LIGHT INTENSITY EFFECTS IN GROWTH AND DEVELOPMENT OF TULIPS, IN COMPARISON WITH THOSE IN *GLADIOLUS*

E. C. WASSINK

*Laboratory of Plant Physiological Research,
Agricultural University, Wageningen, The Netherlands;
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The same technique as earlier with *Gladiolus* (four different light intensities obtained by gauze screens (1)) was applied to Tulips. Individually weighed bulbs of the cultivar 'Rose Copland' were planted 7.11.60 (7th November, 1960), in fields 2 $\times$ 2 m with side rows. Harvests were taken at various dates between 22.2 (22nd February) and 15.6.61 (15th June, 1961). Dry weights of different parts as well as data on formative effects were determined (general aspect of plants at different harvests, see plate I).

1. DRY WEIGHT PRODUCTION

At the first harvest (22.2.61) (Fig. 1) total dry weight shows some decrease in relation to light intensity which may be related to dry weight of the bulbs initially planted. Total dry weight is closely paralleled by dry weight of the old bulb; dry weight of the organs developed shows no relation to light intensity. At the second harvest, 13.3.61, much the same still holds, with somewhat increased values, especially for the leaves. At the harvest of 4.4.61, the first apparent deviation between total and old bulb dry weight, and the first sign of light intensity influence on total dry weight shows up, and remarkably, the light intensity effect is manifest practically only in the *new bulb*! In the next harvest, 24.4.61, more or less at the peak of flowering, total dry weight is clearly related to light intensity, and very strongly so again in the new bulb which already has the highest proportion of all organs, except at the lowest light intensity. A clear effect is also on flower stalk and flower;

over the range of light intensities (including darkness) they together increase about 2.7 times, the new bulb about 3.5 times. Excluding darkness, flower stalk and flower increase about 2.0 times, the new bulb about 3.8 times. Old bulb, roots and leaves do not show any appreciable light intensity effect. The next harvest (17.5) emphasizes the excessive predominance of the new bulb over all other organs, especially at the higher light intensities. The formation of additional, small new bulbs (+) shows up at the higher light intensities. Leaves show some, probably mainly incidental relation to light intensity, flower stalk weight has somewhat, and flower weight appreciably decreased as compared with the previous harvest. The 5-9.6.61 harvest is the last before death of the aerial parts (plants without definite signs of dying were selected for this harvest); new bulb weight predominates, and is strongly related to light intensity; the same holds for the small bulbs. Stem weight still shows some relation to light intensity, aerial weights and old bulb make up only a minor part at this stage. Total dry weight seems to continue to increase at much the same rate up to the very end, and so does new bulb weight. At 14.6.61 charac-
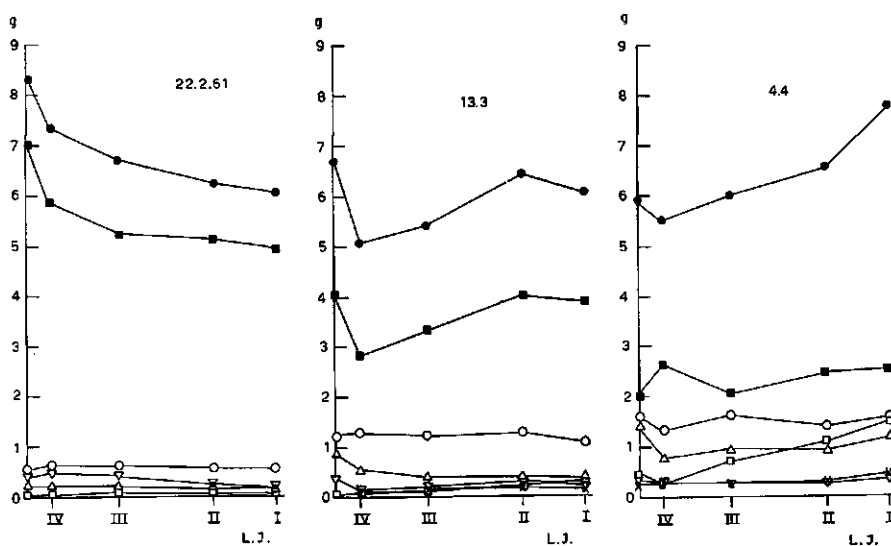

Fig. 1a, b. Tulip. Field experiment with artificial shading. Dry weight development of various (pp. 2, 3) parts and total at successive harvests. Planted 7.11.1960. Legend: ▽ —— ▽ roots, ○ —— ○ leaves, △ —— △ stem, × —— × flowers, ■ —— ■ old bulb, □ — □ new bulb, + —— + small new bulbs, ● —— ● total. Light intensities, I, II, III, IV: 100, 75, 37, and 10–21 % of full daylight, and darkness (zero light intensity).

teristics of decayed plants are determined. They give much the same picture as obtained at the preceding harvest.

This picture of the development is interesting in relation to some well-known characteristics of the tulip plant. As established earlier in this labora-
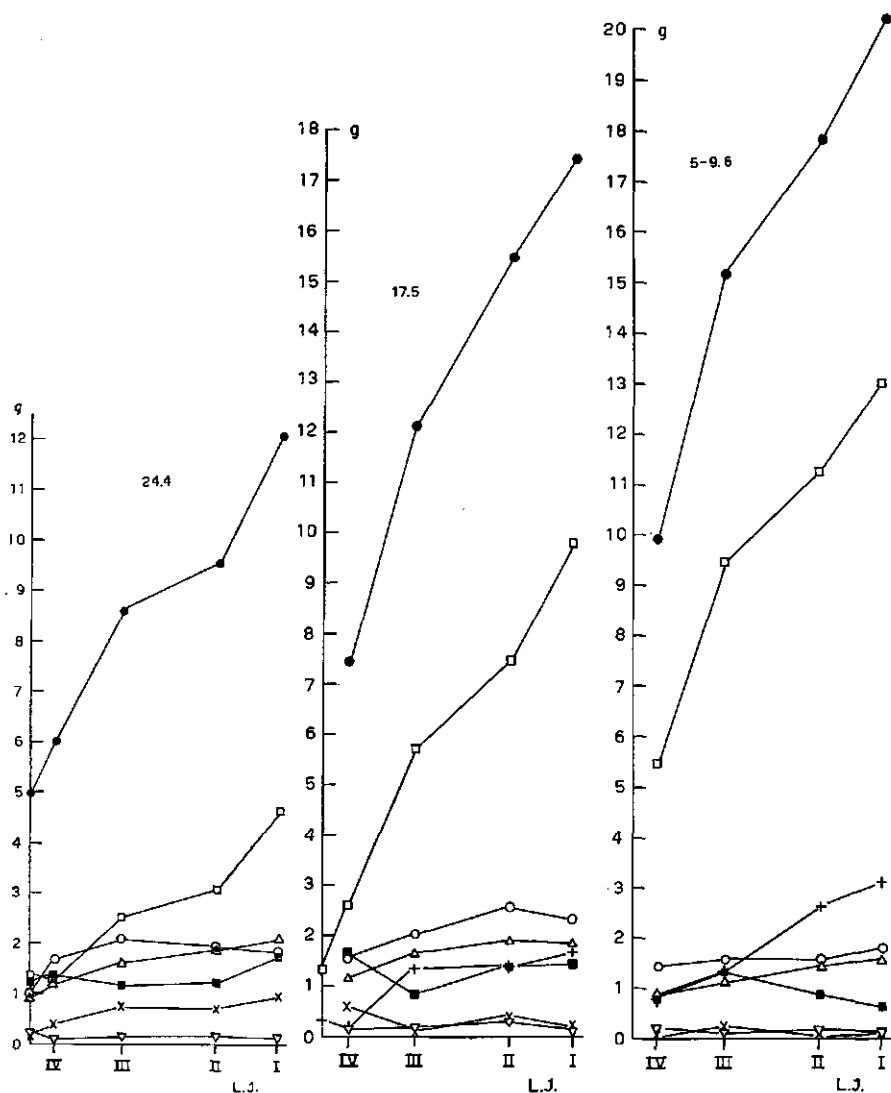
FIG. 1b. Legend, see p. 2.

tory, the flower has completed its initiation before the planting date. Further-
more, forcing practice has shown that tulips require only low light intensity for
complete development (Nonetheless, light intensity dependent formative effects
are present in the aerial parts of the plant; we will come back to this below).

The observations discussed above show that the main achievement of these
tulips during their active life is to build up the new bulb; the aerial parts mainly
develop at the expense of the old bulb. The size (however, not the shape, see
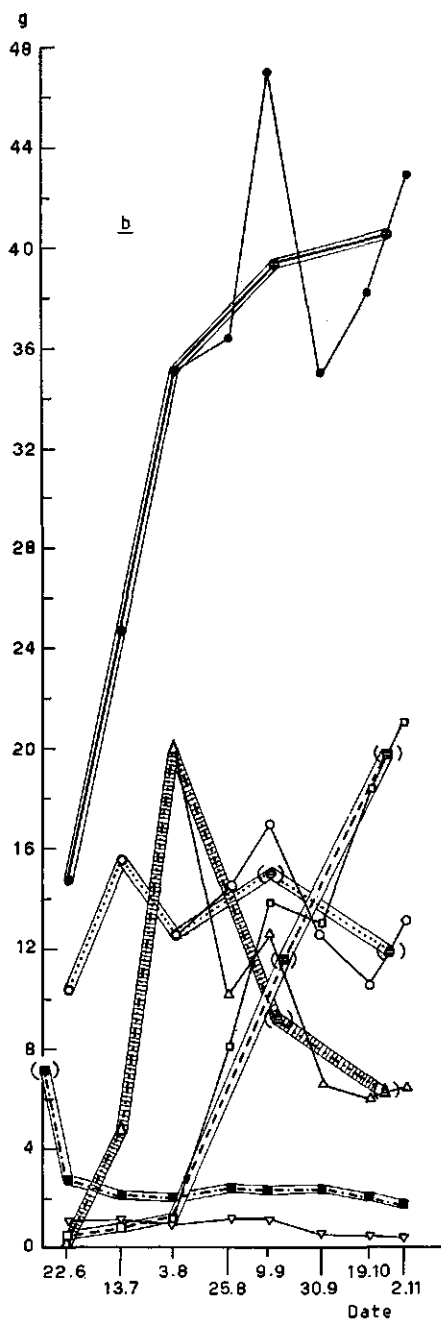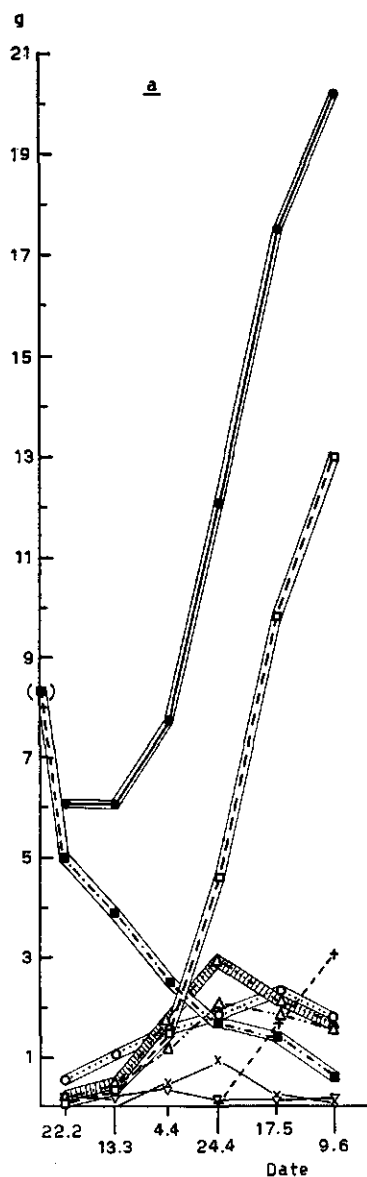below) of the leaves is not appreciably light-intensity dependent; the stem is,

Fig. 2. Dry weight development during season of various organs at full daylight in field experiments. a. Tulip, season 1960–61; b. *Gladiolus*, season 1959. Legend: see figure 1. (Some streamlining in *Gladiolus* by averaging some neighbouring values).

though its size, in relation to the new bulb is relatively small. It is remarkable that the new bulb starts its light intensity dependent growth already at an early stage, even before the flower stalk shows a marked relation to light (4.4.61).

