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# AN ATTEMPT AT SEPARATING PRODUCTIVE AND MORPHOGENETIC EFFECTS IN THE GROWTH OF SOME BULB PLANTS

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## 1. Introduction

The contents of this paper have been presented at the International Symposium 'Productivity of Photosynthetic Systems', part II, Theoretical Foundations of optimization of Photosynthetic productivity, held at Moscow, USSR, September 23–29, 1969. This Symposium was organized in close contact with the subsection PP-photos. of IBP and was directly preceded by a similarly organized technical meeting at Třeboň, Czechoslovakia. The proceedings of this part have been published in English in 1971 (see, e.g. ref. 11); those of the Moscow part have been recently published in Russian (see, e.g. ref. 13). Publication of these Proceedings in English was also envisaged but it appears probable that this is not near at hand. It, therefore, seemed justified to recall in mind the material contents of this contribution as briefly as possible in the present article.

## 2. Discussion of some data

In the past years, our laboratory has studied the effect of light intensity on growth and development. Among the objects were 'bulb' plants, e.g. gladiolus, tulip, bulbous Irises, and onions (3, 5, 10, 8). In periodic harvests, production data of the different plant organs are determined, as well as morphogenetic characters. For details of the experimental technique see refs. 2, 7, 10, 11.

By special methods of analysis it is possible to extract from the data relationships indicating characteristic differences between plant species, and also to distinguish between directly productive, and morphogenetic effects of light intensity, and to follow up these differences throughout the season and the species.

This ultimately leads to a further analysis of contentions like N.A.R. and R.G.R., by referring them to single organs, and recognizing that they contain a mixture of productive and formative aspects, which may be differently affected by environmental factors.

In this paper, I will restrict myself to some examples of this type of growth and production analysis, in tulip, bulbous iris, and gladiolus. A similar analysis of shape factors is possible, as I have shown at the International Photobiology Congress at Hanover, U.S.A. (1968, see ref. 10).

Graphs representing the growth of plant organs against light intensity at successive dates are rather similar for the three mentioned bulb plants. As the season proceeds, the effect of light intensity on total dry weight production becomes increasingly pronounced, and the organ, ultimately making up for most of the total weight, is the new bulb (or corm), in all three species, be it to a different extent (figs. 1–3; for a detailed discussion of these graphs, see refs. 3, 5 and 10 respectively).

The picture for the other organs at first sight is less clear. This is mainly so, since those develop largely at the expense of the reserves in the old bulb or corm, especially in their initial stages, and decreasingly so in the order tulip-iris-gladiolus.

In all cases, the new bulb largely grows at the expense of actual photosynthesis, as indicated by its strong relation to light intensity, but also here, the degree of dependency upon the light factor, and the start of new bulb (corm) development mutually differ.

Increase in light intensity generally leads to increase in dry weight of all plant organs. Apart of that, it is of interest to see whether differences in the distribution pattern occur in relation to light intensity during the growth period.

Therefore, some series of graphs are presented, showing the dry weight of some plant organs at various closely corresponding points of seasonal development, and at different light intensities, expressed *in percents (%) of total dry weight*. This eliminates the direct effect of light intensity on production, and, therefore, brings about more clearly the formative, developmental, and species effects.

Fig. 4 shows this for leaves, stems, flowers, stems + flowers, old bulb (corm), and new bulb (corm) as % of actual total dry weight of the plant, for five representative stages of development in relation to light intensity. Moreover, in each case, the *actual total dry weight*, as % of that reached at 100% light intensity has been represented, to remind the importance of the productivity factor. The trends in the remaining graphs multiplied by those just mentioned, yield the actual production values of the different organs.

Fig. 4 shows that the percentage of total dry weight in the leaves increases in the direction tulip-iris-gladiolus; in each species it reaches its highest values in the first parts of the season, and later decreases continually. There is, in all cases, at all dates, a slight but unmistakable decrease with increase in light intensity.

The percentage of total weight in the flowering stem gradually increases during the season and reaches its maximum – as might be expected – at the time of flowering. After this, it decreases in all three species, and, together with the

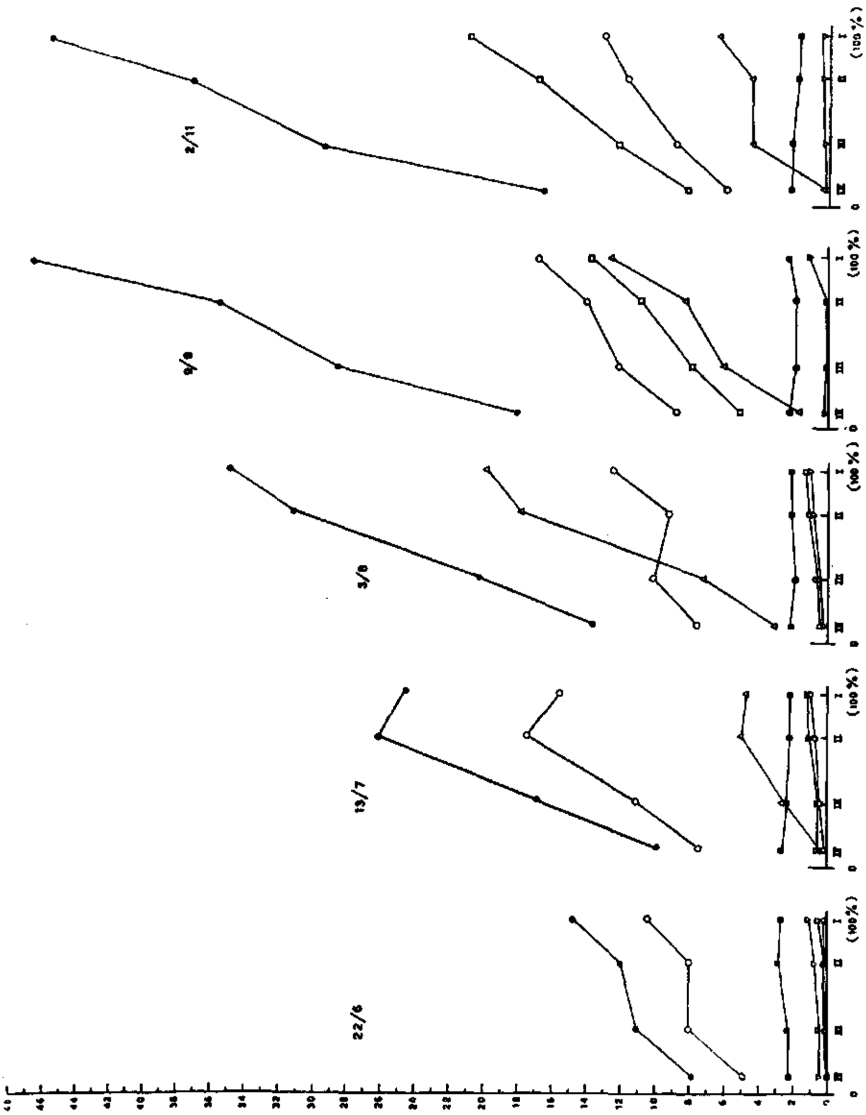



FIG. 1. *Gladiolus*. Field experiment with artificial shading. Dry weight development at choice (5 out of 8) of successive harvests. Planted May, 1959. ▽ roots, ○ leaves, △ stem, ■ old corm, □ new corm, ● total. Light intensities I, II, III, IV: 100, ~ 75, ~ 37, ~ 12% of full daylight respectively.

