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THE INFLUENCE OF LIGHT INTENSITY ON MORPHOLOGY AND GROWTH RATE OF BEAN SEEDLINGS

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SUMMARY

Experiments with bean seedlings were made to explain the fact that plants grown at low light intensities which show a delay in plant weight reach the same relative growth rates (RGR) as controls at high light level.

The experiments confirmed the conclusion of EVANS & HUGHES (1961) that the constancy of RGR along a rather broad light intensity range can be explained by morphogenetic effects resulting in large differences in leaf area ratio (LAR).

The delay in plant weight at lower light levels appears to arise in the early seedling stage when the morphogenetic adaptations are not yet accomplished.

1. INTRODUCTION

When the natural radiation received by a young plant grown under favourable conditions is weakened from the seedling stage onward by some intercepting agent the weight during the vegetative stage will generally be lowered in comparison with controls. When, however, relative growth rates (RGR) are calculated from successive harvests according to the exponential growth model as described by WILLIAMS (1946) for free standing plants it may appear that during large parts of the vegetative stage this value is constant over a broad radiation range. This phenomenon has been observed by BLACKMAN & WILSON (1951), EVANS & HUGHES (1961) and HUXLEY (1967) and is discussed by PONS (1977). According to Evans & Hughes it can be explained by morphogenetic effects of the radiation level leading to high leaf area ratio's (LAR = leaf area per unit dry matter) in weak light which may compensate a low net assimilation rate (NAR = net gain in total dry plant weight per unit leaf area per day). The above-mentioned authors worked with shade-tolerant species but there are indications that also other species may show a light saturation curve for RGR from some radiation level onwards. RGR can only be accepted as a useful specific reference value as done by GRIME & HUNT (1975) when it is measured at this light saturation level, apart from optimal temperature and nutritional conditions.

Differences in final weight shown by young plants grown at different radiation levels with the same RGR must be explained by developments in the early seedling stage. One can expect that adaptations of leaf thickness and shoot-root ratio which both lead to a change in LAR take some time during which a seedling in weak light will lag behind. This retarded growth cannot be made up when later the RGR is brought at the level of controls. On the contrary the difference in absolute terms will increase with time.

The main purpose of this study is to analyse the development of seedlings at different levels of radiation. An agricultural variety of *Phaseolus* beans has been chosen because of its uniformity and large seed weight, which facilitates the evaluation of the role seed reserves play during the development of seedlings in different light regimes.

2. METHODS

Phaseolus beans of the agricultural variety Berna ('brown beans') were germinated in a climate room at 20 °C and fluorescent light (40 W/m^2). After six days, when the seedling leaves were unfolded, the seedlings were placed on an aerated nutrient solution (pH 6.5) containing 5.95 me/l NO_3^-, 0.5 me/l $H_2PO_4^-$, 3.45 me/l SO_4^{--}, 3.6 me/l K^+, 4.5 me/l Ca^{++}, 2.0 me/l Mg^{++} and the trace elements: 0.5 ppm B, 0.7 ppm Mn, 2.5 ppm Fe, 0.1 ppm Zn, 0.02 ppm Cu and 0.05 ppm Mo.

During the experiments in June (1) and July 1979 (2) the night temperature in the glasshouse was 20 °C, whereas the temperature rose at sunny afternoons up to 30 °C or somewhat higher.

