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Relation Between the Development Of Root System and Shoot Under Long- And Short-Day Illumination

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RELATION BETWEEN THE DEVELOPMENT OF ROOT SYSTEM AND SHOOT UNDER LONG- AND SHORT-DAY ILLUMINATION

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(WITH SEVEN FIGURES)

Relatively few investigations have been made to determine the factors which affect the relation of the growth of roots to tops. A more exact knowledge of the relations between aerial and subterranean plant parts and the degree to which these may be modified through cultural practices is of great scientific and practical importance. Extensive investigations have shown that plants exhibit marked specific and varietal differences with respect to relative development of roots when grown under the same environmental conditions. Intensive studies on the growth of wheat by WEAVER, KRAMER, and REED (**20**) and of certain other plants by CRIST and STOUT (**3**) have also made clear that there is a persistent tendency towards a positive correlation between roots and shoots, increase in size of tops being accompanied by increase in size of roots. Although significant variations in the relative distribution of the growth rate of tops and roots occur in nature and may readily be induced by change in environment, the fact remains that there is a persistent positive correlation in size of tops and roots regardless of the wide variations induced by special conditions.

The maintenance of a proper balance between root and shoot is of very great importance. If either is too limited or too great in extent, the other will not thrive. The root system must be sufficiently widespread to absorb enough water and nutrients for the stem and leaves, which, in turn, must manufacture sufficient food for the maintenance of the root system. The plant is a biological unit although it is frequently not treated as such. It is often mutilated by pruning, cutting or injuring the root system, frequently without much regard to the effect upon the remaining portion.

JEAN and WEAVER (**7**), HARRIS (**6**), and others have shown that the general effect of decreased water content of soil, providing enough is available to promote moderate growth, is to accelerate root development in relation to growth of tops. Low humidity resulting in high transpiration gives similar effects. MAXIMOW and LEBEDINCEV (**13**), MAXIMOW *et al* (**14**), and TURNER (**18**), have found that plants grown in shade have a less extensive root system and a greater ratio of dry weight of tops to roots. MOELLER (**15**), GERICKE (**5**), and LIVINGSTON (**9**) have shown that in sterile soils or in dilute nutrient solutions, roots develop extensively in relation to tops and the ratio of dry weight of tops to roots is greatly decreased. Conversely, a generally enriched soil or one with an abundance of nitrates increases the ratio of tops to roots (**6, 18, 3**). CHANDLER (**2**), for example, found that "while the nitrate has increased both top and root growth, it has not increased root growth to as large an extent as it has increased top growth. Thus, while the top growth of fertilized trees [peaches] is twice as great as that of the unfertilized trees, the root growth is only 50 per cent. greater." As pointed out by TURNER (**18**), the decreased root growth in the presence of an abundance of nitrogen may result from a low supply of carbohydrates. As regards the roots of seedlings, it has been shown that their development is greatly influenced by the nature of the reserve food supply in the seed. The more nitrogen a seed contains, the greater is its shoot growth as compared to roots. REID (**17**) has shown that an abundance of carbohydrate foods and a somewhat limited nitrogen supply promote rapid root development.

Cultural practices such as pruning the tops, etc., may affect the normal correlation between the development of root and stem in a very definite manner. AUSTIN (**1**), for example, reports experiments with 3-year-old almond trees where the development of both the tops and root systems was inversely proportional to the severity of the pruning of tops. The spread of the roots was over one-third greater where the pruning was light than where it was severe.

The preceding data are sufficient to indicate that a plant is a very plastic organism and that any factor that influences the development of either root or shoot may also profoundly affect the other. The extensive researches of GARNER and ALLARD, which have since been supplemented by those of several other investigators, show clearly the profound effect that the period of daily illumination exerts upon the vegetative and reproductive activities of plants. However, so far as the writers are aware, relatively little attention has been given to the effect upon the root systems. GARNER and ALLARD (**4**) state that "preliminary observations indicate that the duration of the daily illumination period may exert a marked effect on the relative development of the root and the aerial portions of the plant. For example, a cutting of Biloxi soybeans made no top growth at all through the winter months and the original leaves assumed a very dark color and generally unthrifty appearance. Apparently new buds were unable to develop. Upon examination of the underground portion of the plant in the spring it was seen that the soil contained a large mass of roots altogether out of proportion to the top of the plant, as judged by the usual summer growth. Other similar cases have been observed in which a light duration unfavorable to aerial development has caused extensive root growth.

Growth of root and shoot, therefore, are not necessarily contemporaneous with respect to season, and arrested development of the exposed portion of the plant caused by suboptimal light duration need not be accompanied by checking of root growth."