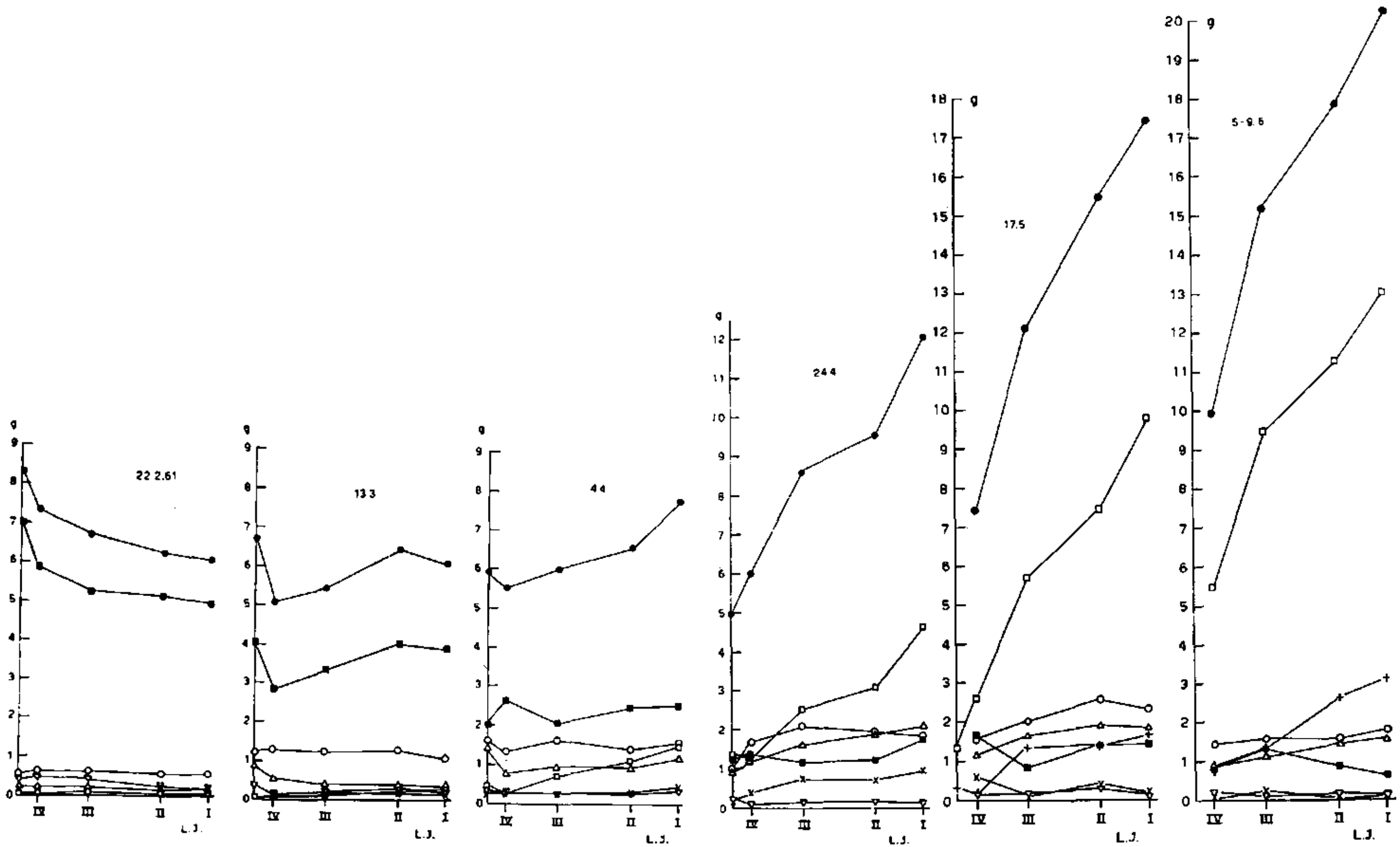



FIG. 2. Tulip. Field experiment with artificial shading. Dry weight development of various parts and total at successive harvests. Planted 7.11.1960; △ roots, ○ leaves, △ stem, × flowers, ■ old bulb, □ new bulb, + small new bulbs, ● total. Light intensities I, II, III, IV: 100, 75, 37 and 10–12% of full daylight, and darkness (zero light intensity).