During this period the radiation measured about noon in full sunshine amoun-

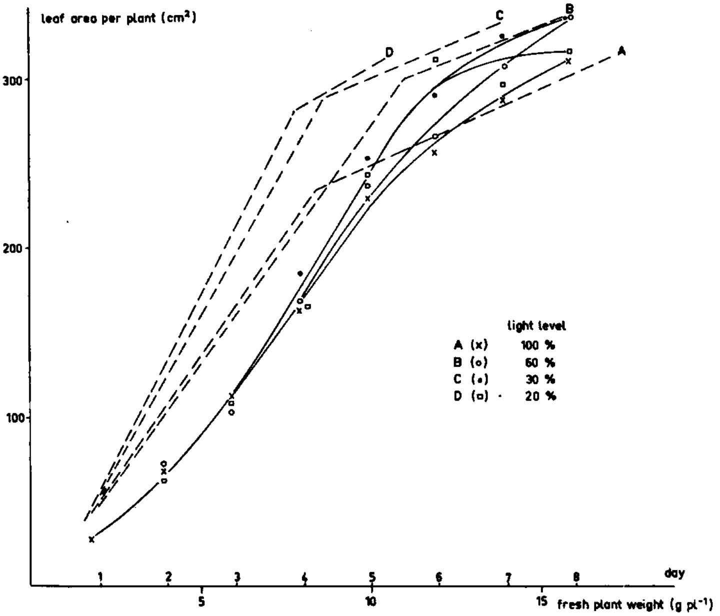


Fig. 1. Leaf area reached by the first two leaves of bean seedlings at several radiation levels plotted against time (——) and against fresh plant weight (— —). Experiment 1.

ted to about 300 W/m^2. In the glasshouse 195 W/m^2 was measured at this moment (level A). This light level was reduced by shading with white cheese cloth to 60% (B), 30% (C), and 20% (D).

Night temperature and during sunny weather also day temperature in all shaded rooms (B, C, D) could rise 2°C above the glasshouse temperature (A). The maximum air humidity in the glasshouse was about 60%, the minimum 30%; in the shaded rooms 90% and 40% respectively.

The accordance in plant weight and development rate between the objects unshaded (A) and shaded (B) indicates that these climatic differences had no significant influence.

Ten plants were harvested daily from each treatment. Fresh and dry weight of several organs and leaf surfaces were measured.

3. RESULTS AND DISCUSSION

3.1. The morphogenetic effects of light energy level

Differences in radiation level appear to have a significant effect on plant form. The final surface of the two first seedling leaves shows only small differences but it is reached at a lower plant weight in weak light (*fig. 1*). This leads to a relatively high leaf area ratio (LAR) that is reached at about the sixth day of the experiment (*fig. 2*).

In *fig. 3* the value for fresh leaf volume/leaf surface is plotted against time. This value gives the average leaf thickness. The leaf volume was calculated from fresh weight divided by SG (specific weight). This last value was measured by immersion of leaves in a calibrated cup. It appeared to fall from about 1 to 0.66 during leaf development. Direct measurements of leaf thickness showed the same tendency.

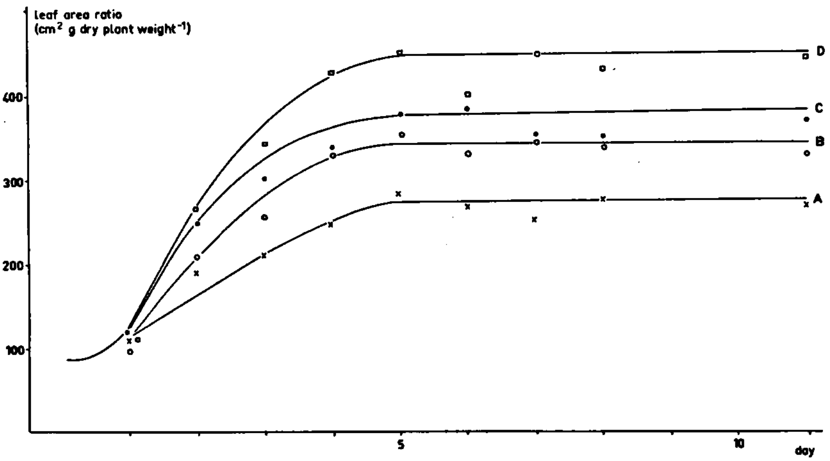


Fig. 2. Leaf area ratio of the bean seedlings recorded in *fig. 1*, in cm^2 leaf area per g dry weight of the total plant.

Leaf thickness falls in all cases during the first day of the experiment and rises steeply from the second day onward, at least in strong light. The weakest light energy level (D) reaches only 60% of the value observed in strong light (A). These findings are in agreement with numerous data recorded in literature e.g. BROUWER (1968) and PIETERS (1974).

The forming of thin leaves in weak light is generally accepted as a useful adaptation enabling a plant to enlarge its relative leaf surface and therefore to improve light interception.