Under periods of illumination varying from 5 to 24 hours duration, PFEIFFER (**16**) found that the amount of development in the fibrous root systems of tomato and buckwheat appeared roughly comparable with that of the aerial parts of the same plants.

JOHANSSON (**8**) showed that root development, in proportion to the total weight of the plant, increased with an increase in light intensity. For intensities of 39 and 70 per cent. there is a falling off in the rate of increase, in proportion to total weight, at 10 or more hours daily illumination and for an intensity of 23 per cent. a decrease begins at 12 hours daily illumination.

LUBIMENKO and SZEGLOVA (**12**) found that the weight of the roots increased in proportion to the weight of the whole plant as the length of the daylight periods became progressively longer.

CRIST and STOUT (**3**) grew plants in 6-inch pots at East Lansing, Michigan. They found in the case of lettuce and radish that shortened periods of illumination (6 hours daily) gave a greater ratio of tops to roots, based on dry weight, than either the normal length of day in cloudy weather of winter or one prolonged 6 hours by means of artificial illumination. Moreover, the plants grown under the longest period of illumination had the lowest top-root ratios while the short-day plants had the lowest actual weight of both tops and roots.

Undoubtedly the most significant criterion for judging the efficiency of root development is measurement of the actual absorbing surface. Because of the great difficulties of procedure this has been accomplished only in a few instances (**20, 19**). The method of determining dry weights has a twofold handicap. Where roots are grown in the soil it is practically impossible to free them completely from adhering rock particles without losing some of the roots. But a much more serious objection is encountered in the fact that this method when applied to maturing plants gives little idea of root efficiency. The woody tissues of a single main root that had ceased functioning often far outweighs an extensive network of actively absorbing rootlets. Consequently, it was deemed best in these experiments to use containers sufficiently large to hold a mass of soil in which the roots could develop in a somewhat natural manner. By accurately measuring and comparing root lengths and diameters, and the number, size, and degree of branching, a close approximation to the relative root development of plants grown under different conditions was obtained. To check out variations within the individual, several plants of each species were grown.

Procedure

In these experiments, the following plants were employed: red clover (*Trifolium pratense*), white icicle radish (*Raphanus sativus*), an iris (*Iris germanica*), common sunflower (*Helianthus annuus*), yellow duke dahlia (*Dahlia pinnata*), great ragweed (*Ambrosia trifida*), white Kherson oats (*Avena sativa*), and an early flowering cosmos (*Cosmos bipinnatus*). These were grown in heavy galvanized containers, 30 cm. square and 60 cm. deep, into the top of each of which was inserted a tight wooden frame in such a manner that the soil depth was increased 20 cm. The crevices were luted with plasticine. The containers were filled with a rich loam soil of optimum and uniform water content, which was well screened and exceptionally free from partially decayed roots or other debris. The water-holding capacity of the soil was about 50 per cent. (Hilgard method) and the hygroscopic coefficient 8.2. In filling the containers, the soil was moderately compacted, and the original water content was maintained by adding water from time to time in sufficient amounts to restore the original weight. Two containers were used for each species.

The ragweeds were transplanted from the field in the early seedling stage without injury to the root system. Iris was propagated by rhizomes 1 to 1.5 inches long, carefully selected for uniformity in size, the leafy tops being cut back to within 4 inches of the rhizome. The dahlias were grown from uniformly selected fleshy roots, and all of the other species from seed. After sowing or transplanting, the soil was covered with a fine gravel mulch to retard surface evaporation. The dahlias were planted on May 3, cosmos and clover on May 5, iris on May 8, and the others on May 16. On May 20, one container of each species was placed on an improvised truck so arranged that they could be placed alongside of the other containers from 9:00 A. M. until 4:00 P. M. each day and kept in an adjacent, well ventilated dark room the rest of the time. Thus, one-half of the plants were subjected to a short day of 7 hours' duration, and the rest to the normal 13- to 15-hour day during May and June.

Results

Red clover

The 20 clover seedlings in each container had developed only a single leaf per plant when the difference in length of day was imposed upon them. Within a week the long-day plants had twice the stature of those of the short-day and thereafter differentiation was marked. On June 19, when the containers were opened and the roots excavated, the long-day plants were 28.4 cm. high and in full bloom but the paler colored short-day plants were only 9.8 cm. tall (fig. 1). Leaflets of the short-day plants averaged 1.75 by 2 cm.; those of the long-day 2.5 by 3.5 cm. The larger plants had

FIG. 1. Long-day and short-day plants of red clover 7-weeks old. The long-day plants are in blossom.

