Experimental Researches on Vegetable Assimilation and Respiration.—XV. The Development of Photosynthetic Activity during Germination of Different Types of Seeds.

By G. E. Briggs, Fellow of St. John's College, Cambridge.

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In a previous paper (2) the writer has shown that the photosynthetic activity of the seedling leaves of *Phaseolus vulgaris*, *Vicia Faba* and *Avena sativa* is zero or very small for some time after their first appearance, and that even when further development of chlorophyll is inhibited the activity increases from day to day. Although the photosynthetic activity was measured under such conditions that carbon dioxide was not limiting the rate of assimilation, yet an investigation of the results of growth experiments (3) indicates that under natural conditions of carbon dioxide supply the assimilation of the seedling leaves of maize is very much smaller than that of mature leaves. Tables I, which contains results of experiments carried out by the writer on maize, and I*a*, a collection of scattered results from Willstätter's work (8), show that some considerable lapse of time is necessary before the seedling leaves of maize attain their full activity, whether light or temperature be limiting; in Willstätter's experiments temperature was limiting. Experiments recorded by Brenchley (1) show that in the case of *Pisum sativum* it is some time before the seedling attains a dry weight equal to that of the seed.

Table I.—Apparent Assimilation of Maize with Low Intensities of Illumination. Young Leaves.

Age from sowing.	Intensity of illumination.	Temperature.	Assimilation in c.c. of oxygen per hour.	
			Per 50 sq. cm.	Per grm. dry-weight.
days.	lux.	° C.		
8	9,000	10	0·06	—
19	16,000	13	0·65	7·8
	9,000	13	0·56	6·7
	2,200	12·8	0·39	4·7
	1,260	12·6	0·23	2·75
29	16,000	12·4	0·68	5·2
	9,000	12·6	0·61	4·7
	2,200	11·5	0·32	2·5

Note.—The plants were grown in February, and when growth was slow.

Table IA.—Collected Results of Willstätter for Maize. High Intensities of Illumination—25° C., 48,000 lux.

Age from sowing.	Assimilation per hour in c.c., CO_2.	
	Per 50 sq. cm.	Per grm. dry-weight.
2-3 weeks	2·25	22
5 "	5·5	56

Note.—Plants grown in summer.

In the case of *Helianthus,* however, the evidence from growth experiments (4) indicates that in this plant the seedling leaves, here the cotyledons, assimilate quite actively as soon as they appear above ground, or that at most hardly a day elapses before they reach their full activity.* This evidence from growth experiments suggested an investigation of the case of *Helianthus* on the same lines as that of *Phaseolus* described in the previous paper. The results of the experiments are recorded in Table II. The same method and apparatus was used as in the previous case (2).

Table II.—Assimilatory Power of Young Cotyledons and Mature Leaves of *Helianthus annuus.*

Date.	Leaf.		Intensity of illumination.	Temperature.	Assimilation c.c., O_2 per hour.		Remarks.
	Area.	Dry weight.			Per 50 cm.^{2}	Per grm. dry-weight.	
	cm.^{2}	mgrm.	lux.	° C.			
30.1.20	1·73	—.	9,000	10·7	3·08	—	Four cotyledons still yellowish. Sown 23.1.20.
			9,000	11·1	3·37	—	
19.6.20	2·2	52·5	9,000	21·3	2·65	2·23	Eight yellowish cotyledons sown 14.6.20.
			36,000	20·8	7·3	6·10	
			2,200	19·0	0·30	0·25	
20.6.20	2·2	52·5	9,000	19·6	3·00	2·50	
			36,000	19·8	8·30	7·00	
			2,200	18·4	0·90	0·76	
16.6.20	16·7	78	9,000	18·8	3·83	16·4	First leaf when about half grown.
			36,000	19·0	9·33	40·0	

* Since carrying out the assimilation experiments described below, growth experiments carried out by Messrs. Kidd and West and the present writer have shown that the increase in dry-weight per sq. cm. per week for the first week after germination was 8·3, and for subsequent weeks 5·6, 8·7 and 8·0.