To illustrate the influence of the light energy level on the relations between several plant organs the figs. 4–7 are designed according to recommandations of VAN DE SANDE BAKHUYZEN (1937) and WITTENROOD (1957) who plotted the weight of separate organs against total plant weight. The result is a 'distribution diagram'. This method generally shows straight lines for separate phases of plant development which means that the weight increase of the organs (or decrease in the case of cotyledons) is proportional to the increase of total plant weight, in other words: the distribution of matter over the plant organs is constant within a phase. In our case a logarithmic scale is chosen to do justice especially to the first phases of seedling development.

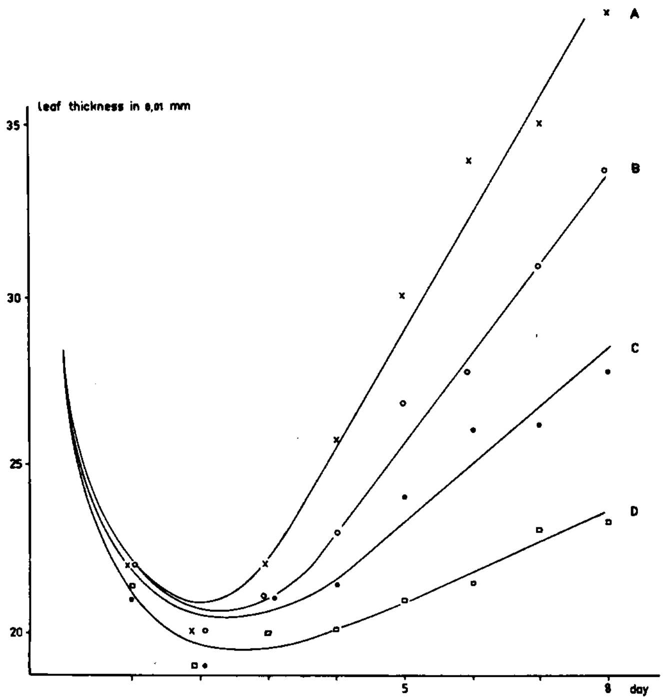
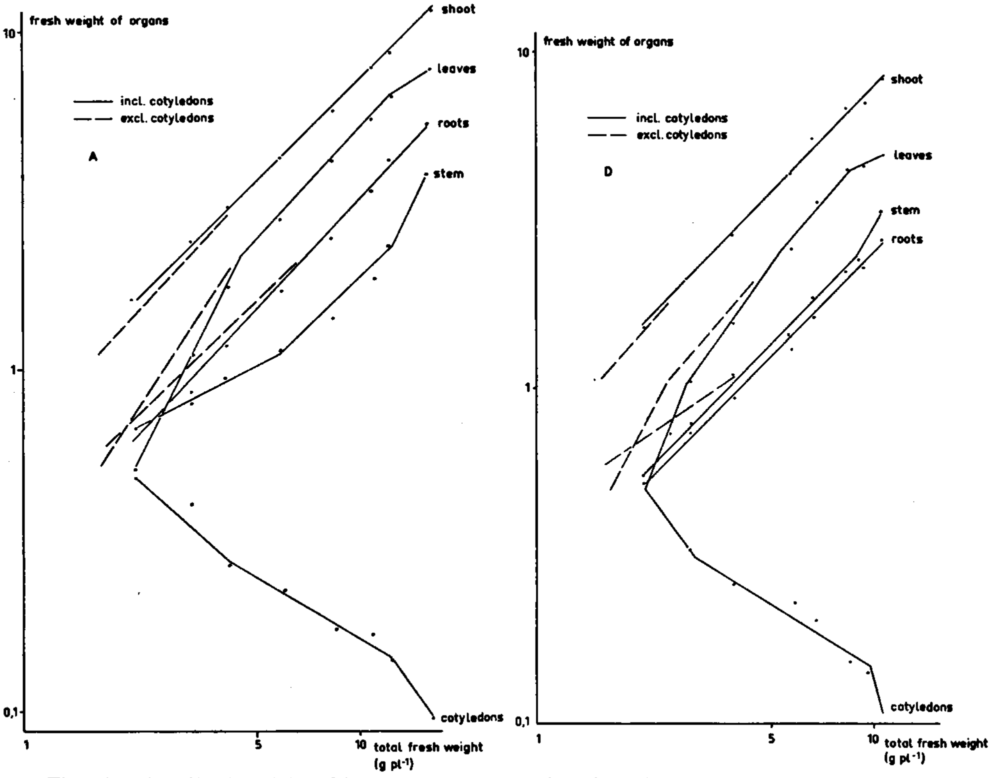


Fig. 3. Calculated leaf thickness of the bean seedlings recorded in *fig. 1*.