25 leaves each, the smaller ones only 12. The result of this difference in photosynthetic surface was clearly shown in the dry weight of tops which was 34.1 and 4.1 grams for the two lots respectively.

Red clover develops a strong taproot from which major laterals arise mostly in the surface 15 cm. of soil. These extend outward more or less horizontally or obliquely and then turn downward and penetrate deeply. At greater depths the primary laterals are smaller and do not spread widely.

The taproots on the short-day plants were only 1.5 mm. thick as compared with 4 mm. for those on the long-day plants. All but one, which barely reached the bottom of the container, ended at 62 cm. or above, while all those of the larger plants extended to and ran along the bottom of the container. The number of major laterals on the proximal 15 cm. of taproot was 3 to 5 per plant, and the total number of laterals was about 40 in both cases. On the short-day plants, however, very few of these extended below the 25 cm. level, a maximum depth of 45 cm. being determined. But those of the other group were as large as the taproots of the smaller plants and most of them extended much deeper, often running along the bottom of the container. The long-day plants alone had root branches of the third order. Below 15 cm. depth, laterals on the short-day taproots were mostly 1 cm. or less in length while both the main roots and primary

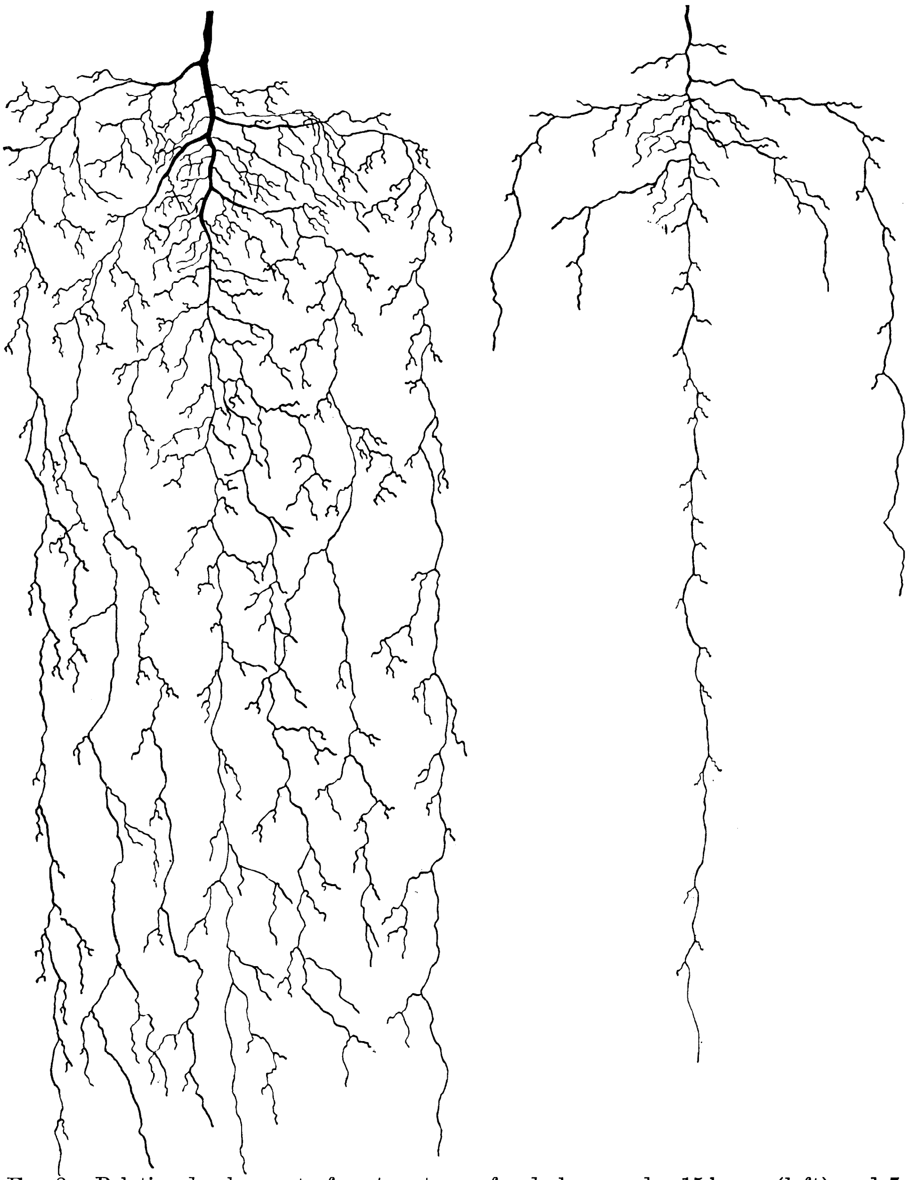

FIG. 2. Relative development of root systems of red clover under 15-hours (left) and 7-hours daily illumination.