Fig. 2a shows dry weight development at successive dates at the highest light intensity. Leaves are the first to develop (roots very probably still earlier, before our first record); then stem, flower and new bulb weight starting to increase at the same time, new bulb weight soon overtaking all others as stated above. Leaf weight increases gradually until late in the season.

Stem and flower weight decline after flowering, no seed development being recorded. Additional small new bulbs start developing only after the peak of flowering is past.

It is interesting to note similarities and differences of this behaviour with respect to that of *Gladiolus*. *Gladiolus* has no initiated flower before planting, and, for forcing, requires high light intensities. Natural daylight at our latitude is hardly sufficient in January through March. The developmental pattern of the various organs illustrates this in some respects (See, e.g. (1), fig. 1, 1959 experiment). Before flower initiation, old corm weight is much more reduced already than is Tulip bulb weight at a corresponding stage and stays so during the rest of the growing season. (Fig. 2b). Leaf weight is relatively much more important, and more markedly dependent on light intensity. Next to leaf development, the flower stalk temporarily plays a much more predominant rôle than it does in tulip. New corm development starts only after the peak of flowering, in contrast to Tulip where bulb development was found to start simultaneously with flower stalk development (cf. figs. 2a, 2b). Like the leaves, the flower stalk in *Gladiolus* reaches relatively much higher dry weight, which, moreover, is more dependent on light intensity than in Tulip. Total dry weight tends to reach a final level well before the end of season in *Gladiolus;* most of corm development takes place in this period, in sharp contrast to Tulip where it starts early in the season. Relative to the other organs, new corm weight predominates in the end of the season, but less markedly so than new bulb weight in Tulip.

Figs. 3a and b illustrate the same relationships as figs. 2a and b, but expressed on the basis of per cents of total dry weight.

A very interesting picture is obtained when comparing relative total bulb (or corm) weight (old and new together), in per cents, with relative total aerial weight (stems and leaves) as is shown in fig. 4, for full daylight. This picture clearly reveals a very marked difference, in accordance with what has been exposed above. In Tulip, bulb weight (old and new) always predominates the combined weight of stem and leaves, whereas in *Gladiolus,* during the major part of the season, stem and leaves are very strongly predominant. This is in accordance with what has been exposed above, viz., that in *Gladiolus* stems and leaves develop to a smaller extent at the expense of the old corm than in the case of Tulip with respect to the old bulb, and is in accordance with the fact that the new stem, inclusive the flower, is initiated in Tulip at an earlier developmental stage. One might say that, in this respect, *Gladiolus* is nearer to
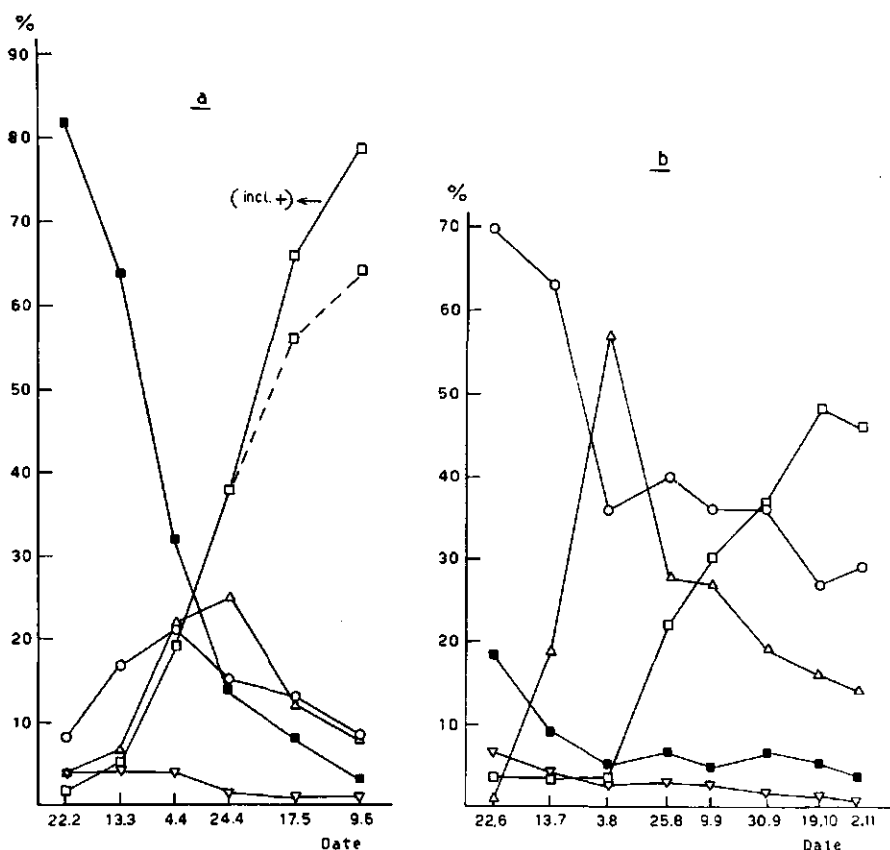
FIG. 3. Same as fig. 2, expressed as per cent of total dry weight. a. Tulip, season 1960–61;
b. *Gladiolus*, season 1959.

a seed plant which also has to develop a vegetative apparatus first in order to produce flowers.

Additionally, we have computed the same relationship for 12% daylight. The situation is mainly unchanged, but the picture is somewhat less extreme: some approach occurs between the situations in Tulip and in *Gladiolus* (See fig. 5).

Total dry weight tends to reach a final level well before the end of the season in *Gladiolus* and most of the corm development takes place in this period (1), in sharp contrast to Tulip, where it starts early in the season (see above). Dry weight increase in the later phases of development in Tulip continues (Fig. 6); it is practically entirely on account of the new bulb and, after flowering, additional small bulbs; it goes on until the plant, rapidly, decays. The picture of dry weight development thus is rather different in both plants (Fig. 6). Partly, this will no doubt be due to genetically determined differences in the type of

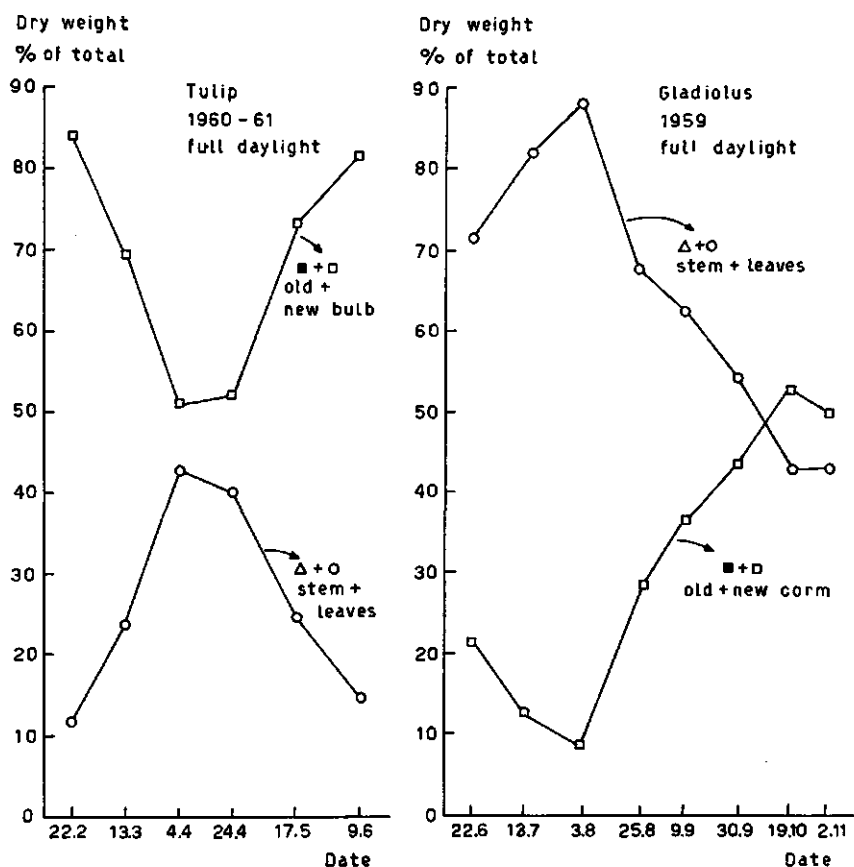6   *Meded. Landbouwhogeschool Wageningen 65-15 (1965)*

FIG. 4. Sum of dry weight fractions of old + new bulb (corm) compared with same of stem + leaves, in Tulip and *Gladiolus* at full daylight. Field experiments of 1960–61, and 1959 respectively. Root weights not represented.

development, but also the fact that this phase in Tulip, in a field experiment, takes place under increasing amounts of light energy and increasing temperature, such in contrast to *Gladiolus,* may play a role. Experiments under fully controlled conditions will contribute to a further analysis of these observations.