3.2. Fresh weights

Figs. 4 and *5* give a comparison between the light levels A and D with respect to the fresh weight ratio. The other levels are intermediate.

According to expectation the cotyledons show a rapid decline. This decline appears steepest in weak light. About the eighth day the cotyledons dissicate. The drawn lines represent values plotted against total weight inclusive cotyledons. Total weight here also includes the cotyledons. The dotted lines represent values without cotyledons, therefore lower values for total weight and total top weight. At the moment the influence of the cotyledons practically disappears, the data for total tops and for roots show straight lines at an angle of about 45° with the axis which (at a log scale) means that shoot weight ratio (and therefore also root weight ratio) is constant. At this moment the same applies to leaf and stem weight ratio. In the first day leaf weight ratio goes up and stem weight ratio falls (the last applies only to the high light level). From the fourth until the seventh day a fairly constant weight ratio is attained in both organs. In the last days the leaf weight ratio falls and the stem weight ratio rises. This last rise is at least partly caused by the inclusion of the emerging third leaf in stem weight. The simultaneous drop in leaf weight ratio applies to the two seedling leaves which approach their final weight at this moment.



Figs. 4 and 5. Fresh weight of bean seedling parts plotted against total weight. A = high radiation level, D = low radiation level. Logarithmic scale. Experiment 2.

The total top weight ratio (and therefore the top-root weight ratio) appears to be higher in weak light (*table 1*). In *figs. 4* and *5* the difference is best visible in the root weight ratio because of the logarithmic scale. Stem weight is mainly responsible for the high top weight ratio in weak light and this may be connected with the growth form of the genus *Phaseolus*, where even bush beans are easily induced to winding by weak light. In weak light the stem weight lies above root weight. Strong light shows the reverse.

The increase in top weight ratio is a well known reaction to weak light (BROUWER 1963, 1968) and can be interpreted as an adaptation just as the thinning of leaves. Under conditions of low transpiration a plant can economise on root weight ratio to the benefit of the top.

The adaptation which results in a higher top-root ratio must take place in the first days of the experiment and should demonstrate itself in a falling root weight ratio. This is visible only when we omit the cotyledon from the ratio data (dotted lines in *figs. 4* and *5*) so that the cotyledons are treated as an external dry matter source, and restrict ourselves to the growing plant parts. When the cotyledons are included this fall of the root weight ratio (which as expected is strongest in weak light) is confounded because root growth then appears as a transfer of dry matter not from 'outside' (the cotyledons) but from total top to root, which lowers the level of the root weight ratio already in the initial phase. After the third day the influence of cotyledons is more and more negligible, so that dotted and drawn lines fall together.

3.3. Dry weight

Figs. 6 and *7* give the distribution of dry matter over the plant organs. At both radiation levels leaf ratio shows a strong increase until the sixth day. This increase is particularly strong in the first days and coincides with a steep decline in cotyledon weight ratio which indicates that especially the leaves benefit from the rapid transfer of dry matter from the cotyledon to the growing organs. In weak light the decline in cotyledon ratio is still steeper, the exhaustion is apparently

Table 1. Root weight ratio and top-root weight ratio from the fourth day of the experiment onwards. Without cotyledons.

			Experiment 1	Experiment 2
Fresh weight	root ratio	high radiation	0.25	0.30
		low radiation	0.22	0.25
	top-root ratio	high radiation	3.0	2.3
		low radiation	3.6	3.0
Dry weight	root ratio	high radiation	0.19	0.17
		low radiation	0.18	0.17
	top-root ratio	high radiation	4.2	4.9
		low radiation	4.5	4.9

