7. At the *16 hour photoperiod* the ears grow slender. The *c*- and *a*-mutants have about the same spike length as under continuous light, whereas the sensitive *b*-mutants obtain extremely long ears (in b^7 the average value is 106.1 mm).

The evidence presented in this chapter indicates that for the eight early mutants tested the thermoperiod 15—10° leads to the best results in phytotron cultivation, just as is the case in Bonus, the parent variety itself. Continuous light, or a 16 hour photoperiod, give approximately the same results at this thermoperiod. However, in the early mutants as well as in Bonus a change from 16 hours to continuous light speeds up development and shortens the time from sowing to maturity with 7—8 days.

Dry weights at maturity

Dry weights were recorded for vegetative and generative parts (1 and 2) according to principles outlined in our work on Mari barley (DORMLING *et al.*, l.c., p. 231). "Vegetative parts" comprise straws and leaves of a plant up to the base of the spikes. Consequently the "generative parts" include in addition to kernels also glumes, rachis and awns. In fertile spikes the kernel matter predominates. Root system was not included in the analysis. The ratio between 1 and 2 is an indication of the generative efficiency. The lower the ratio, the higher is the generative efficiency, and *vice versa.* The results previously reported led to the conclusion that with 8 and 16 hours of light Mari barley was consistently superior to Bonus in generative efficiency. It was also superior, in the case of continuous light, at nine out of ten temperature conditions.

In order to facilitate the discussion Table 4 only gives the sequence of dry matter production for each climatic condition, beginning with the highest and ending with the lowest value of dry weight.

First the reaction of individual alleles and loci. Consider for instance mutant a^8. With 24 hours of light its vegetative and generative dry weights balance each other at all thermoperiods. Its produce of vegetative matter gives a relative mark of 9 (4 + 1 + 4); that of generative matter is also 9 (4 + 2 + 3). With 16 and 8 hours of light the situation is markedly changed. In the 16 hour photoperiod the values are 23 (8 + 8 + 7) for vegetative matter, but 5 (1 + 1 + 3) for generative matter. With 8 hours of light its vegetative produce has a value of 24 (8 + 8 + 8), its generative produce lies at 9 (4 + 4 + 1).

A different behaviour is shown by the mutant b^{13}, insensitive like the *a*-mutants. With 24 hours of light it has a high vegetative produce (4 = 1 + 2 + 1), but its generative capacity is low at 20—15° (8) and 20—10° (8), high at 15—10° (2). With 16 hours of light its vegetative production is low (20 = 6 + 6 + 8), its generative yield relatively good (11 = 3 + 2 + 6). With 8 hours of light it behaves like the *a*-mutants is vegetatively better (18) and generatively at least as well (8) as a^8. The mutants b^{13} and a^{12} approximately react in the same way.

Mutant c^{19} may illustrate the behaviour of the *c*-locus. With 24 hours of light and high temperatures it produces less vegetative matter than the other seven mutants, but is fairly high in generative yield. With 16 hours of light it is medium with regard to vegetative matter, low in generative yield at high temperatures but best of all eight mutants at 15—10°. With a photoperiod of 8 hours like b^7, b^{10} and c^{16} it is rich in vegetative matter but, as previously shown, produces little grain.