Stem dry weight during the season, and especially at its peak seems less dependent on light intensity in Tulip than in *Gladiolus* (Fig. 7). The weight at the lowest light intensity in Tulip at the peak of development is about 60% of that reached at the highest intensity, in *Gladiolus* it was (in 1959) only about 16%. This seems in accordance with the picture derived above, as stem in Tulip mainly thrives on the old bulb, whereas in *Gladiolus,* the achievement of the new leaves appears to contribute largely to the development of the flower stalk. Stem length and stem diameter will be discussed under formative effects (see below).
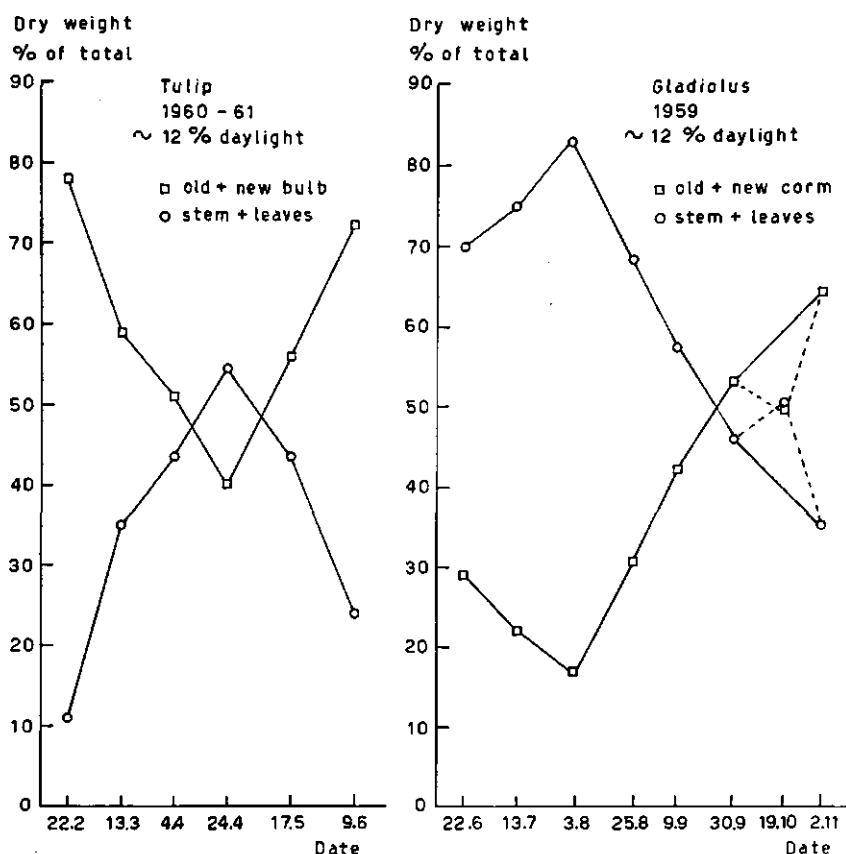
FIG. 5. Sum of dry weight fractions of old + new bulb (corm) compared with same of stem + leaves, in Tulip and *Gladiolus* at 12% daylight. Field experiments of 1960-61, and 1959 respectively. Root weights not represented.

Remarkably, bulb (or corm) weight at the lowest light intensity in both plant types (in the later phases of development) is about 40% of that at the highest intensity. This indicates that in both plants, bulb (and corm) development is ruled by much the same type of phenomenon. In bulb (and corm) formation, in both cases the light intensity dependent photosynthesis of the leaves (of the same year) is involved; in stem growth this is more so in *Gladiolus;* in Tulip stem development seems mainly to proceed at the expense of the old bulb.

The relations for bulb development in both plants are pictured in fig. 8. A comparison with figs. 6, and 7 illustrates the above. However, while bulb increase in Tulip provokes an increase in total dry weight as well, increase in corm weight in *Gladiolus,* mainly took place under conditions of fairly constant total dry weight, indicating that the corm grew mainly owing to trans-
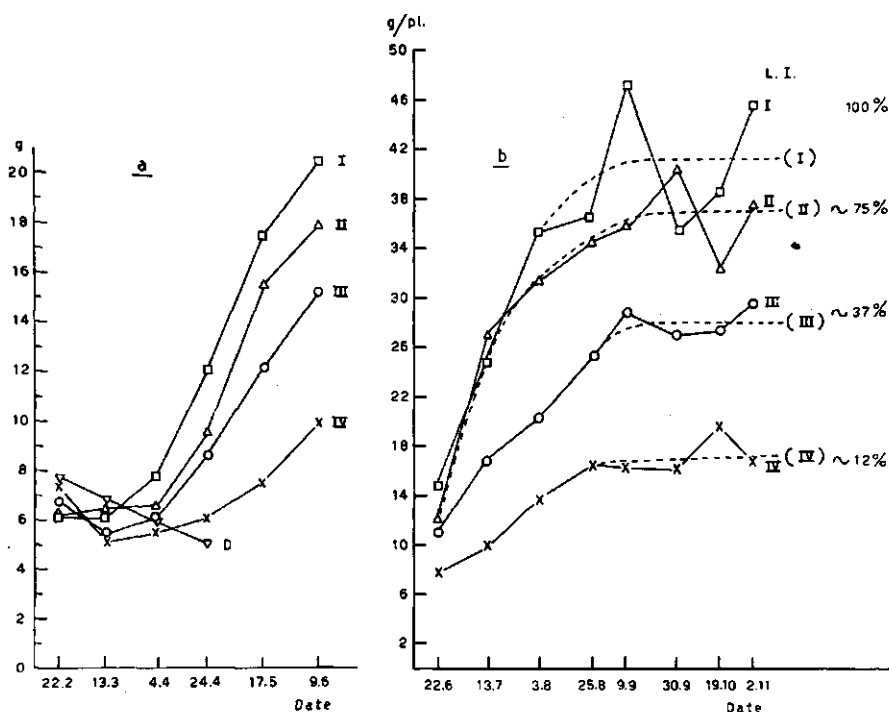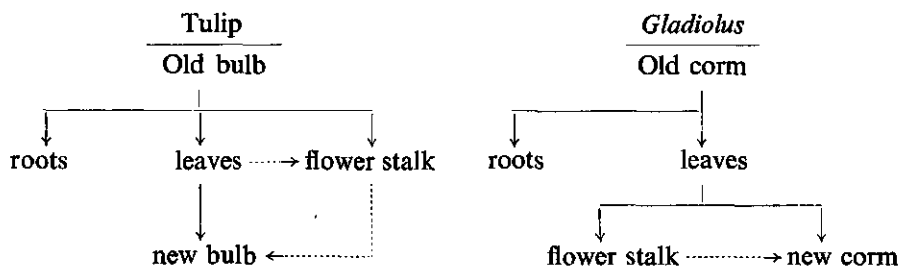
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FIG. 6. Total dry weight development during season at different light intensities in field experiments. a. Tulip, season 1960–61; b. *Gladiolus*, season 1959. □ I (100% daylight), △ II (75%), ○ III (37%), × IV (10–12%), and (Tulip) ▽ total darkness (D).

location processes from the aerial parts of the plants for which actual photo-synthesis provided the energy. Apart from genetically determined differences, also here the different types of season may have played a role which will have to be sorted out further under completely controlled conditions as now available in our laboratory.

The difference between Tulip and *Gladiolus* may be rendered in the following scheme, indicating energy relationships.

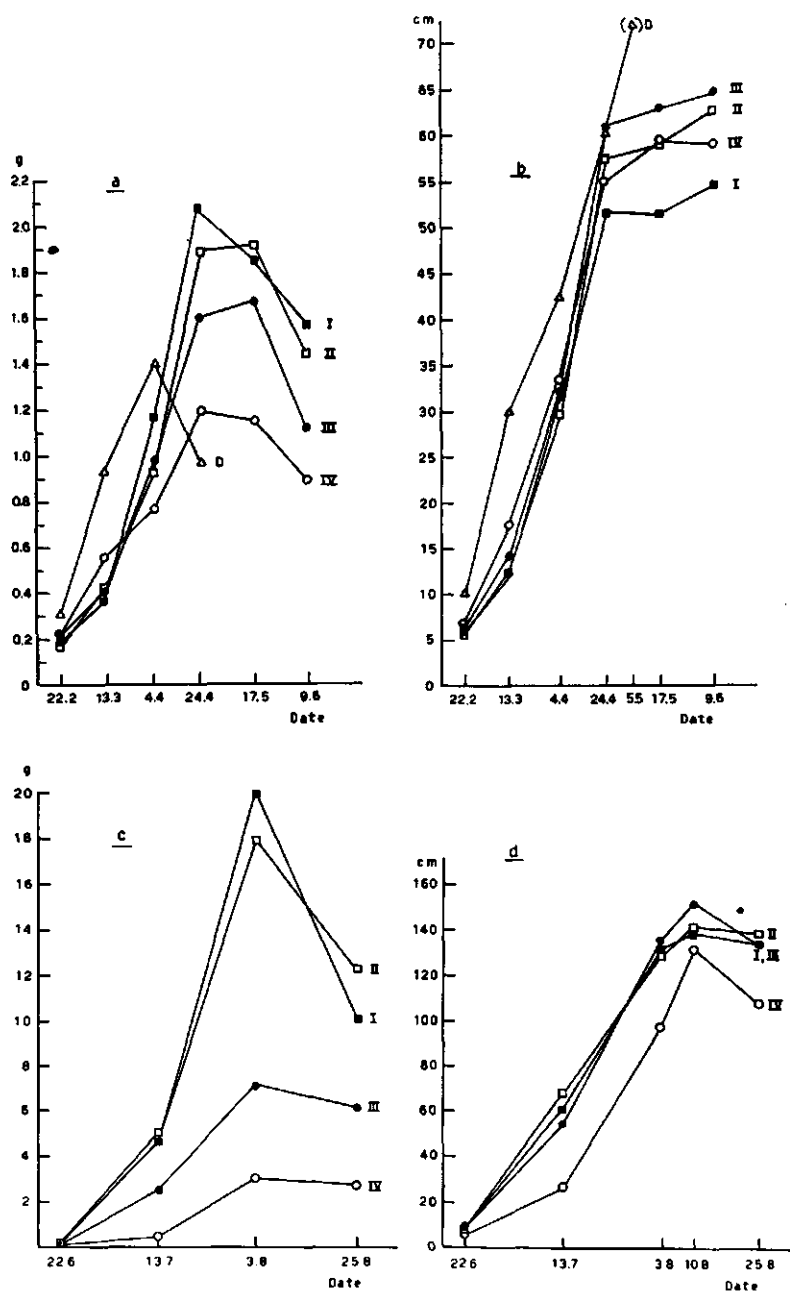Arrows indicate energy relationships; ——→ main effects, ·······→ minor effects.