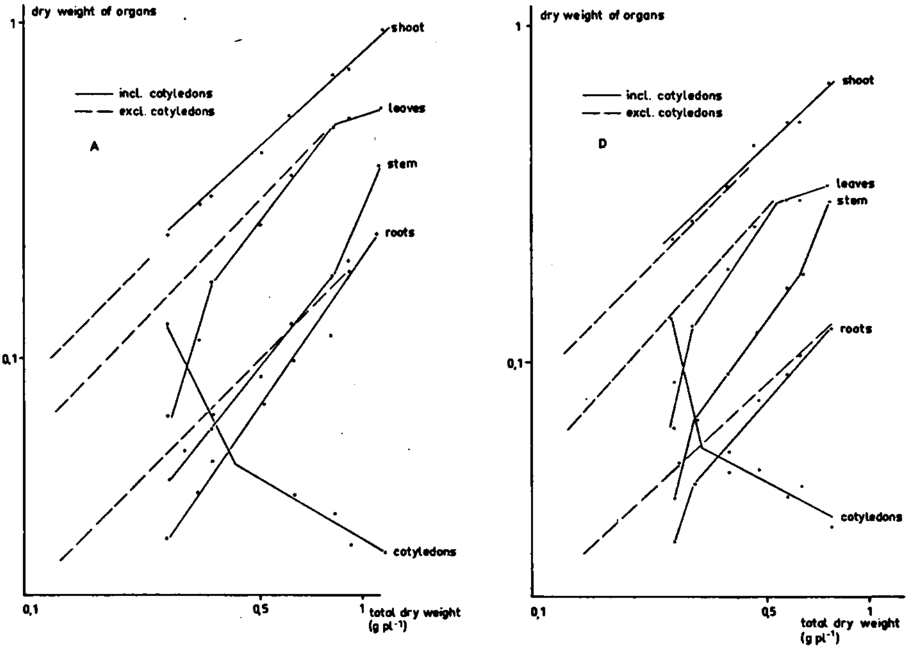
enhanced by weak light conditions and here stem and root also show a relatively strong increase in this phase.

In contrast to fresh weight conditions the weight ratio's of the growing organs are not constant. The root weight ratio is rising (the lines show angles of > 45° with the axis). This contrast can be explained by changes in dry matter content especially in the first phase of seedling development. The transfer of dry matter from the cotyledons to the growing organs results in a dilution, so that the dry matter content of the total plant decreases gradually (*fig. 8*).

When the cotyledons are excluded from the total plant weight (dotted lines in *figs. 6* and *7*) root weight ratio appears to be fairly constant.

In contrast to fresh weight conditions the radiation level has no significant effect on top-root ratio (*table 1*). This can be explained by the fact that the dry matter content of the tops is significantly lower at low radiation level whereas the roots show less difference (*table 2*).

The fact that the radiation level influences shoot-root weight ratio only with respect to fresh weight gives an indirect support to the supposition of BROUWER (1963, 1968) that shoot-root ratio is established as the result of a functional equilibrium. When the plant is short of water because of a high transpiration shoot growth will be retarded more than root growth until the roots are able to compensate the water loss completely. Under conditions of constant radiation and water supply shoot-root ratio's will be constant at a specific level, which will be higher at low radiation because of low transpiration.



Figs. 6 and 7. As *figs. 4* and *5* for dry weight.

Table 2. Average dry matter contents in % at several radiation levels. Compare *fig. 8*.

	Experiment 1		Experiment 2	
Radiation level	A	D	A	D
Shoot (without cotyledons)	8.9	7.7	8.4	7.2
Root	5.2	4.7	4.3	4.6

It is clear that fresh weight relations are decisive for transpiring leaf areas and active root mass and, therefore, for the equilibrium. Dry matter relations may deviate.

3.4. Conclusion with respect to the morphogenetic effects

The morphological differences between bean seedlings in strong and weak light express themselves mainly in LAR and in the stem weight ratio which are much higher in weak light. With respect to top-root ratio (without cotyledons) this is almost constant from the beginning with respect to dry matter weight and does not show a clear influence of light level. The fresh weight ratio, however, is higher in weak light. The difference is caused by relatively higher water content of the sprout, which corresponds, of course, with a lower dry matter content (*table 2*).