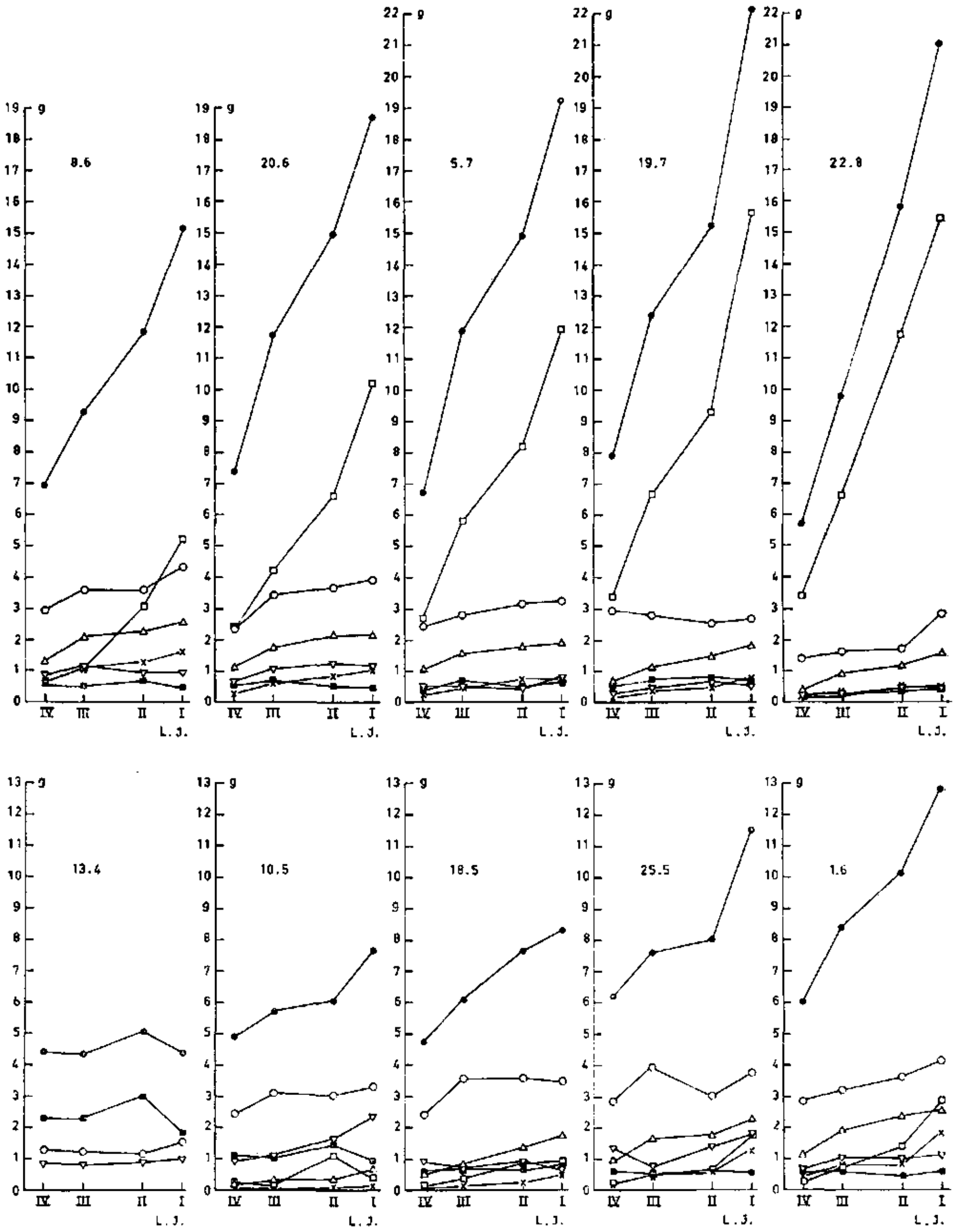
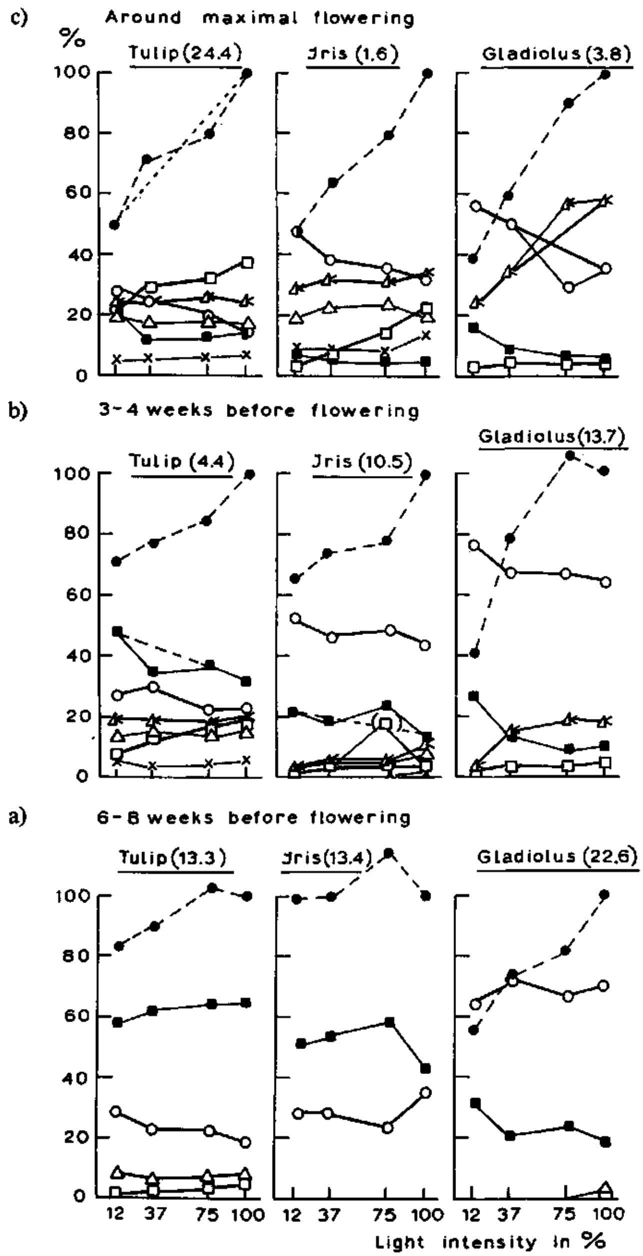



FIG. 3. Iris, var. Wedgwood (bulbous Iris). Field experiment 1966 with artificial shading. Dry weight development of various plant parts and total weight at successive harvests. Planted 8 Dec. 1965. △ roots, ○ leaves, △ stems, × flowers, ■ old bulb, □ new bulb(s), ● total. Light intensities I, II, III, IV, 100, 75, 37 and 10–12% of full daylight.


c)
Around maximal flowering
%
Tulip(24.4)
Jris (1.6)
Gladiolus (3.8)
100
80
60
40
20
0
b)
3-4 weeks before flowering
Gladiolus(13.7)
Tulip (4.4)
Jris (10.5)
100
80
60
40
20
0
a)
6-8 weeks before flowering
Tulip(13.3)
Jris(13.4)
Gladiolus (22.6)
100
80
60
40
20
0
12 37 75 100 12 37 75 100 12 37 75 100
Light intensity in %

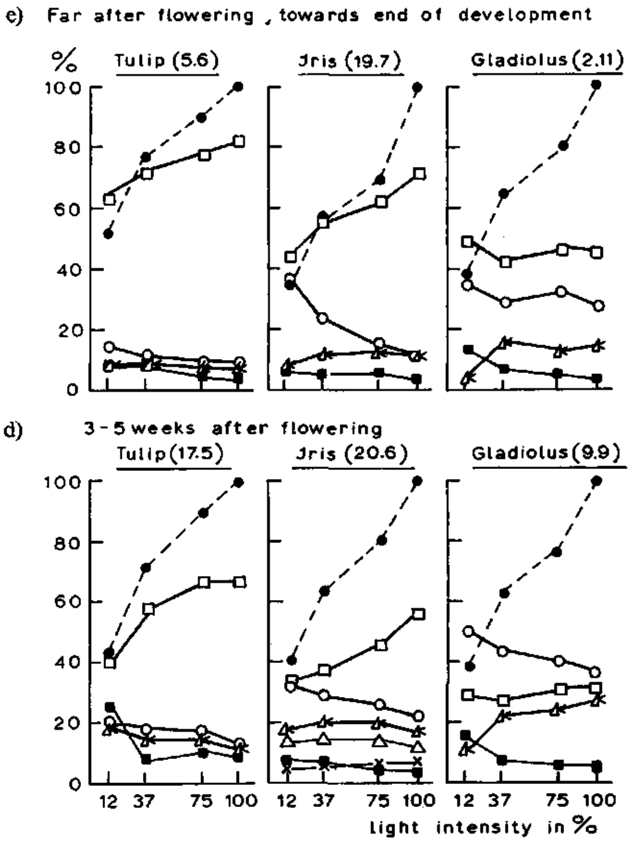



FIG. 4. (a-e, pp. 6 and 7) Dry weight of separate organs in % of corresponding total plant dry weight; ○ leaves, △ stem, × flowers, (△×) stem + flowers, ■ old bulb/corm, □ new bulb/corm; - - - ● - - - total dry weight in % of value at 100% daylight.

data of figs. 1–3 suggests transport of materials from the flowerstalk, probably in favour of the new bulb (or corm), which should be studied further; some preliminary explorations herefor have been made.