FIG. 7. Development of stem dry weight and stem length during season in field experiments at different light intensities. a. Tulip, stem dry weight; b. Tulip, stem length; c, d, same for *Gladiolus*; a and b season 1960–61, c and d season 1959. Light intensities: I 100% daylight, II 75%, III 37%, IV 10–12%, and (Tulip) total darkness (D).
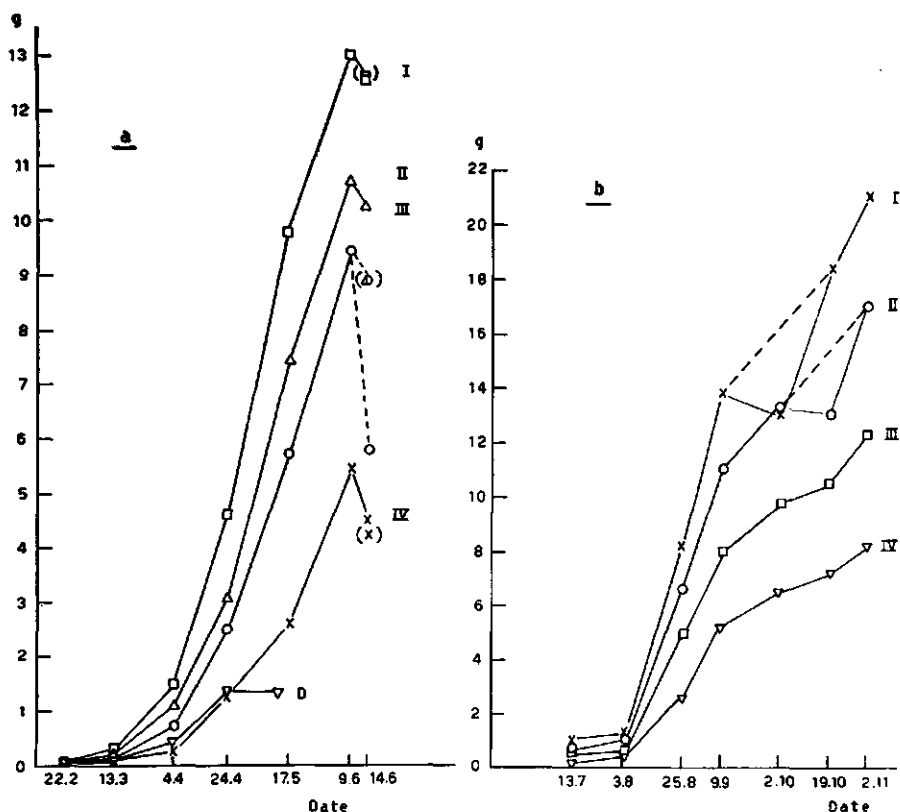
FIG. 8. a. Dry weight development during season of new bulb in Tulip in field experiments, at different light intensities, including darkness (D). Final harvest: died-off plants (14-6), ( ) plants beheaded after flowering. Season 1960–61. b. Same for *Gladiolus* (new corm, no dark experiment), season 1959. I–IV: Light intensities, as figure 7.

2. FORMATIVE EFFECTS

a. L e a f   s h a p e. As in *Gladiolus,* leaf shape has been characterized by the length/width relationship (L/B; fig. 9). Dependency of L/B on light intensity develops gradually, first in the 1st and 2nd leaf, later also in the 3rd and 4th leaf (e.g., 4.4 and after); in the latter it remains somewhat less than in the first two. The largest change in shape is between darkness and 12% light, less so in the range from 12 to 100% light. The relationship appears most fully developed on 24.4 and 5.5.61 (See also plate II). Averages for leaves 1 and 2, and leaves 3 and 4 taken from these two dates are given in table I and in fig. 10. It is remarkable that, in relative measure (putting the 12% light intensity value = 100), the range, and especially so for the first two leaves is very similar to that in *Gladiolus* (no dark values recorded in the
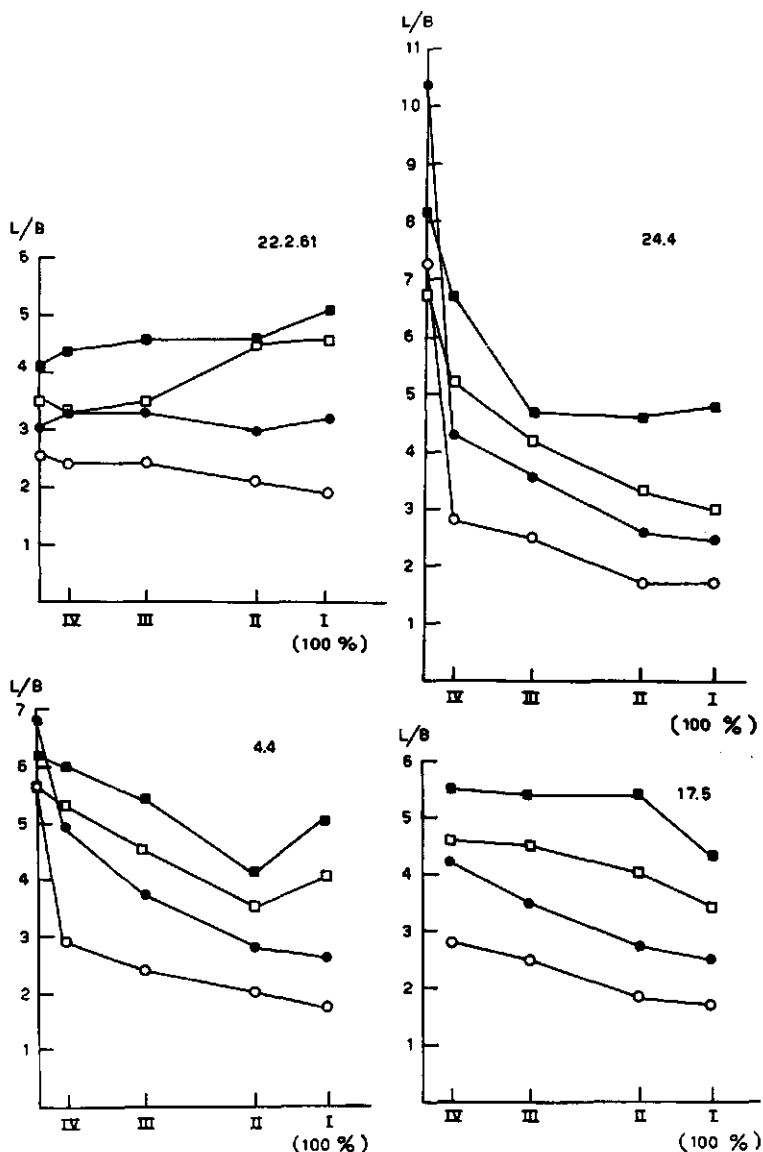
FIG. 9. L/B (= length/width relationship) of leaves in Tulip at different light intensities for different harvests (22.2, 4.4, 24.4, and 17.5.1961 respectively); ○ first, ● second, □ third, and ■ fourth leaf respectively. Field experiment of 1960–61 season.

latter). This indicates that the formative effect of light on leaf shape is of the same order of magnitude in both plants (Fig. 10; Table 1).

Remarkably, like in *Gladiolus,* the reverse relation (B/L, increasing with light intensity) is very closely related to dry weight as produced at the different

TABLE I. Some data for comparison of leaf shape and dry weight as affected by light intensity in Tulip and *Gladiolus*[1].

Date/Item	Leaf nr.	Light intensity				
		D	IV	III	II	I

1. TULIP
A. L/B, averages for 2 dates

Date/Item	Leaf nr.	D	IV	III	II	I
1. 24.4	1	7.25	2.75	2.5	1.7	1.7
2. 24.4	2	10.4	4.25	3.6	2.6	2.5
3. 5.5	1	9.75	3.3	2.4	1.8	1.7
4. 5.5	2	13.75	5.3	4.0	3.1	2.2
5. Average	1/2	10.3	3.9	3.1	2.3	2.0
6. Rel. values	1/2	265	**100**	80	59	51.5
7. B/L. (rel. values)	1/2	0.38	**1.0**	1.25	1.70	1.94
8. B/L (in % of LI I)	1/2	20	52	65	88	**100**
9. 24.4	3	6.7	5.2	4.2	3.3	3.0
10. 24.4	4	8.2	6.7	4.7	4.6	4.8
11. 5.5	3	9.1	6.2	5.3	5.2	3.2
12. 5.5	4	–	7.0	5.3	5.5	4.0
13. Average	3/4	8.0	6.3	4.9	4.65	3.75
14. Rel. values	3/4	127	**100**	78	74	60
15. B/L (rel. values)	3/4	0.785	**1.0**	1.28	1.35	1.66
16. B/L (in % of LI I)	3/4	47	60	77	81	**100**

B. Total dry weight (g). Same dates

Date/Item	Leaf nr.	D	IV	III	II	I
17. 24.4	–	5.0	6.0	8.5	9.5	12.0
18. 5.5	–	–	7.5	12.2	15.5	17.4
19. Average	–	(5.0)	6.75	10.35	12.5	14.7
20. (in % of LI I)	–	(34)	46	71	85	**100**

2. GLADIOLUS
A. L/B (Read from fig. 6, ref. (1)).

Date/Item	Leaf nr.	D	IV	III	II	I
21. L/B		–	34	25	20	18
22. L/B (in % of LI IV)	see ref. (1)	–	**100**	73.5	58.5	53
23. B/L	,,	–	10	13.5	17	19
24. B/L (in % of LI I)	,,	–	53	71	89	**100**

B. Total dry weight (Read from fig. 8, ref. (1))

Date/Item	Leaf nr.	D	IV	III	II	I
25. (in % of LI I)	see ref. (1)	–	42	68	91	**100**

3. COMPILATION OF CRITICAL VALUES (IN PER CENT)

Date/Item	Leaf nr.	D	IV	III	II	I
26. Tulip B/L, leaves 1–4 (av. lines 8 and 16)		(34)	56	71	85	**100**
27. Tulip, total dry wt. (line 20)		(34)	46	71	85	**100**
28. *Gladiolus* B/L leaves 3–5 (line 24)		–	53	71	89	**100**
29. *Gladiolus*, total dry wt. (line 25)		–	42	68	91	**100**

[1] cf. also figs. 10, 11.

light intensities (Fig. 11). Even the slight deviation of dry weight to a lower value at the 12% light intensity also holds for Tulip. (Dry weight at complete darkness, in Tulip does not show this deviation; however, this dry weight value is only founded upon one figure).

b. T o t a l l e a f a r e a. The picture for total leaf area (fig. 12) again reminds very strongly of that of *Gladiolus* (1, fig. 9). Leaf area, contrary to leaf shape, shows relatively little effect of light intensity. There is an optimum at 37% of daylight; already at an early stage these features show up. The maximum difference, however, at the optimal development, is not more than 20%. The average sequence is: 100% − 75% − 37% (optimum) − 12% − dark. Obviously, at the lowest light intensity and in darkness there is a competition between the elongating tendency and the energy available to realize it. Much the same holds in *Gladiolus* in which, however, the lowest light intensity lags further behind, probably, because leaf development, in its later stages, relies less on the corm than is the case in Tulip with respect to the bulb.