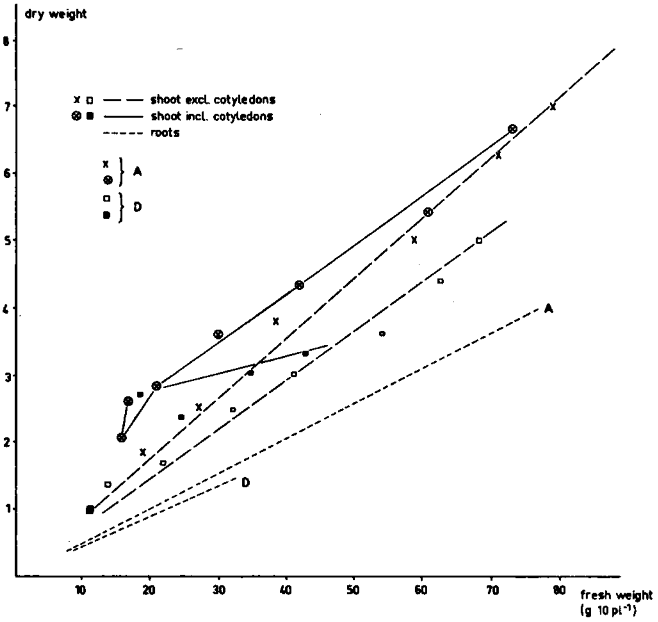


Fig. 8. Dry matter weight in grammes of bean seedling sprouts (10 plants) plotted against fresh weight. Experiment 1. Sprouts inclusive cotyledon begin with a dry matter content of 15.5%, which falls gradually to a constant level of 8.9% (A) and 7.7% (D) when the cotyledons are exhausted. This process ends earlier in weak light (D). When the cotyledons are omitted sprouts show the constant dry matter content from the beginning.

3.5. The increase of fresh plant weight

In *figs. 9* and *10* logarithmic values for total seedling weight from the daily harvests are plotted against time. RGR values are recorded in *table 3*. It appears that the light levels A and B do not show a significant difference. C and D are at a lower position and these arrears become manifest immediately in the first days of the experiment when the formative adaptations take place.

The dotted lines again show plant weights without cotyledons. This makes a large difference in the first days. About the sixth day of the experiment this difference expires because of the exhaustion of the cotyledons. At the same time RGR values are lowered. The initial high RGR can be explained by the fact that in the first days the increase in fresh weight has two components: a gain in dry weight and an increase in water content. At zero day the dry matter content of the seedlings is high, 13% in experiment 1 and 14.8% in experiment 2. In the period until the sixth day this drops to 8% (experiment 1) and 7.3% (experiment 2). From this moment onwards dry matter contents remain about constant with the result that the RGR's of dry and fresh weight do not show significant differences. The initial high dry matter contents are mainly caused by the cotyledons as *fig. 8* shows. As already observed the transfer of matter from the cotyledons to the growing organs implies dilution with water, which enhances the increase in fresh weight.

During the first days the RGR for the light level (D) is lower than that of the higher light levels. When, however, cotyledons are excluded from all weight data (dotted lines) this difference disappears. This can be explained by the more rapid exhaustion of the cotyledons in weak light (*fig. 8*). After the sixth day only object C in experiment 2 is able to maintain a RGR close that of A and B.

3.6. The increase of dry plant weight

It appears that in the first day of the experiment the seedlings loose dry weight. This may be explained by respiration excess in the initial germination phase

Table 3. Relative growth rates (mg $g^{-1}day^{-1}$) of bean seedlings grown at several light levels at temperatures of about 24 °C (June) and 22 °C (July). Average values.

Before exhaustion													after exhaustion of cotyledons		
	fresh weight						dry weight						fresh and dry weight		
	cotyledons inclusive			exclusive			cotyledons inclusive			exclusive					
	AB	C	D	AB	C	D	AB	C	D	AB	C	D	AB	C	D
June (exp. 1)	325	325	290	340	340	340	210	220	135	350	350	270	192	135	78
July (exp. 2)	333	354	270	355	365	365	208	300	230	350	354	325	207	191	137