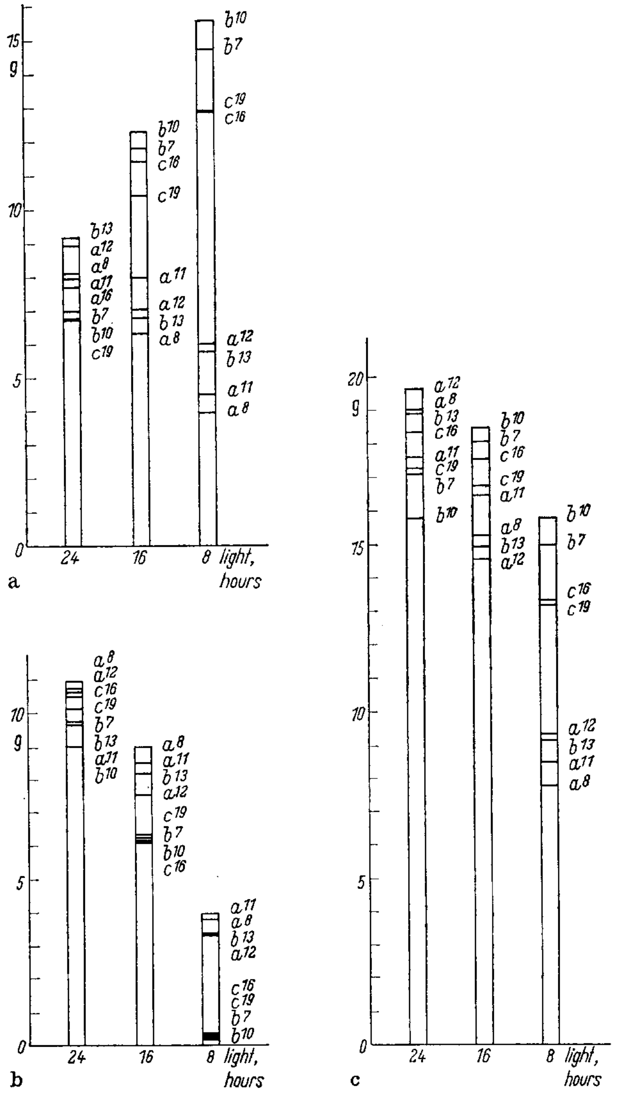

Fig. 1. Dry matter production per plant in different *photoperiods.* Means of 15 plants (5 from each thermoperiod). a: vegetative matter, b: generative matter, c: total production

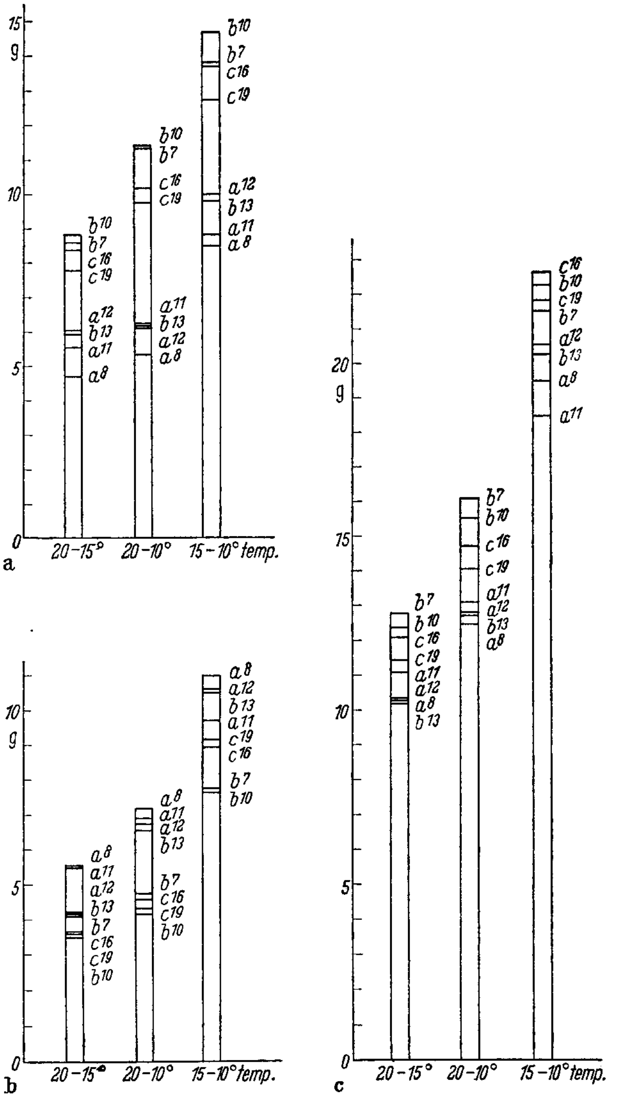

Fig. 2. Dry matter production per plant in different *thermoperiods*. Means of 15 plants (5 from each photoperiod). a: vegetative matter, b: generative matter, c: total production

Dividing the nine climatic variables into two groups: (1) with regard to *photoperiod*, (2) with regard to *thermoperiod*, we obtain a sequence of production as illustrated in Figs. 1 and 2.

These data show that in the case of *photoperiod variations* the four insensitive mutants are, on the whole, leading in generative production (Fig. 1 b), the best mutant being a^8 (Mari). With 24 hours the differences of the eight mutants are slight. At other photoperiods the four sensitive mutants decrease considerably. With regard to vegetative matter (Fig. 1 a) the situation is unclear at 24 hours of light, but at 16 and 8 hours the insensitive mutants drop down. Taking total production into account (Fig. 1 c), the insensitive mutants occupy the three first places with continuous light but all of them drop to the bottom with 16 and 8 hours of light. In vegetative and total production with 16 and 8 hours mutant b^{10} (having a translocation) leads the series but is the last one with 24 hours of light.

