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ABSTRACT — During the course of 13 days of germination and growth, the dry weights of roots, hypocotyl, and epicotyl increased in soybeans grown both in the light and in the dark. The roots of etiolated 13-day-old soybeans were only 50 per cent of the weights of roots from similar plants grown in the light. The epicotyls of etiolated plants were only 18 per cent of the dry weight of epicotyls of light-grown plants, but the hypocoyl weights of etiolated plants were greater than those grown in the light. Cotyledon dry weight of light-grown plants was reduced by 70 per cent during the 13-day period while the cotyledon weight of the etiolated plants was reduced only 60 per cent. Cotyledon removal materially reduced the subsequent growth of soybean seedlings.

During germination of soybean seedlings, the dry weight increases in various parts may be used as a measure of the translocation of reserve materials from the cotyledons and other supply organs to the increased part of the plant. Preliminary to a study of the levels of carbohydrate compounds and carbohydrate precursors in the cotyledons and embryos of germinating soybean seedlings (Abrahamsen, 1964), rates of increase were determined in the dry weights of the root, hypocotyl, and epicotyl of soybean seedlings germinated in the light and dark. Cotyledons were removed to determine effect on the dry weights of plant parts above and below the cotyledons.

Materials and Methods

Seeds of soybean, *Glycine max L.* variety Ottawa Mandarin, were dusted with Arasan, and allowed to germinate between wet, paper towels in an incubator at 25° C ±1° C. After three or four days in the incubator, the seedlings were transferred to one-quart black styrene containers in which was one liter of 1# X Hoagland's solution. The Hoagland's solution contained 0.19 g per liter of Versenol iron chelate (9 per cent expressed as the metal) as an iron source. Six seedlings were grown in one container with a waxed, plywood cover, and aerated by forcing compressed air through a central glass tube.

All plants for studies in light were transferred from the incubator to a controlled environment room three days after the beginning of imbibition. The temperature and relative humidity of the controlled environment room were 24° C ± 1.2° C and 45 per cent ± 3 per cent, respectively, during the 12-hour light cycle and 18° C ± 1.2° C and 97 per cent ± 3 per cent, respectively, during the 12-hour dark cycle. The illumination during the light cycle was 1300 ft-c at the plant level, as measured by a Weston Illuminometer, Model 756. The light source consisted of fluorescent and incandescent bulbs.

Plants for studies in the dark were transferred from the incubator to a plywood dark box (42" x 85" x 30") four days after the beginning of imbibition. This transfer was made under a dim, green light. Longitudinal openings were cut in the top and bottom of the dark box for ventilation, and the openings were baffled to prevent light leaks. The dark box was located in the controlled environment room. The temperature and relative humidity of the dark box were 20° C ± 1.2° C and 48 per cent ± 3 per cent, respectively, during the 12-hour light cycle and 17.5° C ± 1.2° C and 92 per cent ± 3 per cent, respectively, during the 12-hour dark cycle. The plants were divided into different parts for dry weight determinations as described in Figures 1 and 2. From 18 to 24 plants were selected at each harvest day for dry-weight determination. Cotyledons of soybean seedlings were removed and weighed at one or two day intervals throughout the 13-day germination period; all such plants were grown under illumination.

Results and Discussion

The data in Figures 1 and 2 indicate that essentially no dry-weight increase occurred in the embryo between day 0 and day 1 although a slight decrease in the dry weight of the cotyledons occurred during this interval (Figure 3). Presumably, the dry-weight decrease in cotyledons was due to loss of respiratory substrates. Between day 1 and day 3 the soybean radical began to elongate and increase in dry weight. The epicotyl dry weight also increased during this interval but not as much as did the hypocotyl.

At day 3 the plants to be grown in the light and dark were separated. Although the plants were exposed to light and darkness for 24 hours, no differences in growth were detected on day 4. By day 5, differences in the growth patterns of plants growing in the dark and in the light were apparent. The cotyledons of plants growing in the light began to expand at this time although no expan-

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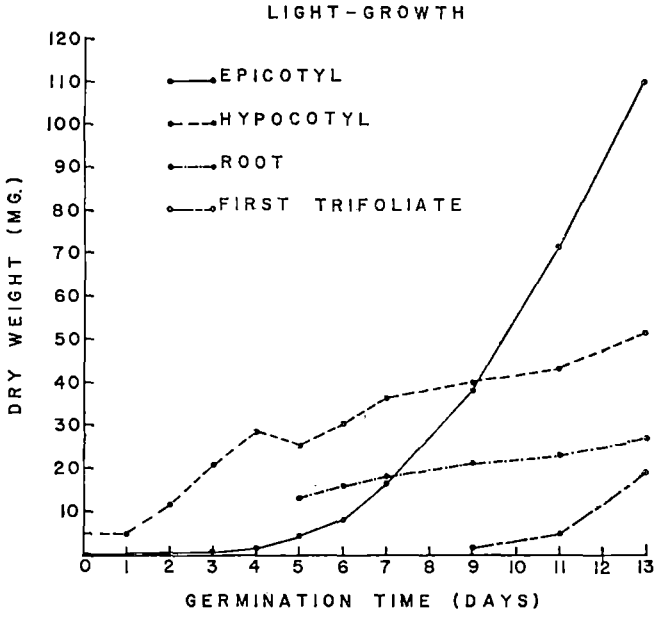