branches of the long-day plants had developed many rootlets 5 to 10 cm. long and some reached a length of 36 cm. and extended to the bottom of the container. In fact, the surface 15 cm. of soil of the short-day container was much more poorly ramified with roots than the last 15 cm. of the other container. Thus while the general plan of the root systems was the same in both cases, roots of the short-day plants, where growth of tops had been inhibited, represented a much earlier stage in development than those of the well developed plants in blossom (fig. 2).

Radish

The radishes were in the cotyledon stage when placed under the two conditions. Within a single week the larger leaves and darker green color of the long-day plants were very noticeable and when the roots were examined at the end of a month marked differences were apparent (fig. 3). Although each of the ten plants possessed the same number of leaves, those of the long-day averaged just three times as large (1,365 sq. cm.) as those of the short-day plants.

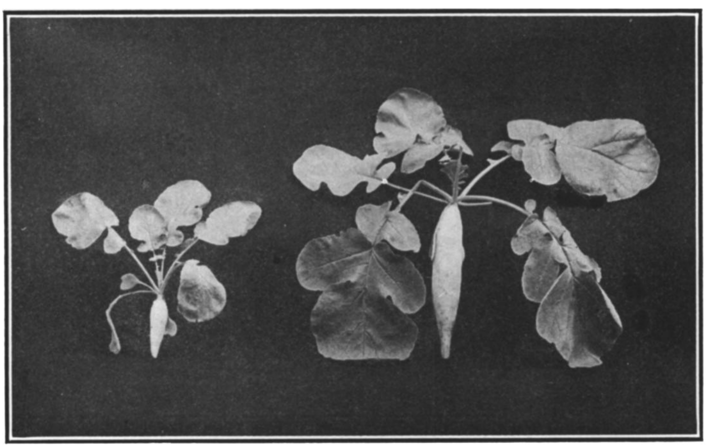

Fig. 3. Average development of tops and fleshy portion of roots of long-day (right) and short-day plants of radish.

The radish is characterized by a rapidly growing and deeply penetrating taproot. Strong, profusely branched laterals arise in the surface 7.5 to 20 cm. of soil and constitute the major portion of the absorbing system, since at greater depths the taproot develops only short laterals.

The taproots of the smaller plants (fig. 3) were 20 to 75 cm. long, those of the larger ones reached greater depths and extended 10 to 15 cm. along the bottom of the container. The thread-like lateral roots and their almost cobwebby network of branches were of nearly equal abundance in both containers in the first 20 cm. of soil. But in the next 25-cm. layer this network of branches continued in the long-day plants while in the others it was absent and there were few branches except very close to the taproot. At 40 cm. depth, branches from the taproots averaged somewhat