In the case of *thermoperiod variations* and generative matter (Fig. 2b) the insensitive strains are even more dominating, with mutant a^8 at the absolute top. Considering vegetative matter (Fig. 2a) the insensitive strains are the least productive ones, with a^8 at the bottom and b^{10} at the top. Similarly, with regard to total production the insensitive strains are inferior. Fig. 3 illustrates the generative productivity at 16 hours of light at different temperatures. The influence of the thermoperiod is most pronounced in the sensitive mutants, especially in c^{19} and c^{16}.

The absolute figures of dry matter production per plant as to *the generative phase* are given in Fig. 4, where the different photoperiods (24, 16 and 8 hours), as well as the thermoperiods (20—15°, 20—10° and 15—10°), are given the numbers 1, 2, 3 for each type of variables. For instance, 24 hours of light and the thermoperiod 20—15° is denoted as 11, 16 hours of light and 15—10° as 23, 8 hours of light and 20—10° as 32.

The production ranges from 15.64 gram per plant in a^{12} down to less than 1 gram in the photoperiodically sensitive mutants. In mutants a^8 and a^{11} seven conditions give a production of 5 grams or more per plant. In a^{12} and b^{13} five conditions surpass this level, and in b^7, b^{10}, c^{16} and c^{19} only four conditions.

Both in the sensitive and insensitive mutants conditions 13 and 23 produce more than 10 grams generative matter per plant (in c^{16} also condition 12). In fact, the parallelism with regard to the productivity at different conditions is pronounced. In the sensitive strains condition 23 gives the highest values. In the insensitive strains, except in a^{11}, the corresponding top values are produced in condition 13.

The highest values of any mutant is reached in the case of a^{12} and b^{13} applying 24 hours of light and a thermoperiod of 15—10°. Considering the four best

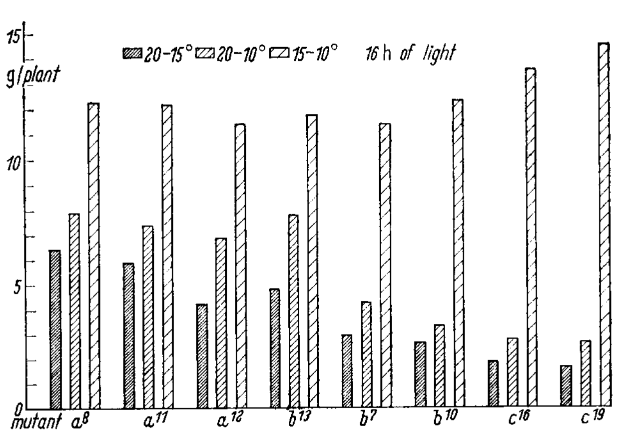

Fig. 3. Dry weights of the generative parts at 16 hours of light and different thermoperiods

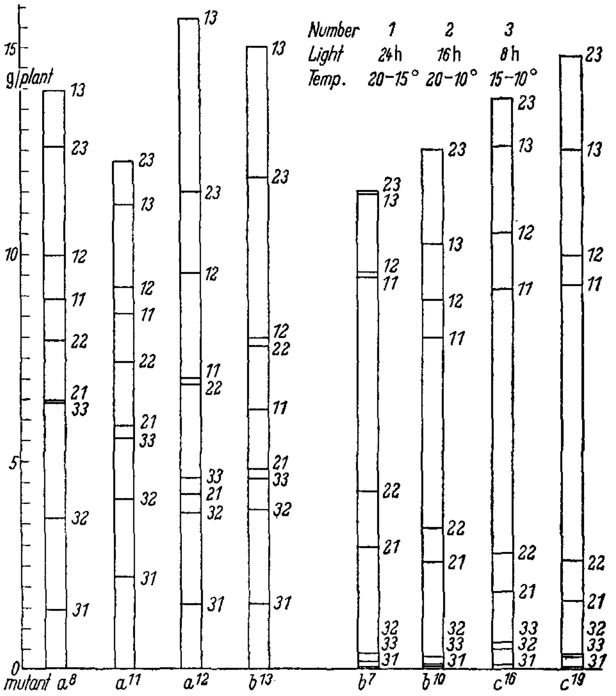

Fig. 4. Dry matter production of the generative phase in different climatic conditions. Further explanations in the text

conditions (generally 13, 23, 12 and 11; in the case of b^{13}, however, 22 instead of 11) the sequence of productivity is:

Mutant	c^{19}	c^{16}	a^8	a^{12}	b^{13}	b^7	a^{11}	b^{10}
g/plant	11.54	11.42	11.35	10.92	10.67	10.48	10.31	9.87

Mutants c^{16} and c^{19} are long-day adapted like their parent variety Bonus and possess no special feature of value except earliness in direct field cultivation. (Possibly they may be used in recombination work intended to lead to very early high-productive long-day types.) The reason why mutant a^8 was directly fit for release into agriculture was its increased earliness, its high lodging resistance (correlated with a kind of semi-dwarf habit), and its high productivity under appropriate field conditions. This high productivity is combined with a wide insensitivity to photo- and thermoperiod.