FIGURE 1. Changes in the dry weight of various plant parts of light grown soybean seedlings during germination and early seedling growth. First trifoliate refers to all plant material above the primary leaves. Epicotyl refers to all plant material above the cotyledons but below the first trifoliate. From day 0 through day 4 hypocotyl refers to all plant material below the cotyledons. From day 5 to day 13 hypocotyl refers to roots. Root refers to all material below and including the first lateral roots. Each point represents the mean of three experiments.

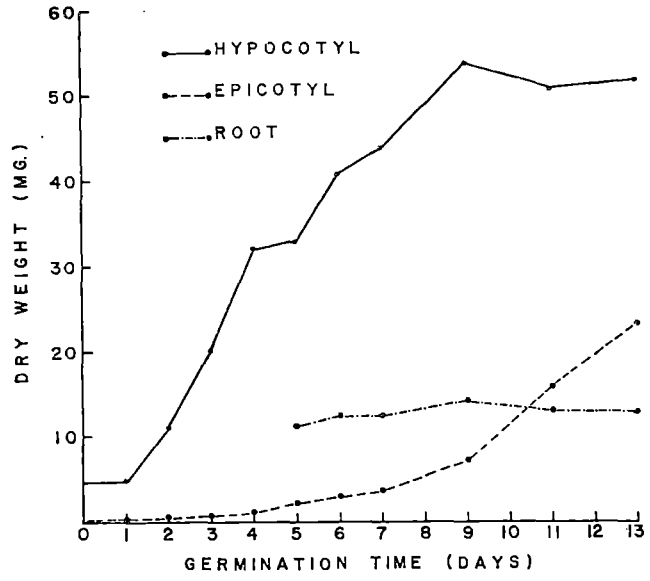

FIGURE 2. Changes in the dry weight of various plant parts of dark grown soybean seedlings during germination and early seedling growth. Epicotyl refers to all plant material above the cotyledons. From day 0 through day 4 hypocotyl refers to all plant material below the cotyledons. From day 5 to day 13 hypocotyl refers to all plant material between the cotyledons and the first lateral roots. Root refers to all material below and including the first lateral roots. Each point represents the mean of three experiments.

sion of the cotyledons of dark-grown plants occurred throughout the 13-day germination period.

The roots of dark-grown plants were shorter and the number and development of lateral roots were markedly reduced in comparison to plants grown in the light. These observations were confirmed by the dry-weight data in Figures 1 and 2. In the dark, the dry weight of the roots increased from 11.3 mg at day 5, to 13.0 mg at day 13, while in the light, root dry weight increased steadily from 13.0 mg at day 5 to 27.0 mg at day 13.

A logarithmic dry-weight increase in the epicotyl of light-grown plants began at day 5 and continued throughout the 13-day germination period. In the dark, slight increases in epicotyl dry weight occurred throughout the germination period, but the rate of increase was much lower than that of light-grown plants. The highest rate of epicotyl dry-weight increase in dark-grown plants occurred between day 9 and 13. This was accompanied by a rapid elongation of the epicotyl and a decrease in dry weight in the hypocotyl (Figure 2).

The dry weight of the first trifoliate leaf of light-grown plants increased rapidly from day 11 to day 13. The dry weight of the first trifoliate leaf of dark-grown plants was not determined because of its extremely small size.

The striking etiolation of the hypocotyl of dark-grown plants was evident by day 5 and it continued throughout the 13-day germination period. The hypocotyl dry weight of dark-grown plants was consistently higher than that of light-grown plants. For example, on days 5 and 9 the hypocotyl dry weights of light-grown plants were 78.6 per cent and 74.5 per cent of corresponding dry weights of dark-grown plants. The results indicate that hypocotyl elongation in etiolated soybean plants is not only an increase in length, but involves a net synthesis of dry matter.