Remarkably, in tulip and iris, much the same percentages go into the flower stem at all light intensities, with slightly higher percentages at the higher light intensities in the earlier parts of the season. In gladiolus, the effect of light intensity on the percentage of weight going into the flower stem is much more pronounced, especially around the peak of flowering. The percentage of the total weight going into the flowering stem (including flowers) slightly increases in the order: tulip-iris-gladiolus, especially towards the peak of flowering.

The percentages of total dry weight going into the new bulb (or corm) increase during the season in all cases. In tulip and iris, moreover, there is a definite increase in these percentages with increase in light intensity, in gladiolus there is not. Moreover, the onset of actual new bulb growth during the season differs; it is well before flowering in tulip (in which, around the flowering date, the new bulb already has the highest percentages of all organs), it is well under way but not yet predominant in iris around flowering, and in gladiolus by this time it has hardly started. By the end of the growing season, these features are clearly pronounced, and, in part as their consequence, the ultimate percentages of total dry weight, covered by the bulb (or corm) decrease in the order tulip-iris-gladiolus.

The presentation of fig. 4 still results in rather complicated pictures, and therefore, in the following figures, some further summarizing is endeavoured.

Figure 5 shows the trends of dry weight acquisition during the season, in percents of total, separately for leaves, stem + flowers, and new bulb (corm) at the various light intensities. To facilitate comparison, the curves at about the maximum of flowering are marked by interrupted lines. The features already briefly discussed show up more clearly.

The percentage weight in the leaves decreases with increasing light intensity, in all three plants, and more or less at all dates in much the same way; their absolute values increase clearly in the order tulip-iris-gladiolus.

The behaviour of the new bulb is fairly the opposite of that of the leaves; its percentage decreases in the order tulip-iris-gladiolus.

In tulip and iris, there is a clear increase in percentage weight in the bulb with increasing light intensity; remarkably, not so in gladiolus.

During the season, the percentages of total dry weight in the bulb increase considerably, probably in part reflecting its function as storage organ, as well as – especially in the later stages – the gradual decline of the aerial organs.

As already observed, stem + flower percentages of dry weight remain rather unaffected by light intensity in tulip and iris during the season, whereas in gladiolus, especially around flowering, a clear sensitivity to light intensity is expressed.

It should be remarked that mirror images are no miracles because of the expression as percents; nevertheless they may be accepted to show trends really present. Their generally coherent appearance throughout the season seems to stress the validity of the expressed trends.

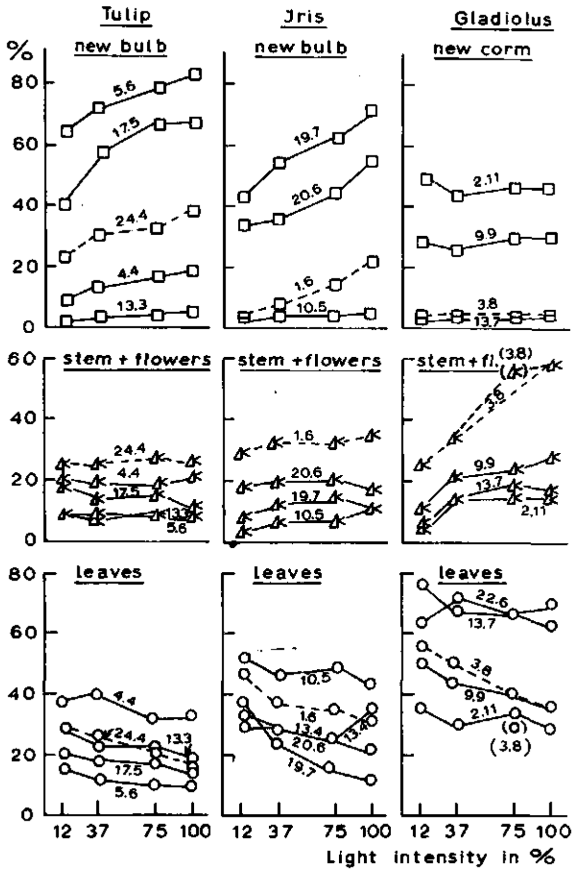



FIG. 5. Time course in the percentages of total dry weight present, as present in leaves, in stems and flowers, and in the new bulb (corm) at successive harvests during the season; - - - - - = time around flowering.

As for the position of the various organs around the flowering stage, the 'stem + flower' curve is at its highest position, the leaves are at intermediate positions with clear differences in order of magnitude in the various species, and are in a declining trend in all cases; the bulb (corm) shows already considerable percentages in tulip, much lower ones (in general) in iris, and hardly any investment yet in this organ in gladiolus, as stated before.

Figure 6 shows the relationship between the percentages of total dry weight in the aerial – mainly photosynthetically active – organs (leaves and stem) and those in the old and new bulb (the sources of reserves) together. Previously published data (10) had indicated that the position in tulip and gladiolus is very different; in gladiolus the aerial organs cover much higher percentages, whereas

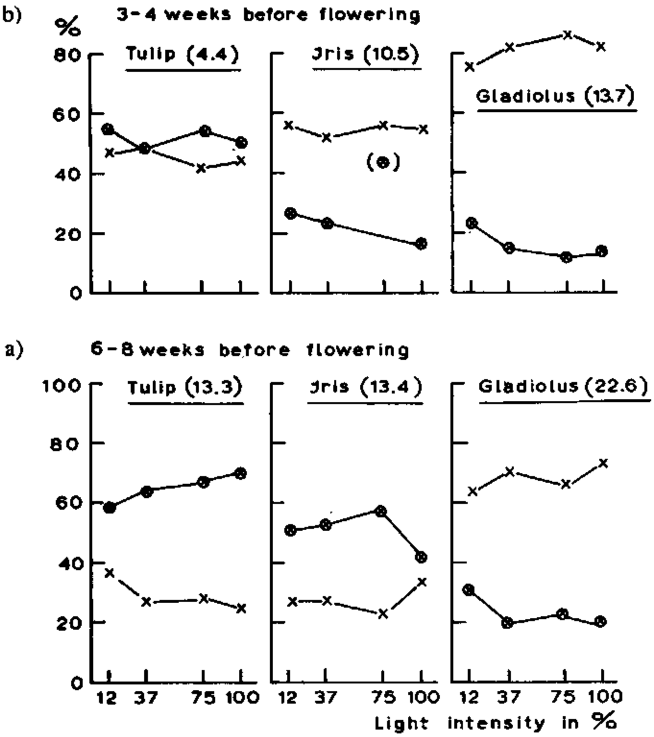
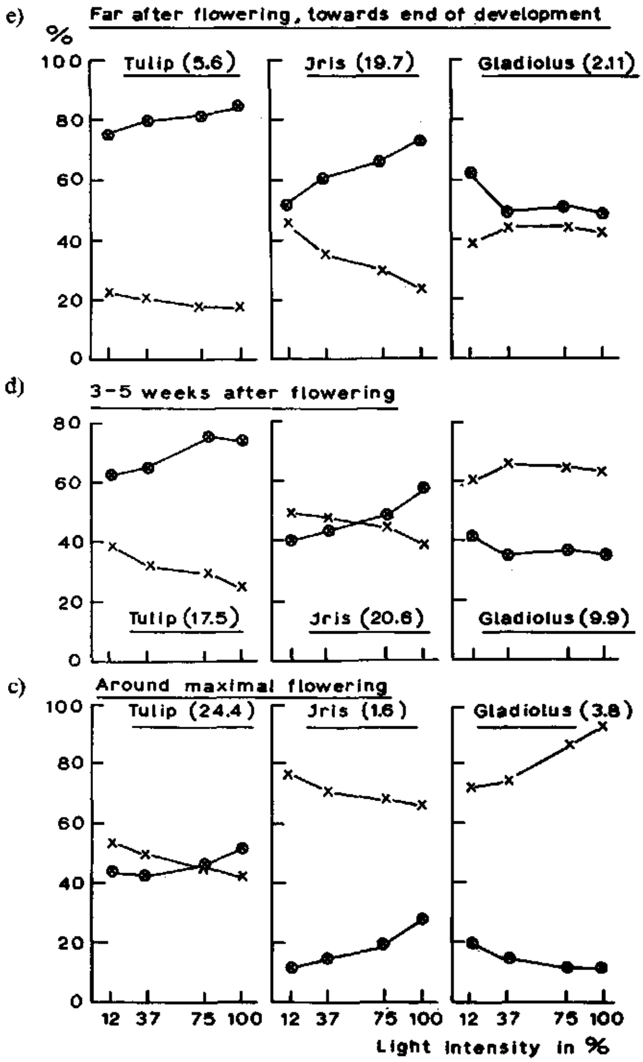