Generative efficiency

Generative efficiency is here determined as the ratios of the dry weights of vegetative *versus* generative matter. These ratios are presented in Table 5. Values below 1.0 indicate that the weight of generative matter of a plant is superior to the weight of vegetative matter.

The data show that the early long-day mutants (sensitives) give a continuous increase in ratio size at shorter photoperiods, independent of thermoperiod. The same holds true of the insensitives at a high thermoperiod (20—15°) and is also evident at the two lowest thermoperiods (20—10° and 15—10°) applying 8 hours of light.

Comparing insensitives and sensitives the conspicuous increase in ratios of sensitives at 16 hours of light is evident. Applying 8 hours of light this increase becomes striking.

Mutant a^8 works more efficiently than the other three insensitives in seven out of nine conditions, and is also better than two of them (a^{12} and b^{13}) in all nine conditions. In seven instances it produces more generative than vegetative matter (ratios below 1). Very low ratios are found with 16 hours of light and thermoperiods of 20—10° and 15—10°. The ratios are relatively low also in the case of all three thermoperiods in continuous light.

Mutants a^{12} and b^{13} deviate from the other insensitives in having some high ratios, especially at the 8 hour photoperiod.

It appears as a rather striking fact that the sensitive mutants have their highest generative efficiency in 24 hours of light at 20—15° and 20—10°, where they show even lower ratios than the insensitive mutants, in fact the lowest values in the whole experiment. Compare for instance the early mutants a^8 and a^{11} with c^{19} and c^{16} in Table 5.

Table 5. *Ratios of generative efficiency (vegetative matter/generative matter; dry weights)*

Thermoperiod	20—15°			20—10°			15—10°		
Photoperiod	24 h	16 h	8 h	24 h	16 h	8 h	24 h	16 h	8 h
a^8	0.72	0.87	1.49	0.74	0.64	0.96	0.75	0.66	1.01
a^{11}	0.87	1.10	1.23	0.78	1.03	0.92	0.82	0.82	1.28
a^{12}	1.08	1.75	2.05	0.75	0.76	1.56	0.78	0.75	1.94
b^{13}	1.28	1.42	1.80	0.91	0.69	1.51	0.82	0.69	1.89
Average insensitives	**0.99**	**1.29**	**1.64**	**0.80**	**0.78**	**1.24**	**0.79**	**0.73**	**1.53**
b^7	0.66	3.98	130.33	0.63	2.83	39.10	0.76	1.01	104.50
b^{10}	0.72	4.45	89.80	0.68	3.63	52.40	0.83	1.05	138.50
c^{16}	0.64	6.04	79.60	0.60	3.76	27.12	0.89	0.92	26.97
c^{19}	0.57	5.90	205.00	0.57	3.89	32.70	0.75	0.75	51.65
Average sensitives	**0.65**	**5.09**	**126.19**	**0.62**	**3.53**	**37.83**	**0.81**	**0.94**	**79.53**

Other properties

With regard to internode number and length there are striking differences in field cultivation between loci and alleles (Gustafsson *et al.*, 1960). Mutant b^7 has a higher internode number than a^8, but a lower one than Bonus. Some differences between Bonus and a^8 (Mari) were reported by Dormling *et al.* (l.c., p. 234), indicating a special thermoresponse of a^8. Photo- and thermoperiods exert a definite influence on internode number. The genotype-environment interactions are evident.

Internode number is definitely lower under continuous light than at 16 and 8 hours of light (the values are 5.6, 6.0 and 6.7 respectively). The photoperiod influence is most marked at 20—10° (5.6, 6.2 and 7.1).

Locus *b*-mutants possess, in agreement with field results, higher internode numbers than the *a*-mutants (6.4 versus 5.8 internodes). This is especially clear in 8 hours of light, where the difference is considerable (7.3 versus 5.9).

Locus *c*-mutants show low internode numbers with continuous light, in fact lower than in the *a*- and *b*-mutants (5.1 versus 5.7 and 5.8). With 8 hours of light the *c*-mutants have higher internode numbers than the *a*- and almost as high as the *b*-mutants (7.1 versus 5.9 and 7.3). The *a*-mutants hold a fair uniformity as to internodes throughout the varying photo- and thermoperiod conditions, although, as mentioned previously, they show a certain increase in internode number at a low temperature combined with extreme short-day.