Although the young cotyledons were removed from their testas as soon as they appeared above ground, and when they had developed only a small portion of their normal chlorophyll-content, yet it will be seen that their photosynthetic activity as measured by oxygen output is quite large. The exact value for respiration depends upon the age; at 10° C. that of the cotyledons is about 1·5 c.c. CO_2 per gramme dry-weight per hour, whilst that of the half-grown leaves is about 0·9 c.c. Thus, it will be seen that the real assimilation of the cotyledons is at least as large as that of the more mature leaves both when light and when temperature are limiting: with the higher light intensity temperature was the limiting factor.

Experiments with *Cucurbita,* the results of which are recorded in Table III, show that this plant behaves similarly to *Helianthus* with regard to the photosynthetic activity of its seedling leaves. Clearly then, from this point of view, *Helianthus* and *Cucurbita* belong to a different class from *Phaseolus.* The former, where the photosynthetic activity is fully, or almost fully, developed when the seedling leaves first appear, we will call for the sake of brevity the "Helianthus type," and the latter, where the photosynthetic activity does not reach its maximum value until some time after the leaves have appeared, the "Phaseolus type."

Table III.—Young Cotyledons of *Cucurbita.*

Date.	Leaf.		Intensity of illumination.	Temperature.	Assimilation c.c. O_2 per hour.		Remarks.
	Area.	Dry weight.			Per 50 cm.^{2}	Per grm. dry-weight.	
	cm.^{2}	mgrm.	lux.	° C.			
12.2.20	5·56	175	2,200	13·4	0·21	0·13	First day after appearance of seedling above ground.
			9,000	13·4	2·31	1·47	
13.2.20	—	—	9,000	13·8	2·18	1·39	

Note.—All intensities of illumination of the same value are comparable; but different values can only be approximately compared, as the values are calculated assuming the inverse square law.

We have already shown that the latter type includes, besides *Phaseolus,* plants such as *Avena, Vicia* and *Zea.* The results of Irving's experiments (5) show that *Hordeum* also is of this type, whilst the analysis of the growth experiments of Kreusler (3) and the work of Brenchley (1) indicate that maize and the pea are to be included.

Since the chief feature distinguishing the "Helianthus type" from the "Phaseolus type" is that in the former the cotyledons function as the first

assimilating organs, it was decided to investigate the case of *Ricinus,* which is like the "Helianthus type" in that its first assimilating leaves are cotyledons, but differs in that they are not the storage organs of the seed. The results of the experiments to decide this point (see Table IV) clearly show that *Ricinus* belongs to the "Phaseolus type," the photosynthetic activity increasing from day to day. It will also be seen that as in the case of *Phaseolus* (2) the activity of the young leaves is smaller than that of the more mature ones at the lower light intensities, thus indicating that the photochemical part of the photosynthetic mechanism is not fully developed in the early stages.

Table IV.—*Ricinus communis,* grown in hot-box, 24–25° C.

Date.	Age from sowing.	Dry-weight.	Area.	Intensity of illumination.	Temperature.	Assimilation per 50 sq. cm. per hour, oxygen.	Remarks.
	days.	mgrm.	sq. cm.	lux.	° C.	c.c.	
5.2.20	14			1,260	13·1	0·14	
				9,000	13·3	0·74	
						0·83	
						0·93	
6.2.20	15			16,000	13·9	2·18	
				9,000	13·7	1·58	
		80	7·68	1,260	13·2	0·18	One cotyledon, fully green.
7.2.20	16			16,000	13·3	2·58	
				9,000	13·3	2·05	
				1,260	12·8	0·22	
8.2.20	17			16,000	12·0	2·35	
				9,000	11·9	1·84	
				1,260	11·4	0·21	
9.2.20	18			9,000	11·7	1·66	
		85	14·8	1,260	11·5	0·34	Other cotyledon, fully green.
10.2.20	19			16,000	13·4	2·88	
				9,000	13·0	2·15	