A linear decrease in the dry weight of soybean cotyledons from plants grown in the light and dark took place for the first seven days of the germination period (Figure 3). On days 9, 11, and 13, the mean dry weights of

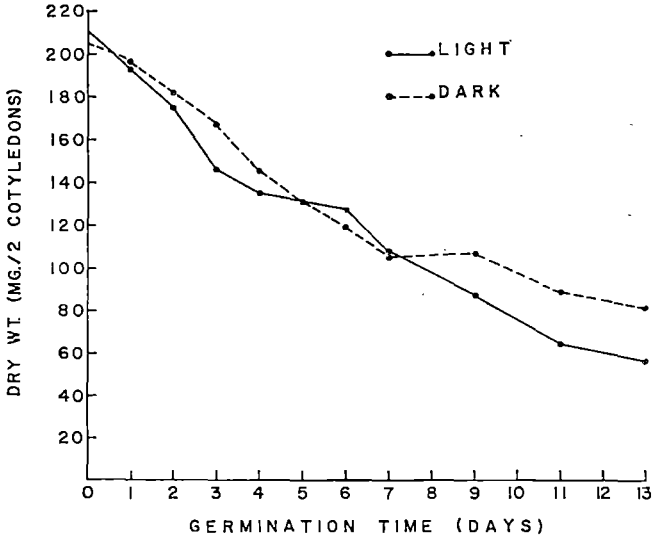

FIGURE 3. Changes in the dry weight of soybean cotyledons during germination and early seedling growth. Seedlings either remained in the dark continuously or were placed under light conditions after the first three days. Each point represents three experiments.

TABLE 1. The effect of cotyledon removal on the dry weight of soybean seedlings.

Day of Cotyledon Removal	Day of Harvest[a] 1		2		3		4		5		6		7		9		11		13	
	Above[b]	Below[c]	Above	Below	Above	Below	Above	Below	Above	Below	Above	Below	Above	Below	Above	Below	Above	Below	Above	Below
1	0.18	4.66	0.19	5.13	0.15	3.76	0.19	4.26	0.20	4.30	0.27	4.79	0.30	4.37	0.41	5.00	0.43	4.27	0.41	4.19
2	0.21	3.86	0.33	13.08	0.29	8.88	0.31	9.15	0.66	11.77	0.88	10.56	1.06	11.36	1.16	11.41	1.30	10.96	1.25	10.28
3	0.24	4.68	0.27	9.93	0.56	20.55	0.85	23.14	1.10	20.87	1.31	19.89	1.75	18.02	2.31	18.04	2.84	18.60	3.82	20.92
4	0.22	5.24	0.35	10.52	0.57	19.98	1.16	26.42	2.00	25.53	2.46	25.53	2.53	25.57	3.10	23.78	2.72	23.29	2.94	24.32
5	0.26	5.21	0.34	11.16	0.67	20.56	1.36	28.37	3.61	36.01	3.97	37.20	4.85	33.14	4.00	27.86	4.40	28.23	4.08	28.54
6	0.22	4.78	0.27	10.77	0.54	18.13	0.84	24.36	2.61	36.73	3.31	41.90	4.89	38.70	5.76	37.41	10.00	36.15	13.44	38.81
7	0.26	5.50	0.31	9.86	0.66	18.54	1.32	33.56	2.52	38.67	4.32	50.28	10.54	55.34	16.89	53.36	26.00	51.27	48.10	62.42
9	0.20	4.42	0.29	12.06	0.65	21.41	1.14	30.55	3.08	42.30	5.98	54.14	10.66	57.99	35.00	72.00	47.20	67.43	84.21	78.01
11	0.24	4.31	0.28	9.41	0.58	23.65	1.33	35.27	2.32	43.47	7.04	56.80	11.71	58.43	32.00	70.00	91.00	87.00	91.00	87.00
Control	0.20	5.00	0.37	11.67	0.67	21.00	1.27	28.67	4.33	38.67	8.33	46.67	16.33	54.33	39.33	61.00	76.67	66.33	129.00	78.67

[a] Data (expressed as mg) are the average of from 6 to 12 plants.
[b] Dry weight of all plant parts above the cotyledons.
[c] Dry weight of all plant parts below the cotyledons.

TABLE 2. Standard Errors of Means in Figures 1, 2, and 3

	Figure 1				Figure 2			Figure 3	
Day	Epicotyl	First Trifoliate Leaf	Hypocotyl	Root	Epicotyl	Hypocotyl	Root	Cotyledons Light	Cotyledons Dark
0	<0.1[a]			<1	<0.1	<1		6	12
1	<0.1			<1	0.1	<1		8	8
2	0.1			<1	0.1	<1		3	6
3	0.1			1	0.1	1		5	3
4	0.3			2	0.1	1		5	8
5	1		1	2	0.2	2	<1	8	3
6	1		1	1	0.3	3	<1	7	9
7	<1		3	1	0.4	3	<1	8	6
9	4	<1	2	2	1.5	3	1	9	9
11	1	1	1	2	3.2	2	1	6	2
13	3	2	5	2	2.2	1	1	2	6

[a] All tabular valves in mg.

cotyledons of dark grown soybean plants were 19 per cent, 28 per cent and 31 per cent higher than those of light-grown plants.