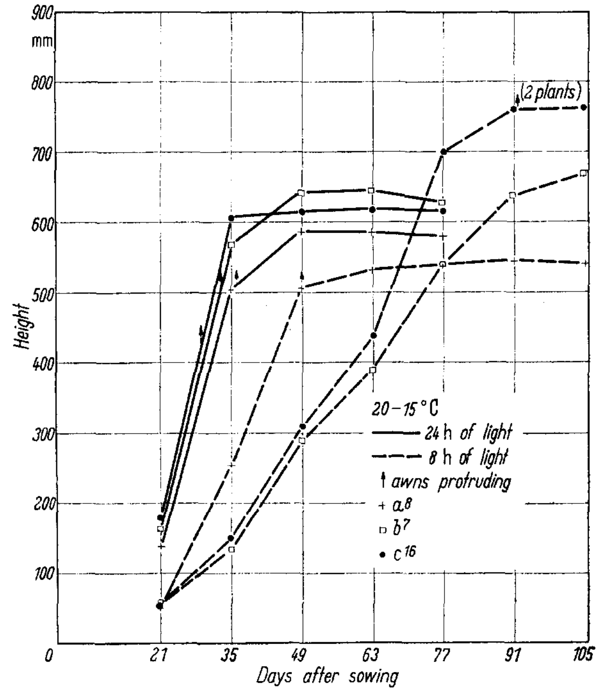

Fig. 5. Height growth at 20—15 °C of mutants a^8, b^7 and c^{16} given 24 and 8 hours of light

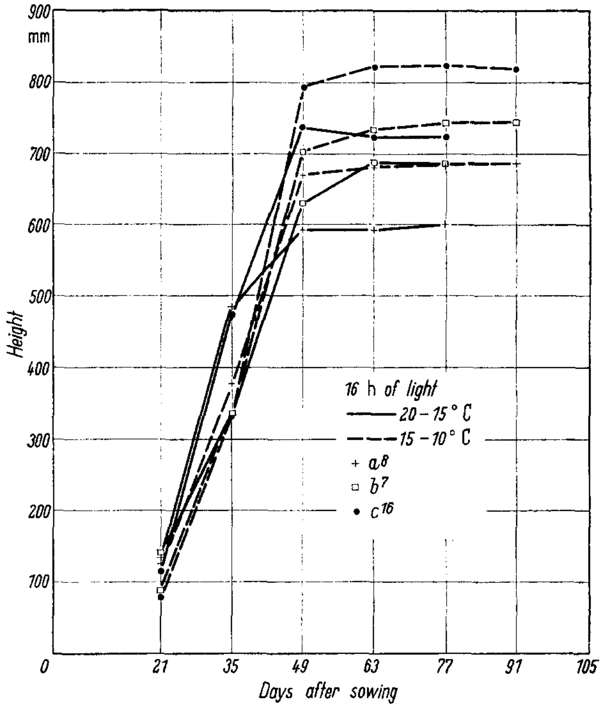

Fig. 6. Height growth at 16 hours of light of mutants a^8, b^7 and c^{16} with 20—15 °C and 15—10 °C

In addition to the locus differences just described there also appear some allelic differences. The insensitive b^{13} behaves like the *a*-mutants and, contrary to the other two *b*-alleles, reacts only slightly to climatic changes, in fact less than any other mutant tested. But despite this it deviates from *a*-mutants, also from a^{12}, by having a higher internode number. This is lower, however, than in b^7 and b^{10}.

Already at an early stage of development, i.e. 2—3 weeks after sowing, striking differences occurred in plant colour at 8 hours of light. The insensitive mutants, later on with heading tillers, were pale yellowish green, whereas the sensitive mutants were pale green in 20—15° but bright green coloured at lower temperatures. At 20—15° the sensitive mutants developed very broad leaves, the mean value being 11.8 mm compared with 9.0 mm for the insensitive mutants. There is no clear difference between the two groups in other climatic conditions, however. They react approximately in the same way, the broadest leaves occurring at 15—10° with 8 hours of light (10.4 mm) and the most narrow ones at 20—15° with 24 hours of light (6.9 mm).

Height development has been followed by measurements every fortnight. In Figs. 5 and 6 the height growth of three mutants, an insensitive one (a^8) and two sensitive ones (b^7 and c^{16}) is illustrated at four different conditions. The measurements are made from the edge of the pot to the top of the leaf sheath.