Fig. 13 shows how length and width contribute to the leaf area. As might be expected, their reactions to light intensity are opposite; leaf length shows a clear inverse relationship to light intensity; leaf width shows a direct relation which, however, is only pronounced below 37% daylight; the values for the three higher light intensities are very near together.

c. S t e m l e n g t h a n d s t e m d i a m e t e r. Figs. 7b and 7d show that both in Tulip and *Gladiolus,* stem length is less affected by light intensity than
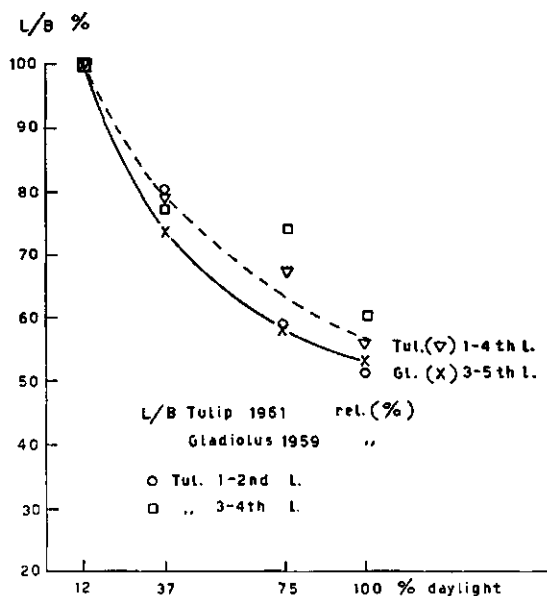

FIG. 10. Length-width relation of leaves (L/B), expressed in % of value at 12% of full daylight, in Tulip and *Gladiolus*.
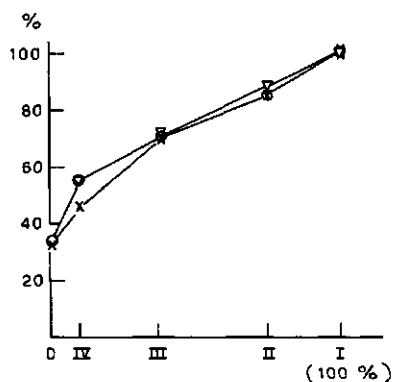
FIG. 11. Leaf shape in Tulip, expressed as B/L (width/length relationship) in per cent, in relation to light intensity, compared with dry weight development, and with similar data in *Gladiolus*.
○ Tulip, average B/L data of leaves 1 to 4, of 24-4 and 17-5-61 ; × Tulip, total dry weight, same harvest dates ; ▽ *Gladiolus*, B/L data average 3rd–5th leaf, expt. of 1959.
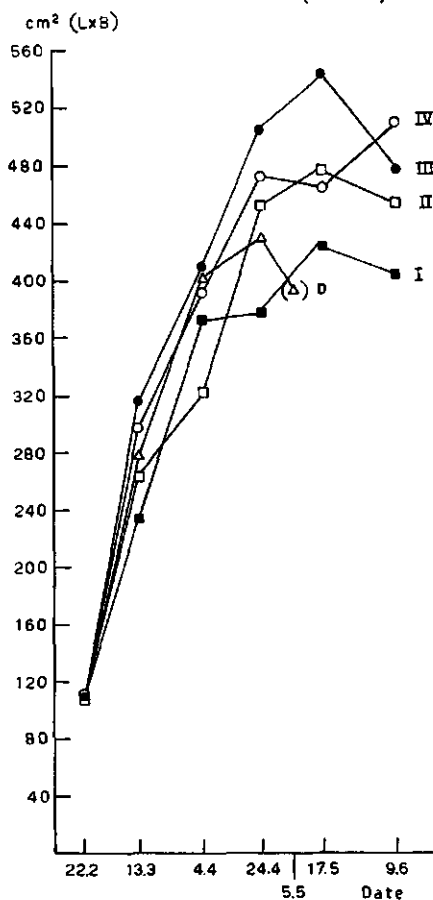

FIG. 12. Total leaf area (as expressed by the product L × B, leaves 1 to 4 added, see also fig. 7) as dependent on season and light intensity in Tulip (light intensities I–IV and darkness, see also legends fig. 7 and 9).
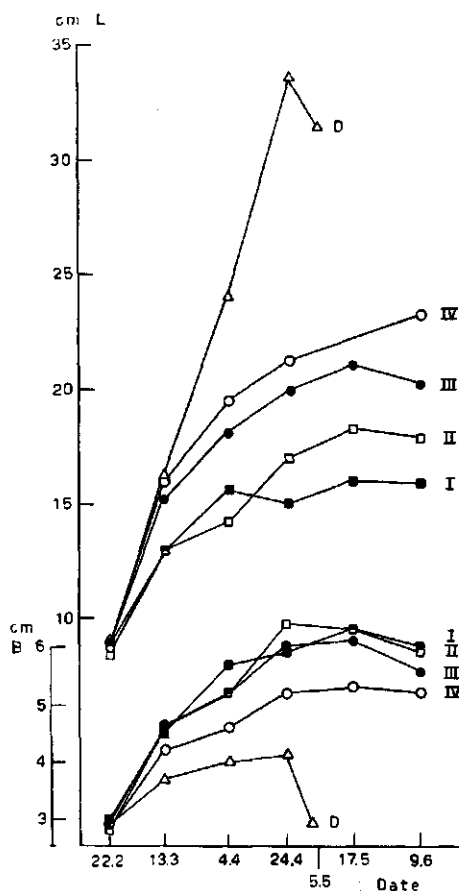
FIG. 13. Average leaf length (L) and leaf width (B) (leaves 1 to 4) in relation to light intensity and season in Tulip (Legend cf. figs. 7, 9, and 12).

is stem dry weight (figs. 7a and 7c). There is some difference, however; in Tulip the highest light intensity produces the shortest stem, the lower ones are somewhat longer, with an indication that 37% daylight (III) produces the longest stem. This seems to be the – for elongation most favourable – balance between elongating tendency ('etiolation') and available energy. Data obtained in darkness (Tulip only) tend to show that elongation may be more excessive still but is stopped sooner because of general weakness of the plants. The higher values obtained in darkness at early dates both for dry weight and length of stem are not well understood; they may be related to somewhat more favourable temperature conditions under dark cages in early spring. Comparable data for *Gladiolus* were not available in the experiment considered.

A comparison of stem length and dry weight data suggests a marked effect of light intensity on stem diameter. This indeed shows up (cf. plate III, and figs. 14, 15, and 16; fig. 16 moreover contains a comparison with *Gladiolus;* there is a definite relationship with light intensity in both Tulip and *Gladiolus* which may be somewhat steeper in the latter. Relations between stem diameter and some anatomical features will be discussed below.

3. SOME ANATOMICAL FEATURES

It has been exposed before (2) that the reflection that anatomical structures (including submicroscopical ones) are in between the initial physico- and biochemical principles that perceive stimuli and initiate reaction chains, and the ultimate differences manifest to the naked eye induced by differences in environment, justifies and stimulates a renewed interest in plant anatomy.

Some features of anatomy in *Gladiolus* in relation to light intensity during growth have been described and have shown that also – as might well be expected – in the microscopical area definite quantitative relationships exist between shape and size of structures and environmental factors (2).

The same features as in *Gladiolus* – size, shape and number of vascular bundles – have been studied in Tulip and are shown on plates III and IV a-e, and figures 14 to 16. The techniques used and the procedure followed are the same as for *Gladiolus* (2). Stems were collected when fully developed and cross sections of the last internode about $1/3$ from below, studied. The items collected are shown, e.g. in fig. 14. Like in *Gladiolus,* several items show a close relation to stem diameter, e.g. bundle length and width (i.e. length and width of the cross section of the bundle as visible on a stem cross section, see also plates IV a-e); the picture may be somewhat less clear than that in *Gladiolus* (2). The only apparent difference between both plants is the number of vascular bundels at the cross section which appears virtually independent of light intensity in Tulip, whereas it was related to r-stem in *Gladiolus* (2). Conversely, average bundle distance (see also plates IV a-e) in Tulip is related to r-stem, whereas in *Gladiolus* it was independent of stem diameter. This, no doubt, is connected with the circumstance that the number of flowers in Tulip – viz. one – is inde-
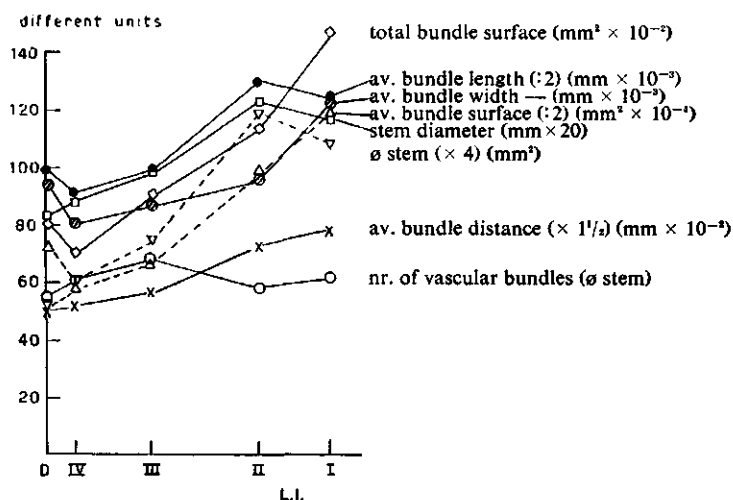
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FIG. 14. Characteristics of vascular bundles in relation to stem cross section in Tulip, last internode, $^1/_3$ from bottom, field experiment 1960–61, at different light intensities (dark, 10–12, 37, 75, and 100% daylight).
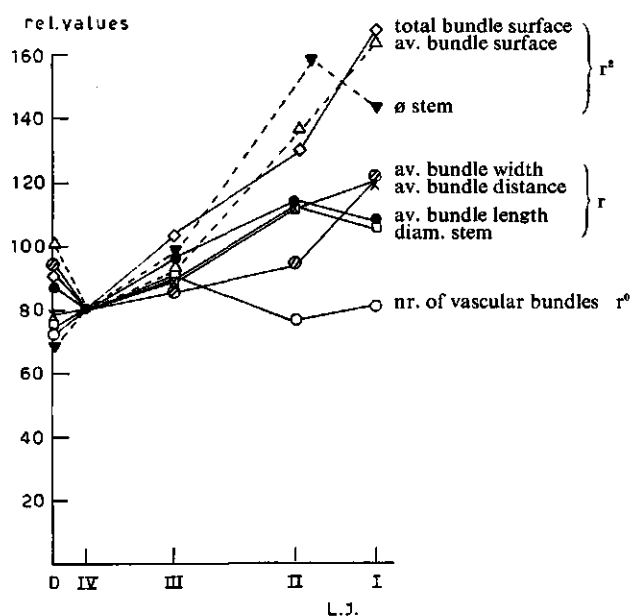

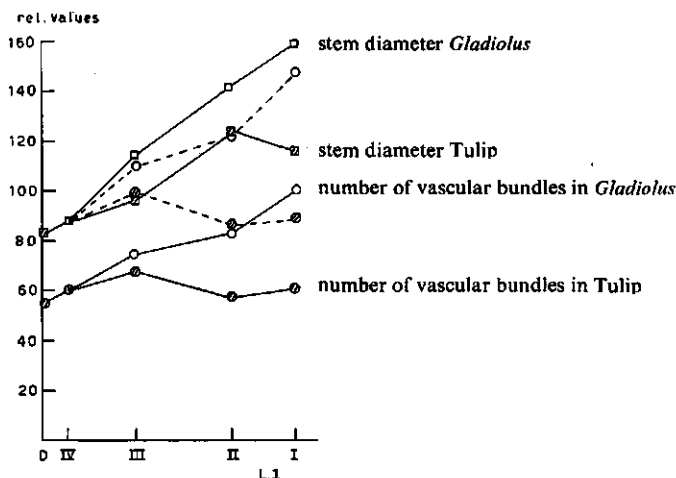FIG. 15. Tulip, same as fig. 14, fixed at same relative value for light intensity IV ($\sim 12\%$ daylight).