The data from one representative experiment on the effect of cotyledon removal at days 1, 2, 3, 4, 5, 6, 7, and 11 appear in Table 1. Eleven lots of soybeans were used for these tests. Of each lot, a fraction of the total number was harvested each day. On successive days and with successive lots, cotyledons were removed so that the soybeans grew normally until the day of cotyledon removal, and then grew without their cotyledons. In the group in which cotyledon removal occurred on the first day, one group was harvested the day of cotyledon removal and succeeding groups were harvested at daily or two daily intervals. In the group in which cotyledon removal occurred on the second day, the plants harvested the first two days had cotyledons, while those harvested on subsequent days did not have cotyledons. This process was continued through 11 days, when, for the last lot, the cotyledons of none of the groups harvested for the first 11 days had cotyledons removed. Only one group of 11-day-old plants had their cotyledons removed and were then harvested two days later. The controls, of which none had had their cotyledons removed, were harvested in similar groups. Removal of cotyledons between day 1 and day 6 inhibited dry-weight increases in plant parts below the cotyledons. Thirteen days after removing cotyledons, the dry weight of plant parts below the cotyledons was usually less than the corresponding dry weights at the time of cotyledon removal. In contrast to plant parts below the cotyledons a slow, steady increase in dry weight of the tops occurred, even when cotyledons were removed as early as day 1. This may be due to both photosynthesis and transport of materials from the roots to the shoots. When cotyledons were removed between days 7 and 11, there was an initial loss of dry weight in plant parts below the cotyledons during the first few days after cotyledon removal, but at day 13, a net increase in dry weight had occurred. This was probably due to the fact that the epicotyl, between days 7 and 11, was more highly developed than in plants of earlier cotyledon removal.

Discussion

During the early stages of seed germination, radicle development dominated seedling growth; between days 6 and 13 epicotyl growth predominated. These growth patterns were modified in etiolated seedlings in which the dry weights of roots and epicotyls were considerably less than those of light-grown plants, but the hypocotyl dry weight in etiolated plants was higher during most of the germination period. Thus, it may be assumed that more of the reserve materials in the cotyledons are translocated to the hypocotyl in the dark than in the light.

It has been shown that substrates are transported predominantly to active growth centers such as the shoot and root apexes, and young developing fruits (Swanson, 1959; Linck and Swanson, 1960). These centers that influence greatly the distribution of metabolites in a plant have been referred to as "sinks." It is possible that in dark-grown seedlings the young apexes (shoot and root) may not be the dominant "sinks" for active transport as they are in the light. This could result in a more random, nonspecific pattern of distribution along the hypocotyl.

The consistently higher cotyledon dry weights in dark-grown plants over light-grown plants between day 9 and day 13 suggest that translocation of materials from the cotyledons is inhibited by dark growth during this interval. It has been shown that removing a site of high metabolic activity that serves as a "sink" for active transport may result in decreased translocation of metabolites from the part of the plant that supplies this "sink" (Linck and Swanson, 1960).

In all experiments, cotyledon removal reduced the size of soybean seedlings. Similar effects were noted by McAlister and Krober (1951), who observed that the removal of soybean cotyledons up to 4 days after emergence resulted in stunted soybean plants. Waters and Atkin (1959), observed that snap-bean seedlings with transversely cracked cotyledons were less vigorous and had a lower yield per plant, than seedlings with undamaged cotyledons. In this work, it was observed that removal of cotyledons resulted in a differential inhibition of root development over shoot development. This indicated that the bulk of the material translocated from the cotyledons moved predominantly to the roots, especially in the early stages of germination. Cotyledon removal later in the 13-day germination period did not seem to have a pronounced effect on seedling development. This indicated that in the later stages of germination after day 7 the leaves assume the function of supplying the growth factors to the root and the rest of the plant.

Summary

The dry weights of the root, hypocotyl, and epicotyl increased throughout the germination period both in the light and in the dark. After 13 days of germination, the root and epicotyl dry weights of dark-grown soybean seedlings were 50 per cent and 18 per cent respectively of the dry weights of similar parts of light-grown plants, while hypocotyl dry weights were higher in the etiolated plants. At the end of the 13-day germination period, the dry weight of soybean cotyledons was reduced by 73 per cent and 60 per cent in light- and dark-green plants respectively. Cotyledon removal reduced the subsequent growth of soybean seedlings.

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