FIG. 6 (a-e, pp. 10 and 11). × Stem (inclusive flowers) + leaves dry weight, ⊗ old + new bulb(s)/corms dry weight, in percent of corresponding total dry weight, at various stages of devel opment. At early dates, sometimes × is only leaves, ⊗ only old bulb/corm, especially in *Iris* and *Gladiolus*.

in tulip the reverse holds. Interestingly, also in this respect, iris is intermediate.

In tulip, both percentages are more or less equal some weeks before flowering, obviously partly owing to the old bulb, but, according to figure 5, also because development of the new bulb has already started. The situation is more or less the same at flowering, but the part of the new bulb has increased (cf. figure 5). Later on, the subsoil parts percentages at all light intensities far exceed those in the aerial parts.

In iris, subsoil and aerial dry weight percentages are about equal 3–5 weeks after flowering; at flowering, the aerial organs still are far in excess.




In gladiolus, percentages of stem and leaves and those of corn weight reached equality only towards the end of the season.

In tulip and iris, the stem and leaves percentages decrease with increasing light intensity (fig. 6) and those for bulb formation increase; in gladiolus, at most data, the percentages of both fractions do not distinctly differ with light intensity, except towards the peak of flowering, when the percentages of the aerial parts strongly increase with light intensity.

Figure 7 expresses the data against time course of season separately for the various light intensities. The trends discussed, and the intermediacy of iris, again

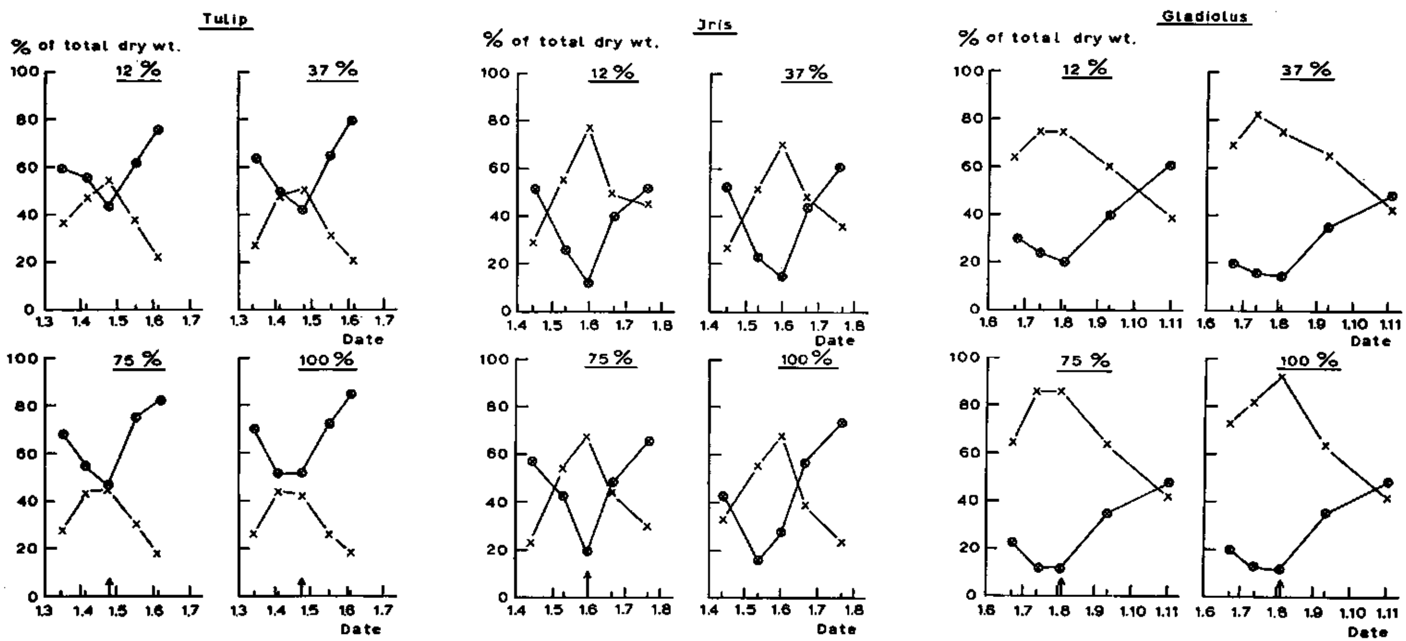



FIG. 7. × Stem (incl. flowers) + leaves, ⊗ old + new bulb/corm, in % of corresponding total dry weight.

show up very clearly. The picture shown earlier (10) is confirmed and extended. In tulip and iris, the subsoil weight percentage curve shows a downward tendency with decrease in light intensity, increasing the 'overlap' between the two curves. In gladiolus, the reverse tendency is observed, and owing to the different position of the curves, this results in much the same sort of picture as in the two other plants. This difference in trend between tulip and iris on the one hand, and gladiolus on the other hand is intriguing, and a satisfactory explanation does not seem easily at hand.

In figure 8 the differences in overlap are expressed in a simplified way, viz. as difference between the two points nearest the maxima (or minima) in each pair of curves against light intensity for all three plants.