and/or by the preceeding manipulation. In the fresh weight data this effect is partly confounded by a rapid uptake of water which results in a decreasing dry matter content, earliest completed under weak light conditions (*fig. 8*). The high radiation plants (A, B) recover during the second day and obtain a RGR (*table 3*), which remains fairly constant despite the fact that LAR in the first days is hardly 60% of the later values. This indicates that the net assimilation rate (NAR = weight increase per unit leaf surface per day) during the first days is high for some reason. In both experiments 1 and 2 the objects A and B show no significant difference in plant weight despite the fact that the radiation level B is 40% lower. It would be undue to conclude that radiation was not yet limiting at this level. As *figs. 2* and *3* show leaf thickness and LAR are significantly different in this sense that plants at the B level have thinner leaves and higher LAR values than those at the A level. When we assume that in the later period NAR for each separate light level is constant and that RGR is proportional to the product of LAR and NAR, a constant RGR demands a constant LAR. Experiment 1 confirms this expectation (*fig. 2*).

These considerations lead to the equation:

$$\mathrm{LAR} \times \mathrm{NAR\,(A)} = \mathrm{LAR} \times \mathrm{NAR\,(B)} \text{ or: } \frac{\mathrm{NAR\,(B)}}{\mathrm{NAR\,(A)}} = \frac{\mathrm{LAR\,(A)}}{\mathrm{LAR\,(B)}}$$

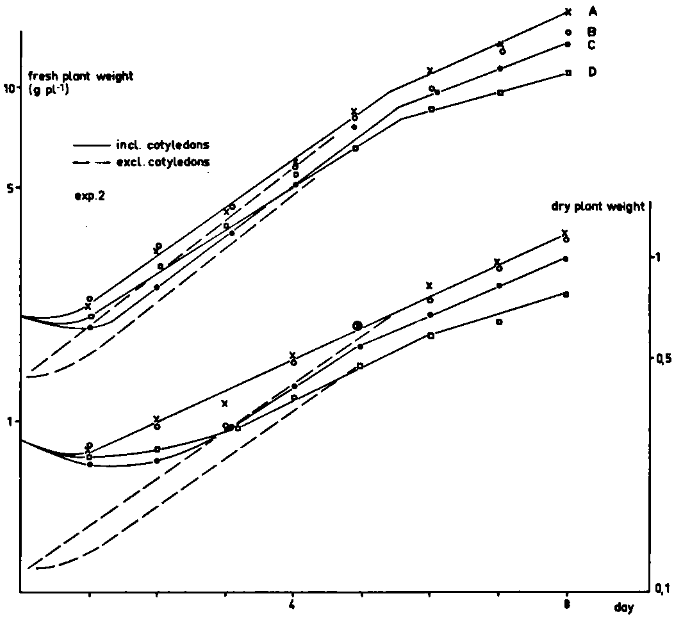


Fig. 9. Logarithmic total plant weight of bean seedlings plotted against time for the July-experiment (2). Legends as *fig. 1*. The light levels A and B fall together (upper broken line). The lower broken line represent the light levels C and D.

When we substitute for LAR the values reached during the experiment on the sixth day from *fig. 2*, we obtain for the relation NAR (B)/NAR (A) in experiment 1 the value 280/340, which means that the NAR of B is 82.3% of level A. For experiment 2 these values are respectively 340/390 and 87%.

This means that a light intensity of 60% still gives a NAR of more than 80%. This discrepancy may be explained by the fact that thinner leaves have a lower compensation point. Moreover it is possible that the two seedling leaves were light-saturated at the highest radiation level because of their horizontal position.

It is remarkable that the formative adaptations of the seedlings of light level B take place without any arrears in plant weight in comparison with the highest level (A). When a RGR as obtained in strong light demands adaptions in weak light it follows that before completion of the adaptations RGR is relatively low.

The lower radiation levels (C, D) satisfy this expectation. They only recover the initial dry weight during the third day. Then a relatively high RGR is reached until the sixth day especially by object C but in experiment 2 even by object D (*table 3*) which agrees with a very high value of LAR, higher than that of the high radiation plants (*fig. 2*). This results in a partial compensation of the arrears of the first days.