The most rapid development is obtained at 20—15° with *24 hours* of light (Fig. 5). c^{16} has reached its

Table 6. *Number of days after sowing for the occurrence of protruding awns on at least 4 of 7 plants per mutant case*

Light hours	24			16			8		
Temp., °C	20—15	20—10	15—10	20—15	20—10	15—10	20—15	20—10	15—10
a^{8}	36	38	45	39	39	43	49	58	63
a^{11}	38	36	44	39	45	45	47	54	61
a^{12}	35	34	41	35	35	44	45	54	60
b^{13}	38	38	41	36	36	42	47	52	60
b^{7}	33	35	41	48	49	49	—	128	133
b^{10}	31	35	43	47	51	51	—	130	(133)[1]
c^{16}	29	31	38	54	49	49	(92)[2]	100	112
c^{19}	29	31	36	50	49	49	—	103	112

[1] 3 plants. — [2] 2 plants.

maximum height already after 35 days, having protruding awns after 29 days (cf. Table 6). b^{7} and a^{8} are somewhat slower. At *8 hours* of light the growth is clearly delayed. The development of a^{8} goes nearly parallel to that in 24 hours of light, and its maximum height is reached only a few days later. The height growth of the sensitive mutants b^{7} and c^{16} is slow and prolonged. The production of vegetative matter — long and broad leaves — is high (see Plate 1c, the left two rows).

Fig. 6 shows the development at 16 hours of light with high and low temperatures (cf. Plate 1b and e). The most striking feature is that the change in temperature does not markedly influence the type of

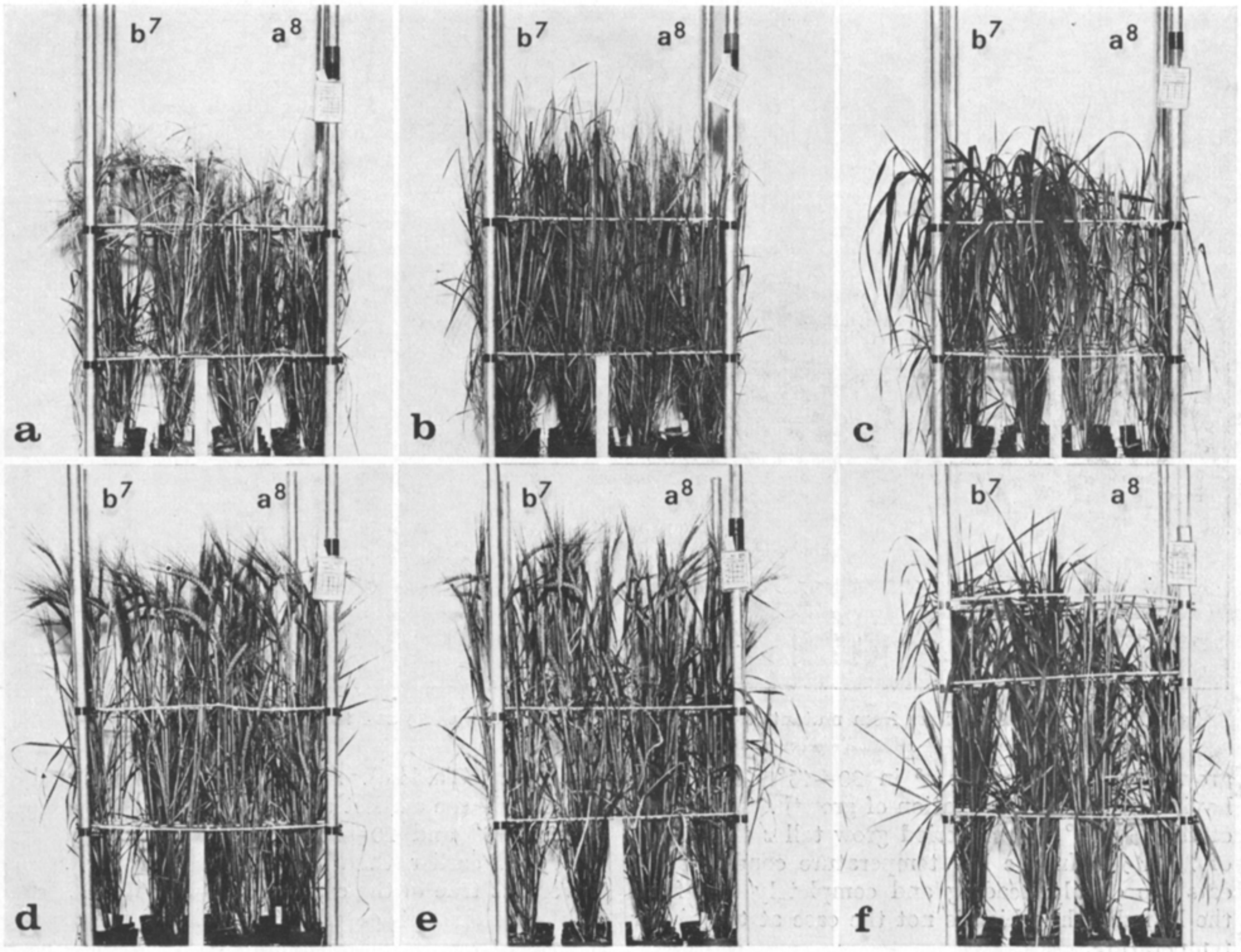

Plate 1. Mutants b^{7} and a^{8} (left and right on the trucks, two rows respectively) in 20—15 °C (top) and 15—10 °C (bottom) with from left to right 24, 16, and 8 hours of light. 84 days after sowing