In general, the type of curves in tulip and iris are similar, while in gladiolus they are different. At present it is not yet possible to reasonably explain this. It may result from the (probably genetically determined) fact that, in gladiolus, the development of the aerial organs is much more governed by the prevailing conditions for photosynthesis than in the two other cases, and this again may be connected with the fact that – at least in our climate – tulip and iris are early season growers whereas gladiolus has its main development in summer.

It may well be asked whether the relationships expressed in figs. 7 and 8 differ in the pre- and post-flowering stages of development, since the growth of the

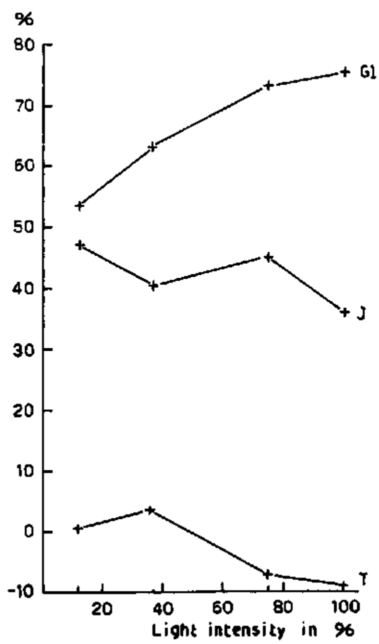



FIG. 8. The distance between the 2 points (averaged) nearest the middle of the × and ⊗ curves in fig. 7, plotted against light intensity.

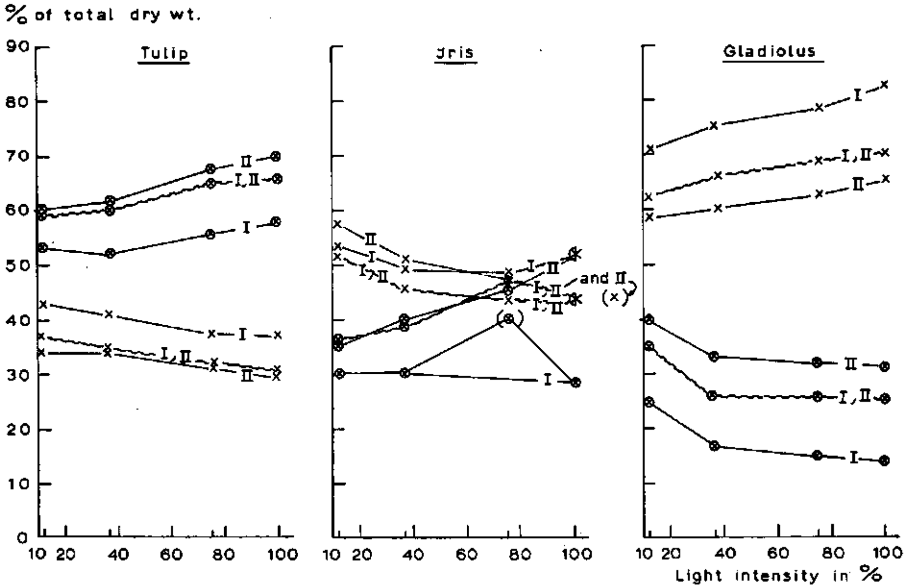



FIG. 9. Stem + leaves (×), old + new bulb (⊗), I: first part of season incl. main flower stage, II: second part of season incl. main flower stage, I, II entire season, as far as represented in fig. 7 (~~).

new bulb (or corm) as the main product of contemporary photosynthesis, for the greater part takes place in the second part of the season.

Therefore, we have averaged the data of fig. 7 for each half of the season separately, including the flowering date in both of them (fig. 9, graphs marked I or II), and compared them with those for the entire season (graphs marked I, II).

In general, the trend of these averages is much the same in both halves, and thus also in the entire season. In tulip, in both halves of the season the subsoil weight prevails, and the more so, the higher the light intensity is. In gladiolus, this is the opposite, and the percentages are further apart. Iris (apart of some irregularities in the data in the first part of the season), again is intermediate, with the position of aerial and subsoil parts reminding of gladiolus, but with slopes more like those of tulip. The average curves for the entire season are shown separately, and thus more clearly, in fig. 10, which reveals the characteristic differences between the three species in a very simple way.

The preceding considerations concerning the relative partition of matter over various plant organs during the season suggest the introduction of *partial net assimilation rates* or *partial relative growth rates*, i.e. the accumulation of matter in the various organs separately per unit leaf present. Similar considerations have been applied in BUTT's work from our laboratory, on onions, as far as we know, for the first time (8).

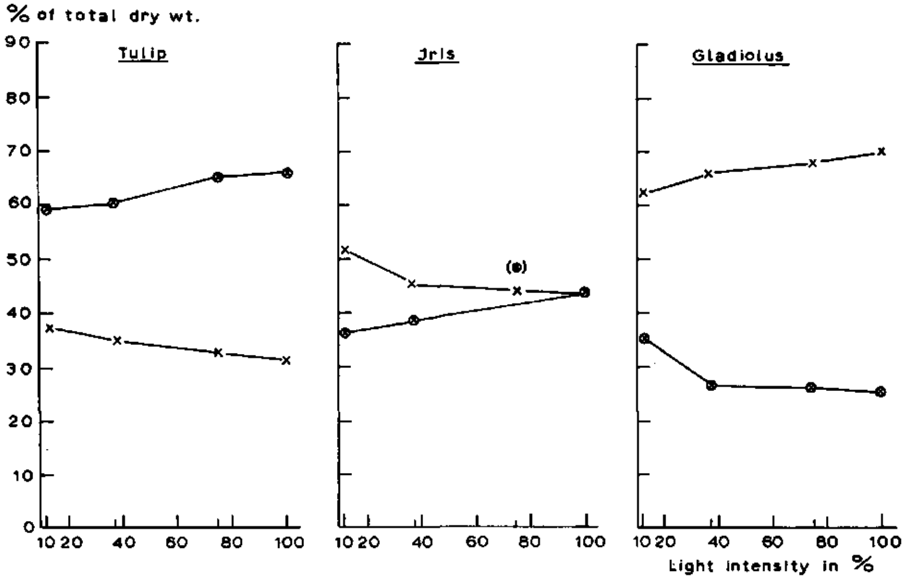



FIG. 10. Stem + leaves (×), old + new bulb (⊗), entire season (taken from fig. 9).

In fig. 11, bulb growth rate in two successive parts of the season is expressed in relation to the average leaf weight present. The data present the daily increase in bulb (corm) weight (in percent) *per unit average leaf weight present* during the period considered, so:

$$\frac{\text{increase new bulb or corm}}{\text{av. leaf weight}} \times 100/\text{day}$$

The value thus calculated may be denoted as the Relative Growth Rate of the new bulb. It is very near to the partial Net Assimilation Rate for the same organ, which would have been obtained if average leaf surface had been used. The 'average leaf weight' taken is the arithmetic middle between the values of the two harvests, at the beginning and at the end of the considered period (see legend fig. 11).

Since bulb growth and leaf weight are taken as absolute values, the production factor of light energy is involved, and not only the formative one as in previous figures, hence the strong expression of light intensity in figure 11.