When we explain the arrears in plant weight by means of the adaptation phase,

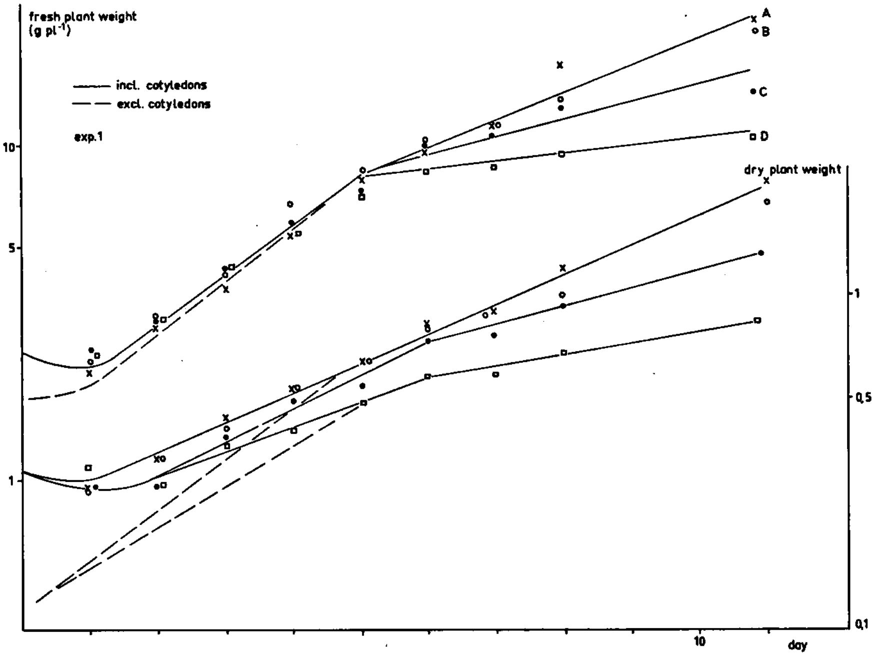


Fig. 10. As *fig. 9* for the June-experiment (1). Fresh weights did not differ significantly between light levels in the phase before the exhaustion of cotyledons. For dry weight the upper broken line represents the light levels A, B and C, the lower line D.

they must be stronger as this phase leads to larger formative shifts (therefore, in weak light). The data agree with this expectation.

From the sixth day onward the low radiation plants show a drop in RGR. In experiment 2 this coincides with a drop in LAR but not in experiment 1. This points again in the direction of a drop in NAR, after high values in the first days.

In experiment 2 the level C attains about the same RGR as A and B (*table 3*) which is also shown by the parallel course of curves in *fig. 9*. The growth curves for the higher radiation values are, however, in a higher position and this is just the situation observed in many preceeding experiments which led to the present design. Beans, by no means shade-tolerant plants, also appear to show a radiation range of constant RGR. The lower position of C appears to be caused by delay arising in the phase when the seedling leaves are still far from their ultimate extension. In both experiments 1 and 2 object D (40 W/m^2) is not able to establish a RGR at the same level as A and B. The same holds for C in experiment 1. It may be that an irradiation of 60 W/m^2 is on the threshold in this respect and that the higher average temperature of experiment 1 turned the scale.

When for experiment 2 we accept that RGR (C) = RGR (A) then:

$$\mathrm{LAR} \times \mathrm{NAR(A)} = \mathrm{LAR} \times \mathrm{NAR(C)} \text{ or: } \frac{\mathrm{NAR(C)}}{\mathrm{NAR(A)}} = \frac{\mathrm{LAR(A)}}{\mathrm{LAR(C)}}$$

When we substitute for LAR the values of *fig. 2* (sixth day) we get NAR(C)/NAR(A) = 340/440, which means that the NAR(C) is 77% of NAR(A). This means that a drop in light intensity to 30% lowers NAR much less than expected. Here again the low compensation point of thin leaves and the possibility of light saturation at level A may offer an explanation.

3.7. Conclusion with regard to growth rates and final seedling weight reached at different light intensities

Seedlings grown at a 60% light level showed the same growth rate and final weight as controls. Their higher LAR apparently gave complete compensation. At light levels of 30 and 20% much lower seedling weights were reached. This delay arose in the early seedling stages during the unfolding of the first leaves and was not made up notwithstanding relatively high RGR's in the period of cotyledon exhaustion.

After cotyledon exhaustion the low light level plants fall back to lower RGR's. Only the 30% level in experiment 2 attained a growth rate comparable to that of higher light levels.

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