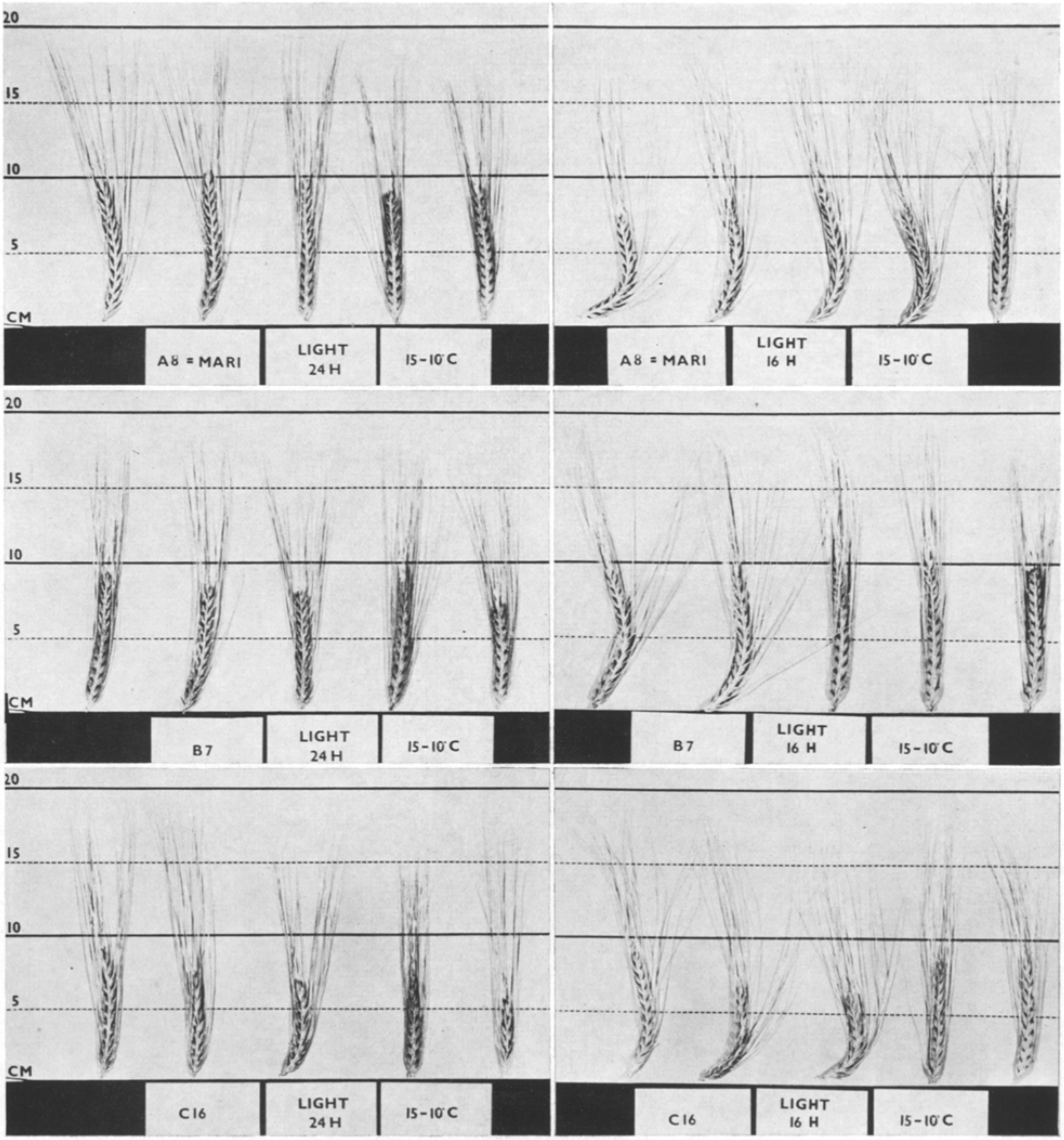

Plate 2. Ears from mutants a^8, b^7 and c^{16} at 15—10 °C with 24 and 16 hours of light

growth — only mutant a^8 in 20—15° deviates in having an earlier termination of growth. The plants of the 15—10° thermoperiod grow taller than those of 20—15°. In the low temperature condition the ears are clearly heading and completely free from the leaf sheaths which is not the case at the higher temperature.