The close agreement of the evidence gained from experiments on the assimilatory power of leaves when carbon dioxide is not limiting, and that from growth experiments under natural conditions of carbon dioxide supply, lead one to expect, in view of the above results, that the rate of increase in dry-weight per unit leaf-area in the case of *Ricinus* would be smaller during the early stages of the plant's growth. Unfortunately, the only evidence with regard to the growth of *Ricinus* appears to be that of Weber (7), whose results are not sufficiently detailed to afford any evidence as to the growth of the plants in the early stages. We have, however, in the sugar-beet a plant of the same type as that of *Ricinus, i.e.,* an albuminous seed with cotyledons which become

assimilatory organs, and whose growth has been investigated by Moritz (6). An examination of the results shows that the rate of increase in dry-weight per unit leaf-area is at first very small and increases considerably as the cotyledons develop. Thus, again, it is found that the assimilation experiments form trustworthy grounds on which to base expectations as to the results of growth experiments.

In view of the whole evidence before us, the significant difference between the seedlings of the two types seems to be that, in the "Helianthus type," the food reserves are in the first assimilating leaves, whilst in the "Phaseolus type" they are stored elsewhere. It may be that the development of the photosynthetic mechanism is delayed in the latter type by the transference of materials from the reserves to the assimilating leaves.

The Case of Acer.

As our previous experience had demonstrated the very small dependence of photosynthetic activity on the chlorophyll-content during germination, it seemed an interesting point to investigate whether the cotyledons of the seedling of such a plant as *Acer* were able to assimilate before the seedling had emerged from the seed and had been exposed to the light; at this stage the cotyledons are already green. For this purpose some sycamore seeds were soaked in water, the testas were removed, and the young seedlings placed in the apparatus with minimum of exposure to light. The results given in Table V show that in this case the photosynthetic mechanism is sufficiently developed to display considerable activity before the cotyledons have emerged from the seed. The oxygen consumption per square centimetre, due to respiration, must have been considerable, since the dry-weight of seedling material per square centimetre of assimilating surface exposed was quite large.

Table V.

Light 9,000 lux. Temperature 13·6–14° C. Oxygen per 50 sq. cm. per hour

Immediately after removal	1·5 c.c.
Next day	1·9 c.c.

In *Acer* the cotyledons are the storehouses of the food, and in view of the previous evidence the photosynthetic activity would be expected to develop early. Had the reserves been stored elsewhere, we might have had before us a case of full development of chlorophyll with no photosynthetic activity.

The Effect of High Light Intensities on the Photosynthetic Activity of Seedling Leaves of Phaseolus.

At the time when the above experiments with *Ricinus* and those with *Phaseolus*, described previously (2), were carried out, it was impossible to decide as to whether the smallness of the photosynthetic activity of the seedling leaves of this type was due purely to the limitations of the photochemical part of the mechanism. To test this point, it was necessary to increase the intensity of illumination to such an extent that the rate of assimilation of the leaves, both young and more mature, was limited no longer by light but by temperature. Under such conditions, had that part of the photosynthetic mechanism concerned with the "dark" phase of the reaction been fully developed in the young leaves, the assimilatory power of the young leaves should have been as great as that of the mature leaves; the temperature being the same in both cases. For such conditions, it was expected that in the case of the young leaves, where a deficiency in the photochemical part of the mechanism had been demonstrated, the intensity of illumination required would be greater than in the case of the mature leaves. The results of the experiments to test this point are given in Table VI.

Table VI.—Effect of High Intensities of Illumination on Assimilation of Young Seedling Leaves of *Phaseolus*.