FIG. 16. Comparison of light intensity relationships of some data in Tulip and. *Gladiolus* in relative values (- - - Light intensity IV data vascular bundles adapted to stem data).

pendent of light intensity, and that all parts are already prepared in the bulb before planting, contrary to the situation in *Gladiolus*. Moreover, since the number of bundles, visible at the cross section, is independent of light intensity, total bundle surface, like individual bundle surface, runs with stem cross section, or with r^2, instead of with r^3 in *Gladiolus* (2).

In fig. 15, the same relationships are pictured, reduced to equal relative basis at 12% light intensity, as had been done in *Gladiolus* (2). The relationships then are brought about still much clearer than in fig. 14. Fig. 16 sets apart the data for stem diameter, and number of vascular bundles at the cross section to show that in both plants stem diameter runs with light intensity (probably somewhat less steeply in Tulip); number of bundles however does so only in *Gladiolus*.

4. DAYLENGTH EFFECTS

Tulip plants were also grown in various daylengths. Among these were some very short daily exposures, viz., $1/2$ and 1 hour, and also complete darkness; furthermore, a 10 h day, and an 18 h day obtained by extending the 10 h day with 8 h low intensity artificial light (two 40 Watt daylight fluorescent tubes on 4 m²). The equipment used for the latter has been described before (3).

Fig. 17 shows dry weight development of various organs (cf. fig. 1) at two harvest dates in the 2nd half of the season. Up to 1 h daylength there is not much effect of the light, except a certain increase in life time as compared with complete darkness (see 17.5), but dry weight, within the experimental error is much the same, and the illumination appears well below compensation of
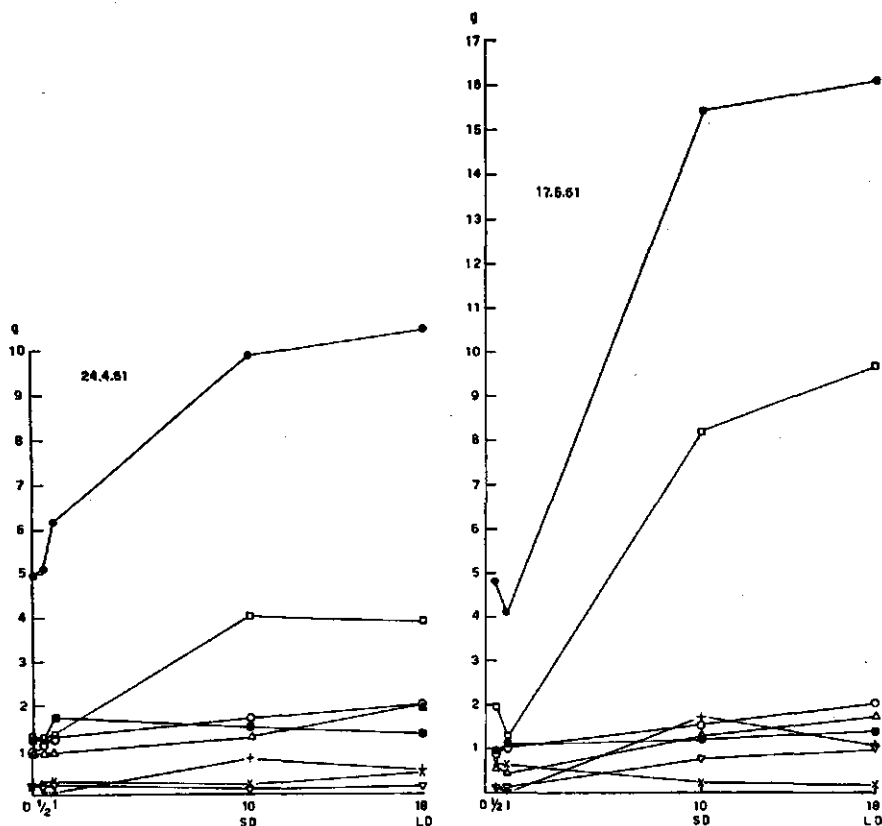
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FIG. 17. Tulip, grown at different daily photoperiods, viz. complete darkness, ½, 1, and 10 hr natural daylight, and 10 hr natural daylight, supplemented by 8 hr artificial light (two 40 Watt daylight fluorescent tubes on 4 m²). Development of various organs, selection of 2 harvests. Legend as fig. 1.

respiration; total weight is definitely lower than initial bulb weight (cf. fig. 1). Not much difference is obtained between 10 and 18 h weights, as might well be expected since the additional energy imput was deliberately kept low. At both 8 h and 18 h, new bulb weight is the predominant item (as in the light intensity series). One feature is probably significant, viz., the fact that the small bulbs (+) show definitely higher weight, at both dates, in the 10 h day than in the 18 h day. This might point to some promotion of bulb formation by short day, but the material is not large enough to make a very definite statement. Whether the main effect is on initiation or on growth, still has to be established. The fact that the large new bulb does not show this effect may point into the direction of initiation.

5. SUMMARY

Tulip has been grown in a field experiment at four different light intensities, viz., ca 12, 37, 75 and 100% of natural daylight, using the same equipment as used in a similar experiment with *Gladiolus*, described earlier (1). The development of the various plant organs has been followed in periodic harvests. Bulb growth was found to play a more important role than corm growth in *Gladiolus*, it also started earlier in the developmental cycle; considerable growth of the new bulb was already observable at the peak of flowering; it was strongly related to light intensity, more so than dry weight development in the aerial organs which, moreover, rarely occupied more than 50% of total dry weight in sharp contract to *Gladiolus* where this could be near 90% around the peak of flowering. In this respect, *Gladiolus* more approaches the situation in a seed plant in which the total vegetative development depends upon contemporary photosynthesis, whereas in Tulip a large part of the vegetative development – but not all – may be accounted for by the old bulb. In this respect, also the initiation of stem and flowers at an earlier stage than in *Gladiolus* – viz., before planting – may be of importance, and the well-known much lower light requirement for forcing to flower fits into the same picture.

Among formative effects, e.g., leaf shape, remarkably, is affected by light intensity in an almost quantitatively identical way as in *Gladiolus*. Also the relation to total dry weight development is practically exactly the same in both cases. Much the same holds for relation between stem length and stem weight in both plants, though the extremes deviate less than in *Gladiolus*.

Stem diameter and stem anatomy (number, size and distance of vascular bundles) have been studied in the same way as in *Gladiolus*. Also in Tulip stem diameter and size of vascular bundles show a quantitative relationship to light intensity. However, in Tulip, the number of vascular bundles was not affected, but the distance was, contrary to what was found in *Gladiolus*. This may be connected with the fact that the number of flowers (one) is not affected by light intensity in Tulip.

Preliminary observations on daylength effects suggest that the formation and/or growth of additional small bulbs is somewhat promoted by short day.

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REFERENCES

1. Wassink, E. C.: *In:* Progress in Photobiology: Ed. B. Chr. Christensen and B. Buchmann. i.e. Proceedings 3rd Internat. Congress on Photobiology, Copenhagen 1960, pp. 371–378.
2. Wassink, E. C.: Mededelingen van de Landbouwhogeschool Wageningen, Nederland 63 (16), 1–8 (1963).
3. Wassink, E. C. and J. A. J. Stolwijk: Mededelingen van de Landbouwhogeschool Wageningen, Nederland 53, 99–112 (1953).

Addition in proof

It was already remarked (p. 11) that L/B shows the largest change in the very low light intensity range, viz., between darkness and 12% light. This is especially clear, e.g. in fig. 9, 24.4, while also at 5.5 (not reproduced) much the same situation holds. It is especially obvious in leaves 1 and 2, and in the B/L ratio of these (Table 1, line 8) the dark average is well below the relative zero dry weight point as shown in fig. 11. (The coincidence of the zero B/L value with dry weight in this figure was brought about by a compensatory effect of leaves 3 and 4, table 1, line 16, in the set of figures used).

In a discussion on the present paper, Mr. R. A. SANCHEZ, guest worker at our laboratory, remarked that the situation as shown especially by leaves 1 and 2 might well point to a dual effect of light on leaf shape in tulip – and most probably also in several other cases –, viz., a truly 'morphogenetic' effect, of great importance, especially operative at low intensities (or amounts) of light, and a second effect, closely related to the imput of photosynthetic energy, thus operating mainly at high light intensities.

This induced me to look further into leaf shape data produced annex to the dry weight data as shown in fig. 17, with extremely short daylengths. It turned out that the biggest L/B shift was between dark and $\frac{1}{2}$ h/day light, and, again, comparing total dry weight (DW) with B/L, the values showed close agreement from $\frac{1}{2}$ h/day upward, while the B/L value in dark (averages of leaves 1–3) was definitely lower. The range of available figures was as follows:

	D	$\frac{1}{2}$ h	1 h	10 h	18 h	Date
B/L (%)	22	48	52	95	100	5.5.61
DW (%)	47.5	48.5	60	93	100	24.4.61

This supports Mr. SANCHEZ' suggestion and, moreover, seems in a line with BATALIN's observations (Bot. Ztg. 29, 669–686 (1871)) who found that short daily irradiations lead to more or less normal leaf shape, even prior to chlorophyll development (see also: WASSINK et al., Atti 2nd Int. Congress Photobiology, Turin, 1957, pp. 343–360, for a discussion of the latter observations).