The time of the occurrence of protruding awns indicates the earliness of the mutants under different conditions (Table 6). At *24 hours* of light c^{16} and c^{19} are clearly the earliest ones, one week earlier than a^8 at 20—15° and 20—10°. Generally, the sensitive group is earlier than the insensitive group. The reverse is true in the case of *16 hours* of light. Here the development of the insensitive mutants was nearly as fast as in continuous light, in some cases even faster, whereas the development of the sensitive mutants was markedly delayed. The extreme short day condition, *8 hours* of light, gave a slower development of the insensitives. Heading tillers occurred in all the plants, however. The sensitives did not produce any heading tillers at all at 20—15° with the exception of two plants of c^{16}. At lower temperatures heading tillers occurred very late, more than 100 days after sowing.

Schlußfolgerungen

Die Autoren untersuchten an acht induzierten frühreifen Gerstenmutanten, die Allele an drei verschiedenen Genloci repräsentieren, die Reaktionen auf unterschiedliche Photo- und Thermoperioden. Die Mutanten, die im Feldanbau ziemlich drastische Frühreife zeigen, wurden im Phytotron unter Anwendung üblicher Kulturmethoden geprüft. Eine dieser Mutanten, *mat-*a^8, ist bereits als schwedische Zuchtsorte unter dem Namen Svalöf's Mari zugelassen. Diese Mutante war bereits früher mit ihrer Ausgangssorte Svalöf's Bonus unter 30 verschiedenen Klimabedingungen verglichen worden (DORMLING et al. 1966). In der vorliegenden Untersuchung wurden drei Photoperioden (24, 16 und 8 Stunden künstliches Licht) mit drei geeigneten Thermoperioden (20—15°, 20—10° und 15—10°) kombiniert.

Die Versuche ergaben, daß bei sehr frühen Gerstenmutanten bezüglich der Merkmale Ährenbildung, Schoßtermin und Kornbildung häufig eine photoperiodische Insensitivität auftritt. Von den 8 untersuchten Mutanten war das bei 4 mehr oder weniger der Fall. 3 davon repräsentieren den Locus *a*, eine gehört zu Locus *b*. Von den beiden *c*-Mutanten war keine insensitiv, sie waren im Gegenteil ausgesprochene Langtagtypen.

Photo- und Thermoperioden üben verschiedenartige Wechselwirkungen aus. Das ist besonders deutlich bei den *c*-Mutanten, die bei Dauerbeleuchtung und hoher Temperatur eine hohe generative Leistung zeigen. Bei 8 Stunden Beleuchtung, unabhängig von der Temperatur, bilden sie keine Körner, produzieren aber eine erhebliche Menge vegetativer Masse, ebenso wie bei 16 Stunden Beleuchtung mit hohen Temperaturen. So unterscheiden sich die Mutanten der Loci *a* und *c* wesentlich hinsichtlich ihrer Reaktionen auf die Klimabedingungen. Die insensitive Mutante b^{13} ist der Mutante a^{12} bemerkenswert ähnlich, aber ihre hohe durchschnittliche Internodienanzahl zeigt, daß sie mit den sensitiven Mutanten b^7 und b^{10} des gleichen Locus gemeinsame Züge aufweist.

Es muß darauf hingewiesen werden, daß die untersuchten Mutanten der 3 Genloci sowohl im Feldanbau wie beim Anbau im Phytotron hinsichtlich ihrer morphologischen und physiologischen Eigenschaften phänotypisch unterschieden werden können. Die *c*-Mutanten sind besonders charakteristisch, aber auch hier scheinen deutliche Reaktionsunterschiede zwischen den allelen Mutanten eines Locus zu bestehen. Tatsächlich scheinen alle 8 untersuchten Mutanten mehr oder weniger unterschiedlich zu reagieren.

Die insensitive Mutante a^8, die bereits für die Praxis zugelassen ist, wird auch in großem Umfange für kombinationszüchterische Arbeiten verwendet, und es konnten bereits aussichtsreiche Linien selektiert werden. Die Eigenschaften, die die Mutante a^8 für die Praxis wertvoll machen, konnten auch in Phytotron-Untersuchungen bestätigt werden. Das gilt besonders für die Frühreife, die generative Leistung und den Ertrag, aber auch für den niedrigeren Wuchs und die Insensitivität gegenüber Veränderungen der Photo- und Thermoperioden.

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