Date.	Age from sowing.	Intensity of illumination.	Temperature.	Assimilation in c.c. O_2 per hour.		Remarks.
				Per 50 cm.^{2}	Per grm. dry-weight.	
	days.	lux.	° C.			
22.3.20	4	9,000	15·3	0	0	Leaves dead at end
	(Expt. I.)	36,000	15·0	0	0	of experiment.
24.3.20	6	36,000	15·0	0	0	Ditto.
	(Expt. II.)					
16.5.20	8	36,000	14·0	1·58	2·17	
	(Expt. III.)	55,000	14·0	1·60	2·19	
17.5.20	9	9,000	14·0	2·90	3·80	
		36,000	14·0	7·00	9·30	
		55,000	14·0	7·00	9·30	

In the case of Experiment 1, the time taken for the seedling leaves to appear was exceptionally short (only four days). With these very young leaves the photosynthetic activity was zero, even when the intensity of

illumination was increased to 36,000 lux, and at the end of the experiment the leaves were dead. Experiment 2 gave the same results. In the case of Experiment 3, it will be seen that, on the eighth day from sowing, the photosynthetic activity of the leaves, although the intensity of illumination was increased to 36,000 lux, was only half as great as it was two days later when the intensity of illumination was but 9,000 lux, and that it increased to more than four times the value in two days when the intensity of illumination was maintained at 36,000 lux. Moreover, no higher value was obtained on either day by further increasing the illumination to 55,000 lux. It is thus definitely shown that, when light is no longer the external limiting factor, it must be that portion of the photosynthetic mechanism of the young seedling leaves of *Phaseolus* which is concerned with the "dark," or chemical, phase of the process that limits the rate of assimilation to a value lower than that of the leaves when more mature.

Discussion.

From the point of view of germination the plants considered may be divided into four classes. In the first class, which contains *Helianthus, Acer* and *Cucurbita*, the cotyledons are the storage organs, and subsequently become the first assimilating organs of the seedling; in the second, of which *Phaseolus* is an example, the cotyledons are again the storage organs, but do not turn green and assimilate; in the third, to which *Ricinus* belongs, the food is stored in an endosperm, and, as in the first class, the cotyledons are the first assimilating organs; whilst in the last class, of which maize and barley have been investigated, the food is stored in an endosperm, but, as in the second class, the first foliage leaf is here the first assimilating organ. In the last three classes we find a *specialised* photosynthetic organ, whilst in the first class the cotyledon serves the dual purpose of storage and assimilation. When the development of the photosynthetic activity is considered biologically, specialisation does not appear to have carried with it any advantage from the point of view of earliness of development, for it is the cotyledon of the first class, which serves as a storage organ also, which is fully equipped for assimilation almost immediately after germination, whilst the specialised photosynthetic organ is some time in attaining its full activity. Since early development of the power of assimilation must count for a great deal in the competition under the conditions holding in nature, one wonders what advantage, if any, this specialisation confers.

As to the immediate cause of the early development in the one class and the delay in the others, it seems as if the translocation of foods from the store to the assimilating organ in the latter and the presence of food in the former may play an important part. Materials are required for the formation

of the protoplasmic part of the chloroplast and for the chlorophyll, although, from what has been said above, a very small portion of the normal chlorophyll-content seems to suffice for full photosynthetic activity.

It is interesting that specialisation and division of labour, such as is usually regarded as constituting a higher evolutionary type, does not seem to make for efficiency in the struggle for existence in the seedling stage, at least as far as assimilatory activity is concerned.

Summary.

In the case of seedlings of plants such as *Helianthus*, where the first assimilating organ is one that also serves as a storage organ, the photosynthetic activity, whether measured when light or when temperature is limiting, is fully developed at germination. Here with this type, assimilation under natural conditions of growth in the field shows no lag behind greening.

In plants such as *Phaseolus*, *Ricinus* and *Zea*, where the seedling develops a specialised photosynthetic organ different from the storage organ, the photosynthetic activity is not developed until some time after germination, and assimilation under natural conditions shows a corresponding lag.

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