It is interesting that at full light intensity, in tulip and (somewhat less) in iris, after flowering, the bulb grows with a daily rate as high as ca. 10% of the leaf weight present. At the lowest light intensity these values are around 4%. In gladiolus, the daily growth rate is much smaller, viz., between 1 and 2 per cent, depending on light intensity.

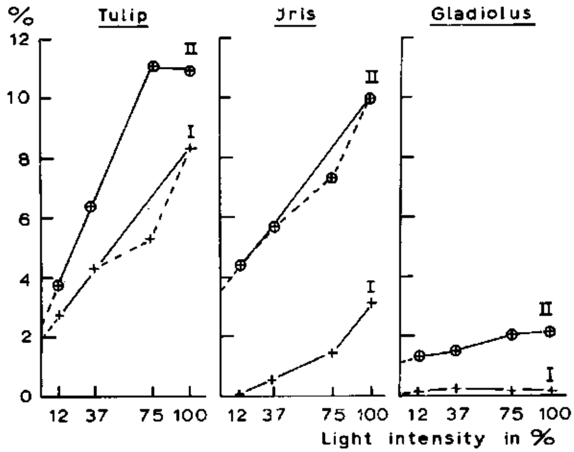



FIG. 11. $\frac{\text{Increase new bulb or corm}}{\text{Leaf weight}} \times 100$/day. (Increase in dry weight of the new bulb, per day in % of the average leaf dry weight present during the period). Period I = from 3–4 weeks before flowering onto flowering; period II = from flowering to 3–5 weeks thereafter.

With the aid of the data on leaf area previously published (10), it is easy to make the calculations with respect to unit leaf area. Since leaf area is not greatly affected by light intensity, the result would not be very different.

Comparison of fig. 11 with fig. 5 shows that the 2nd period represented in fig. 11 is that with the strongest increase in bulb in percentages of total weight. The first period represented in fig. 11 (see legend) clearly expresses the differences in the relative importance of bulb growth in the period just prior to flowering in the three plant types. In tulip it is already very pronounced; in iris it has clearly started, but still is at fairly low rates, especially at the lower light intensities; at 12% daylight it has hardly started. In gladiolus, it has no significance yet in this period.

Herewith, we close our survey which may have shown how plants of similar type, but different in details, react upon the deliberate variation of a definite environmental factor. The reaction type is analogous, however, with distinct differences imposed by the genetic pattern. The tulip may be denoted as the bulb plant 'par excellence' whereas gladiolus shows much more affinity to plants grown from seeds, as during the major part of the season the major part of dry weight is in the aerial (green) parts. Iris is intermediate in several respects.

It seems of interest to carry out this type of studies with other plants, and with various cultivars within one species. Experience with some other plants is available but has not yet been worked out from the viewpoints discussed in this paper.

## 3. Some data on plant density effects in relation to light intensity, in bulbous Iris

The analysis of plant density effects presents difficulties owing to possible variation in the interactions between plants, in the soil with respect to water and minerals, and 'root competition' effects, and in the aerial part with respect to light, carbon dioxide, and VPD effects.

The analysis of density effects may be facilitated in combination with light intensity variation, about which more is already known.

Since plant density studies are included in the IBP 'initial programme', we have carried out (1969) a preliminary experiment with bulbous irises, including simultaneous light intensity and plant density variation. Plants were grown in our normal series of light intensities, at $\frac{1}{2}$ normal, normal, twice normal and four times normal density (or 2, 1, $\frac{1}{2}$, $\frac{1}{4}$ of normal plant distance). For unknown reasons all $\frac{1}{2}$ normal density (twice normal distance) plots failed to develop propeıly and thus could not be used.

A preliminary analysis has been made along the lines of our present discussion.

Fig. 12 shows some data comparable to those of fig. 6, (aerial and subsoil dry weights in % against light intensity).

Seven weeks before flowering, no distinct differences are to be expected, since growth still mainly relies on the old bulbs which had not grown under different conditions. Around flowering, the position of the curves is reversed, and theɪe is a large prepondeıance of the development of the aerial parts over new bulb formation. This preponderance incıeases somewhat with increasing plant density. Seven weeks after flowering, the position of the curves is again reversed, owing to the preponderance of new bulb development (cf. also fig. 6). For some unknown reason bulb development seems somewhat depressed at 100% light which was not so in the experiment at normal plant density only, shown in fig. 6. Clearly, the distance of the curves now narrows towards higher plant densities, which again expresses the relative preference for aerial development at the higher densities also in this period. We have data also for 3 weeks before and after flowering, for simplicity these are left out of the present discussion.

Averaging the distances of the pairs of curves in fig. 12 over all light intensities brings out the density effect as such (fig. 13). The slopes of the curves at flowering and 7 weeks after are nearly the same; their sign being reversed.

Separating the reactions at different light intensities, the *distances of the curves* of fig. 12 at 12 and 37, and at 75 and 100% light intensities respectively have been taken together in order to rule out minor irregularities (fig. 14). At flowering and 7 weeks after, the two light intensity regions are separate, and nearly coincide in the N curve at 37–12% and the 4 N curve at 75–100% light.

The analysis suggests that part of the density effect is light intensity competition by the aerial parts of the plants, and that in the 4 N object the available light is about 25/87 or about 1/3.5 that in normal density. Unfortunately, we have not measured relative light intensities within the crop; the suggested value, however, does not seem unreasonable.

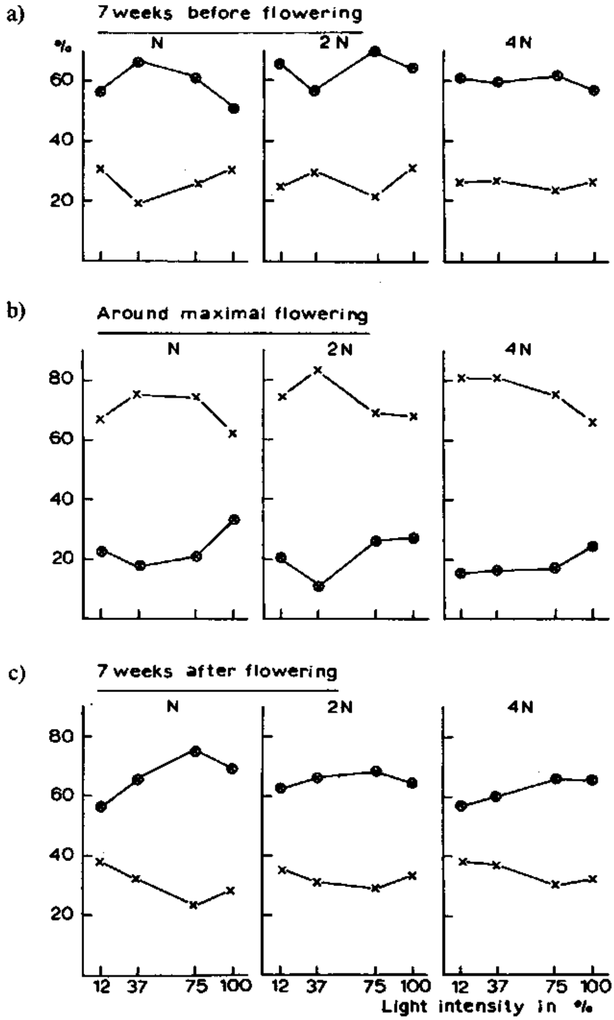



FIG. 12 (a-c). Stem + leaves (×) and old + new bulb (⊗), in relation to light intensity at 3 different moments of the season, in a density experiment (N = normal density, 2 N, 4 N = 2 × and 4 × normal density, or normal, ½ normal and ¼ normal plant distance; normal = ca. 19 × 19 cm).