Certainly, the above suggestion will have to be the object of much further investigation.
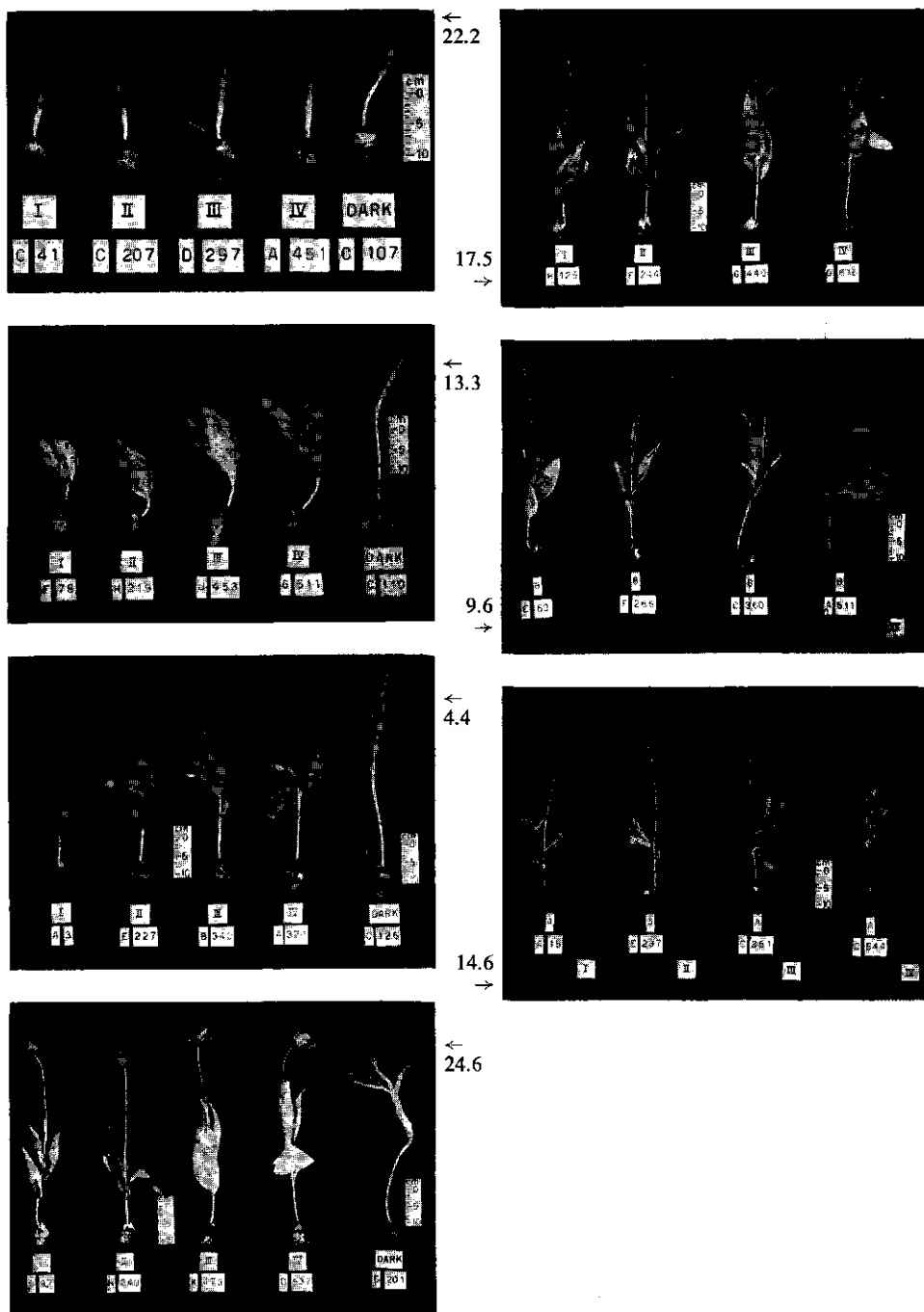
PLATE I. Tulip, field experiment with artificial shading, at 4 different light intensities, and darkness, season 1960–61. Aspects of plants at successive harvests; 9.6 and 14.6 represent still living and already died-off plants, respectively.
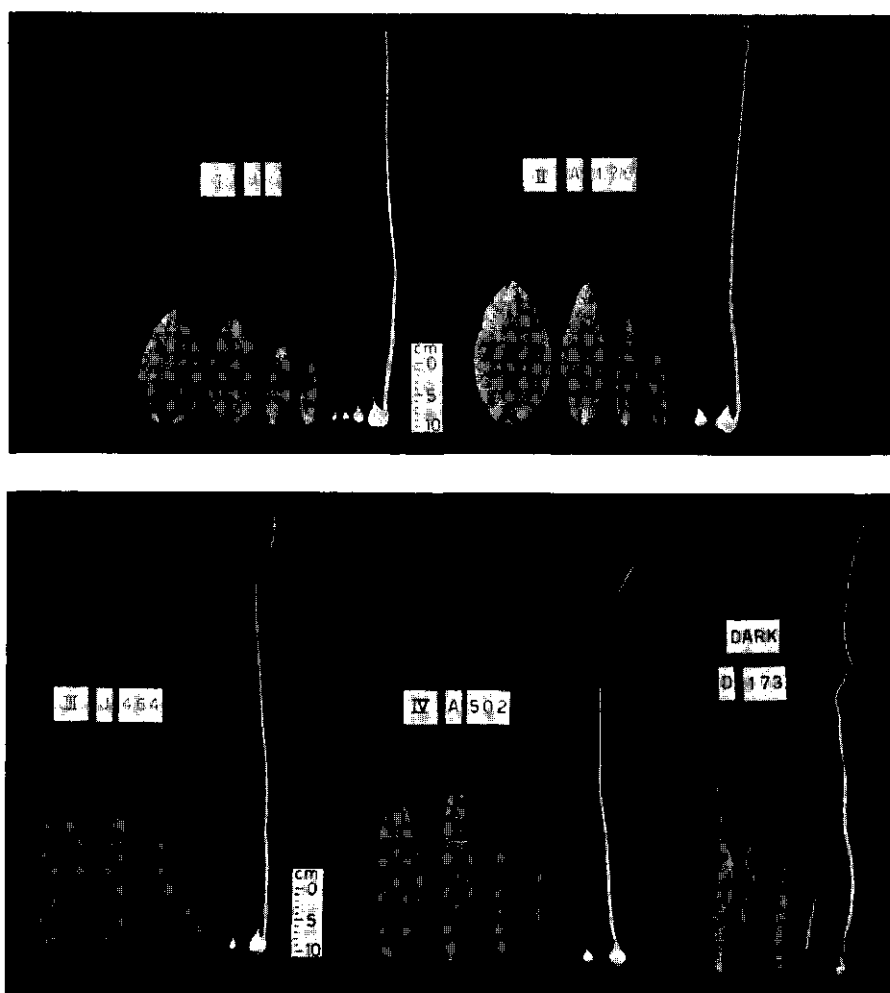
PLATE II. Tulip, as before; details of foliage and stem, grown at different light intensities; Photographed 5.5.1961.
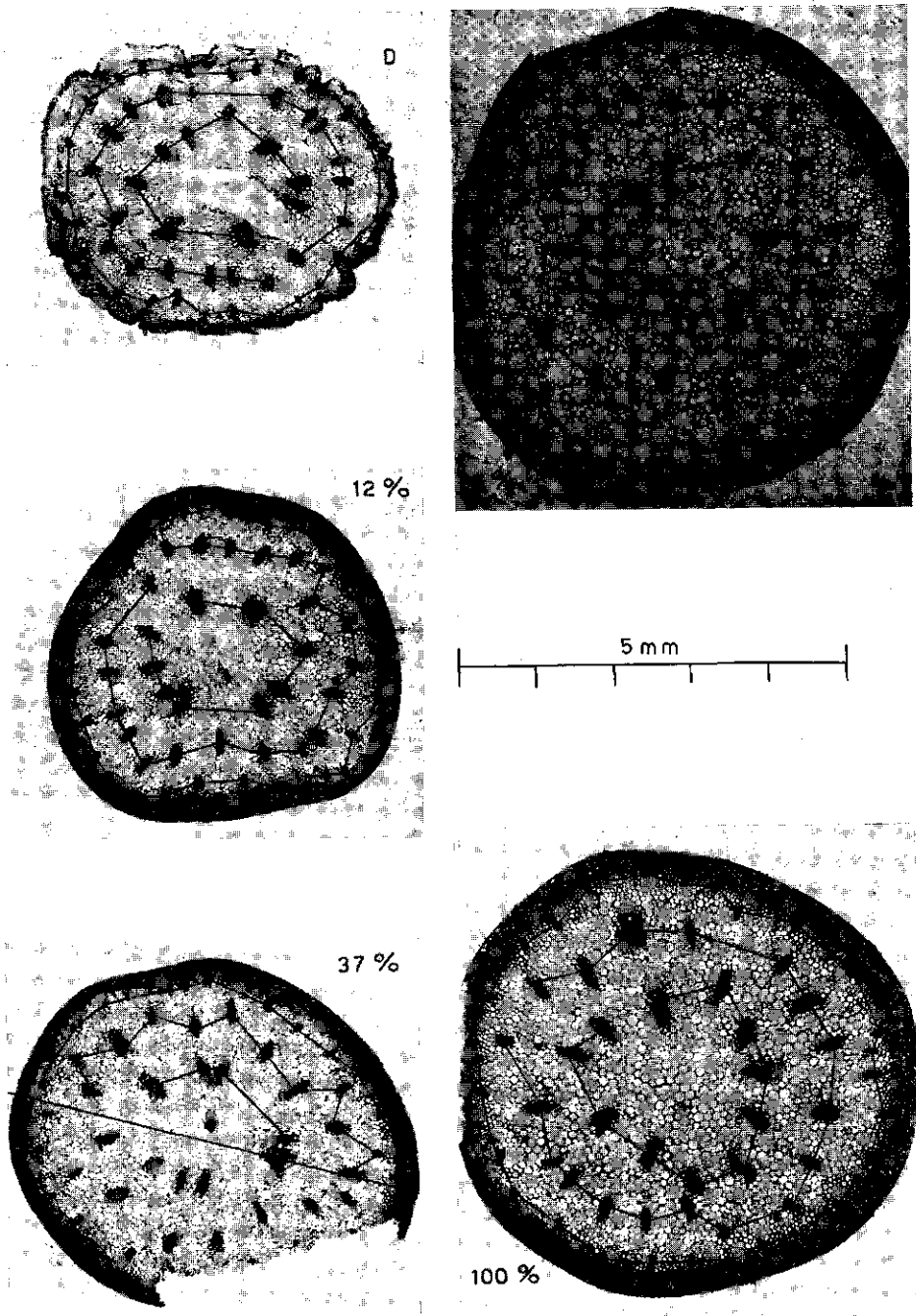
PLATE III. Tulip, sections of top stem internode, ca. $\frac{1}{3}$ from base, grown at different light intensities, used for counting number of vascular bundles, as indicated; 5 mm scale for comparison. Field experiment, season 1960–61, harvested 5.5.1961.
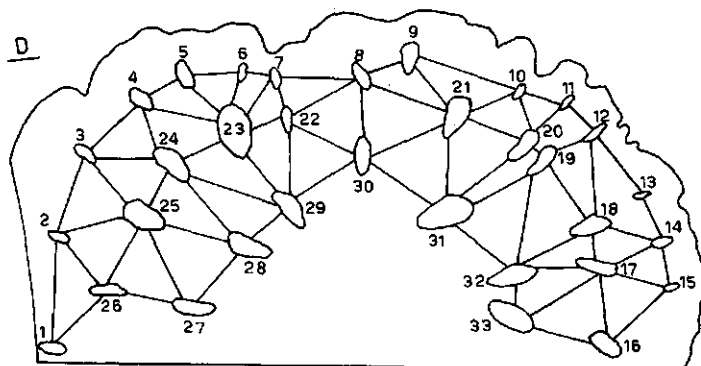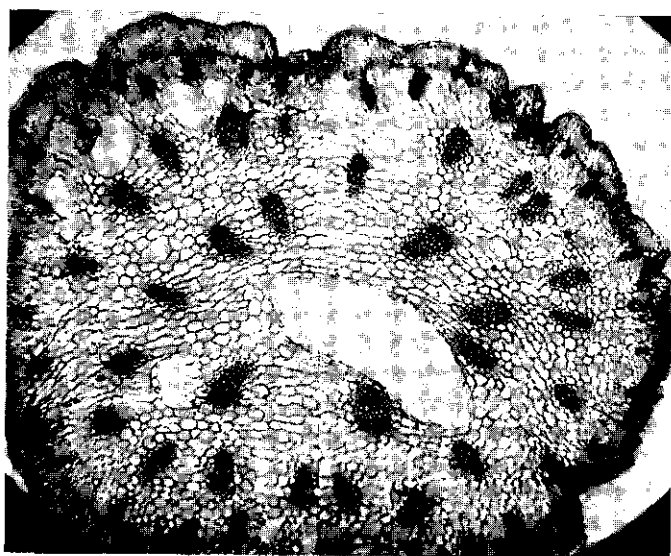
PLATE IVa

PLATE IVa–e. Tulip, sections of top stem internode, as Plate III, used for measuring size of vascular bundles, and schemes used for determining bundle distance as indicated; 1 mm scales for comparison (cf. Plate IVa). Field experiment, season 1960–61, harvested 5.5.1961. Dark (D), and different percentages of daylight as indicated.
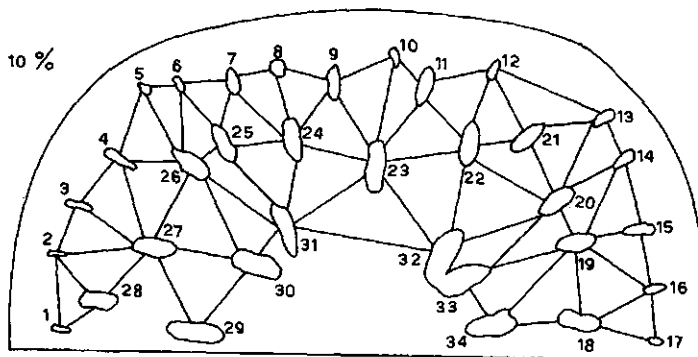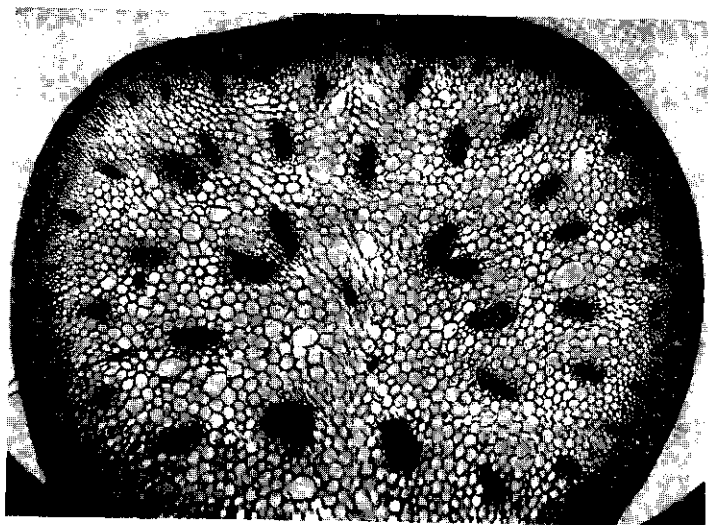
PLATE IVb

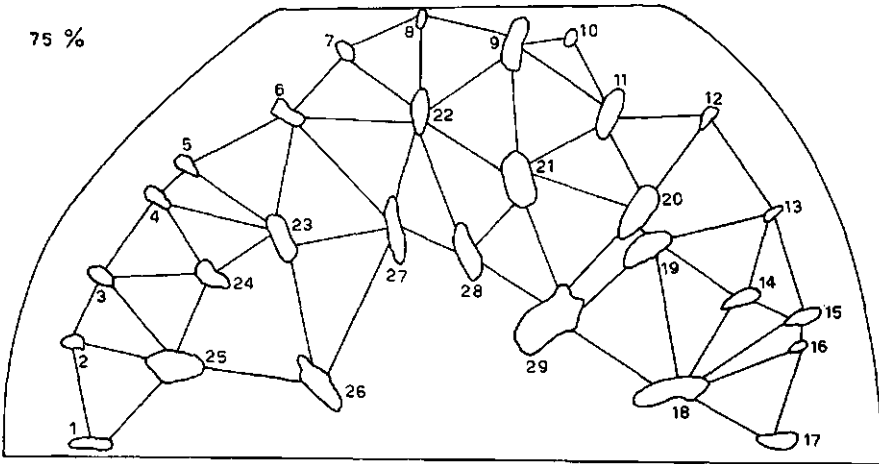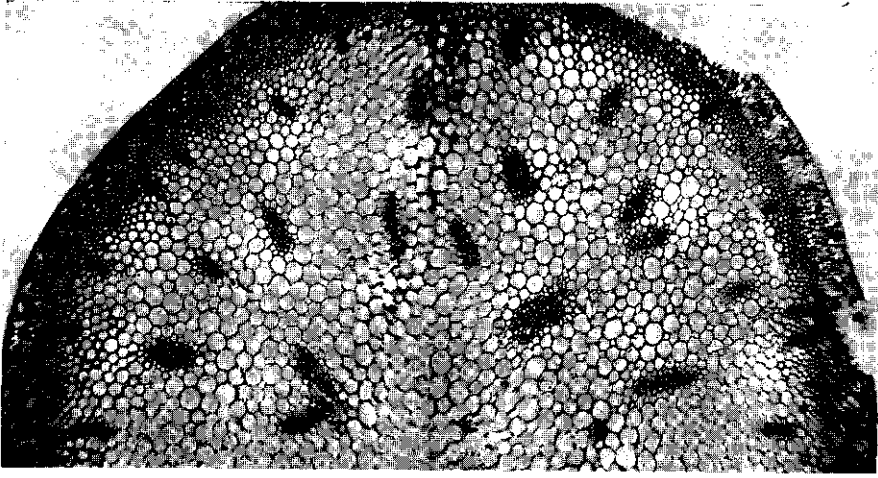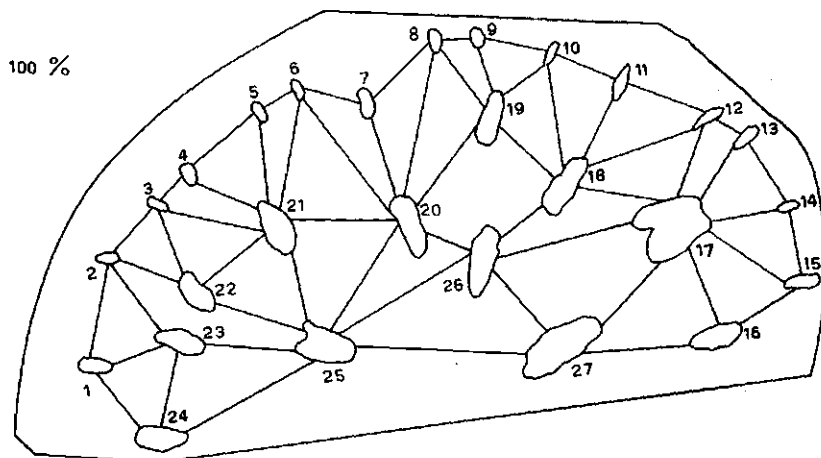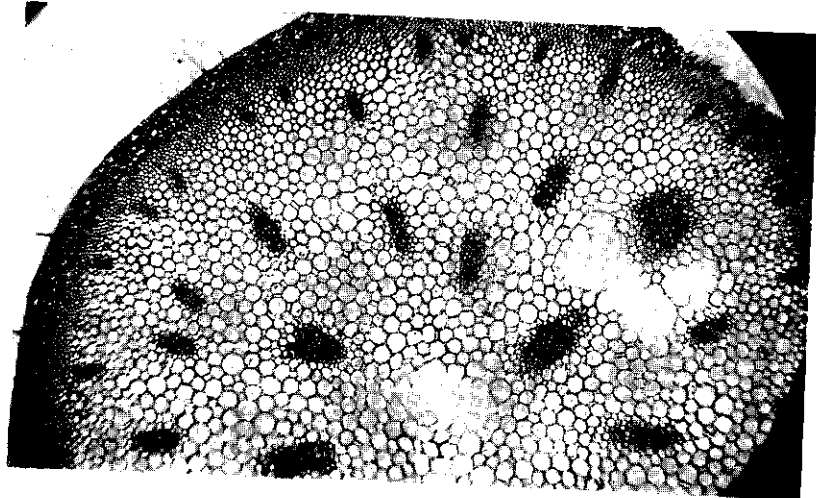Legend: see Plate IVa.
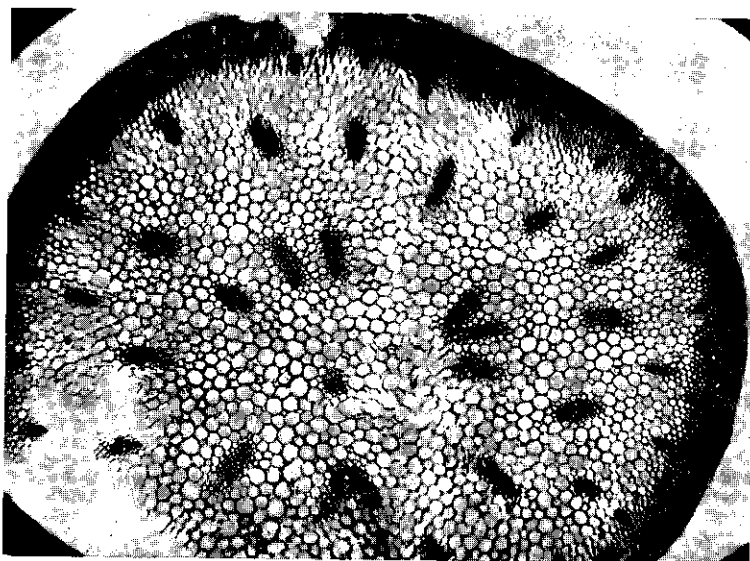
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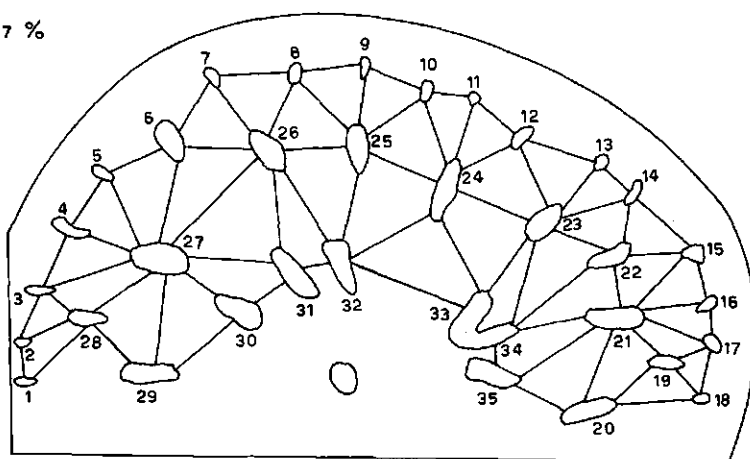
PLATE IVc

Legend: see Plate IVa.

75 %

PLATE IVd

Legend: see Plate IVa.

PLATE IVe

Legend: see Plate IVa.