The data of fig. 14 have been plotted against plant distance in fig. 15 (for flowering and 7 weeks after), and in fig. 16 against light intensity as averaged (medium values 25 and 87.5%). Both figures attempt at a summarized characterization of the data of fig. 12, and bring out the similarity, to a certain extent, of light intensity and plant density effects, as could be expected. In how far the

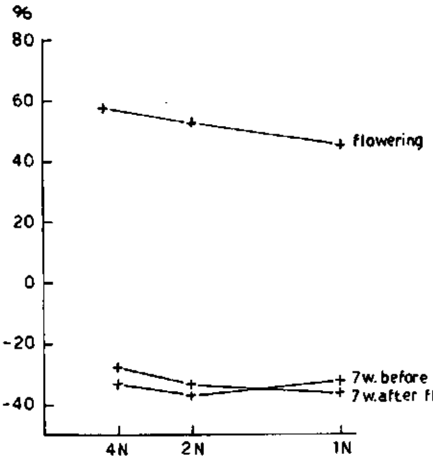



FIG. 13. The distances between each pair of curves ($\times$ minus $\otimes$) in fig. 12, averaged over all light intensities, in relation to plant distance.

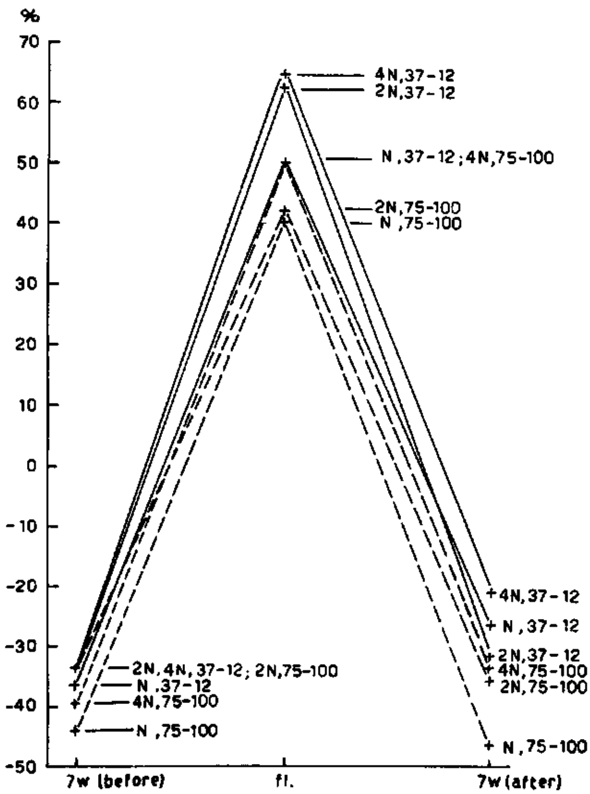



FIG. 14. The distances between each pair of curves ($\times$ minus $\otimes$) in fig. 12, separately for the two lower and the two higher light intensities, plotted against the time of the season. N, 2 N, 4 N, as in fig. 12. (Abscissa: 7 weeks before flowering, at flowering, and 7 weeks after flowering respectively).

plant density effects, in this case, are fully explainable as light intensity effects has to await further experimentation.

The full data of the plant density experiment will be published later on, in the above only some features have been briefly mentioned in connection with the main item of this paper.

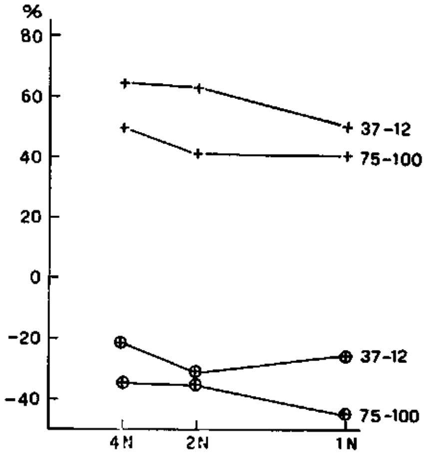



FIG. 15. Data of fig. 14, as a function of plant density (upper pair: at flowering; lower pair 7 weeks after flowering).

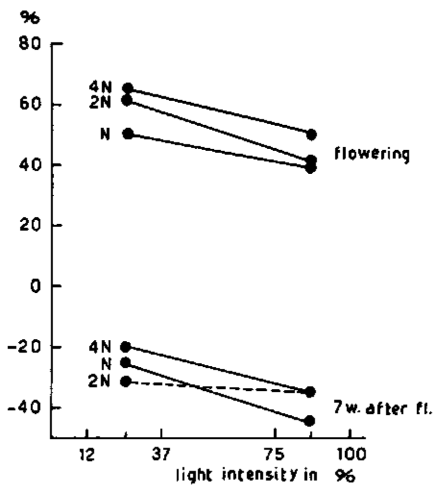



FIG. 16. The same data as in fig. 14, as a function of light intensity.

## 4. Summary

In the present paper, an analysis has been attempted of morphogenetic effects of light intensity in connection with the production pattern, comparatively for three 'bulb' plants: tulip, bulbous iris, and gladiolus (corm).

This could be achieved by expressing growth of various organs at successive stages of development as percents of total increase in dry weight.

It is shown that, in the sequence tulip-iris-gladiolus, the aerial organs (leaves and stem) are of increasing importance, and the reverse holds, obviously, for the bulb/corm.

Light intensity promotes intensively the growth of the new bulb/corm, but, expressed as percents of total, the changes are reduced, and in gladiolus, as far as our experiments go, hardly existent.

Leaves, as a rule, show a decreasing tendency with increased light intensity, during the whole season.

The flowering stem is at maximum percentage weight at flowering, in percentage of total only in gladiolus there is a strong light intensity effect.

The onset of new bulb/corm formation clearly is in the order: tulip, iris, gladiolus, in accordance with the importance as fraction of total dry weight development.

For further details, the reader is referred to the figures and the text of the paper.

Additionally, some data on effects of plant density in relation to light intensity in bulbous iris have been presented and preliminarily discussed. There are similarities between light intensity and plant density effects. At high plant density, as well as at low light intensity, the iris shifts somewhat towards the 'gladiolus' pattern, with more stress on the aerial weight percentages.

## 5. Acknowledgement

The author is much indebted to Miss N. Bok and Miss M. E. van den Noort for skilful and devoted technical assistance.

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