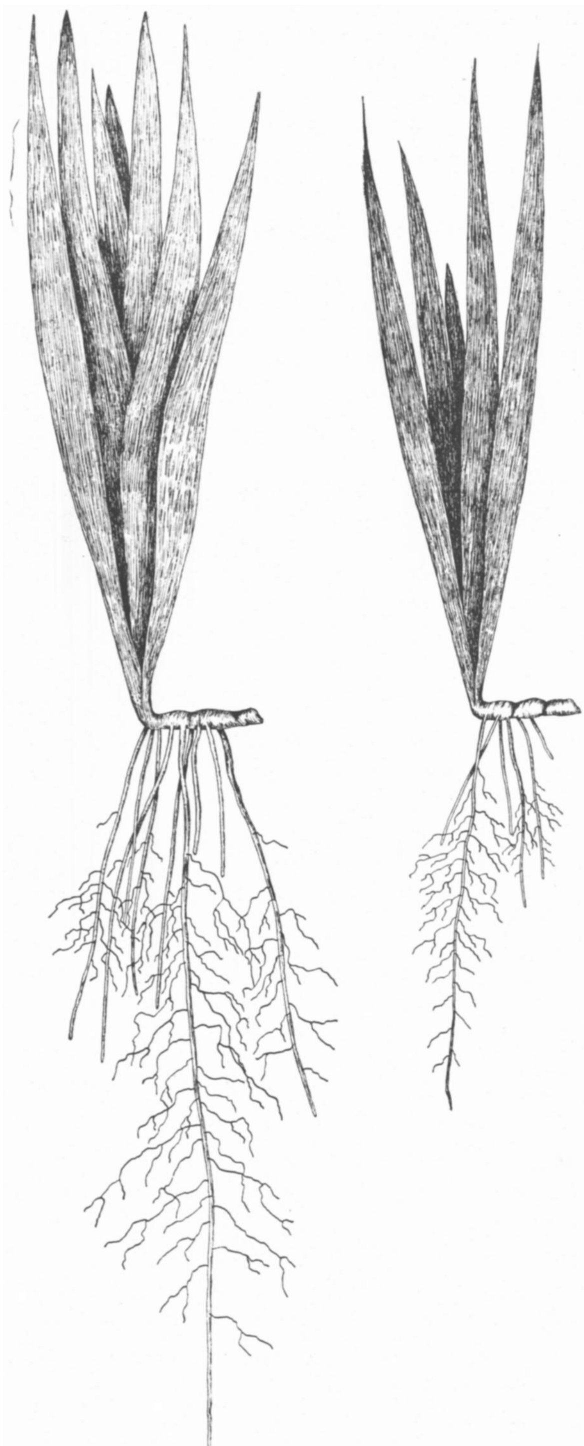

FIG. 4. Relative development of iris under long-day (left) and short-day illumination.

more than twice as long on the larger plants. Even the last 30-cm. layer of soil was penetrated at distant intervals by the vertical ends of these thread-like surface roots.

The fleshy portion of the short-day root system averaged 6 cm. long and 1.7 cm. in diameter; its volume was 58 cc. That of the larger plants was 12 cm. long and 2.7 cm. thick, and the volume 223 cc. Thus the root system of the long-day plants was fully twice as well developed as that of the short-day plants.

Iris

The five rhizomes of iris placed in each of the two containers showed little differentiation of tops until near the time of root excavation on June 19. The average length of leaves of the long-day plants scarcely exceeded that of the short-day but the new leaves were 18 per cent. more abundant. They also averaged about 7 cm. longer and 0.4 cm. wider. The total dry weight of leaves was 2.7 times as great in the long-day plants.

The root system of the iris was very simple. It consisted merely of a few large roots which penetrated rather vertically downward and branched but sparingly. The length and diameter of these roots were carefully measured as they were excavated and counts of the number and measurements of the lengths of the branches were made. On the short-day plants the average number of main roots per rhizome was 6; on the long-day plants 9.2. The former were 1 to 2 mm. in diameter, the latter 1.5 to 3. The average lengths were 13.1 and 22.3 cm. respectively, and the maximum depth of penetration, in the same sequence, 30 and 58 cm. In the short-day container, roots were sparse below 20 cm.; the soil was well filled with roots of the long-day plants to 32 cm. in depth. The younger and shorter roots were unbranched. Primary laterals became more abundant and developed longer branches as the main roots grew longer. Hence, this portion of the absorbing system was much more fully developed in the long-day plants. For example, at 28 cm. depth short-day plants gave off branches only 1 to 4 cm. long, while 12 cm. deeper the larger plants had rootlets 4 to 9 cm. in length which were occasionally rebranched (fig. 4).

Sunflower

Under the long-day illumination the sunflower rapidly developed from the cotyledon stage. The short-day plants were yellowish green and distinctly retarded in their development. They were not attenuated. When the roots were examined on June 17, the long-day plants had a height of 74 cm. and a stem diameter of 15 mm. Each possessed 16 leaves and the average leaf area was 1,924 sq. cm. (fig. 5). The smaller plants were 19 cm. tall and the stems 5 mm. thick. There were only 11 leaves per plant and the average photosynthetic area was only 14 per cent. as great (270 sq. cm.).

The sunflower has a pronounced taproot with numerous strong lateral branches originating almost entirely in the first few inches of soil. The taproots of the short-day plants were 2 mm. in diameter at a depth of 4 cm.; those of the long-day plants were 12 mm. in diameter. The former

FIG. 5. Long-day and short-day plants of dahlia and sunflower about 6 weeks old. The larger plants grew under a long-day illumination. The containers are 80 cm. deep.

tapered to a width of only 1 mm. at 15 cm. depth but extended to the bottom of the container. Those of the long-day plants were 2 mm. thick at the 15 cm. level and 1 mm. in diameter where they grew along the bottom of the container. The largest branches of the short-day plants were 1 mm. or less in diameter and reached a depth of only 28 cm. Those of the long-day plants were 3 mm. thick, they were much more abundant, and some reached the bottom of the container which was covered with a fairly dense network of roots consisting of taproots and the long surface laterals, and the branches of both lots.

The working level of the primary branches (*i.e.* the depth to which most of the roots extended and to which depth maximum absorption occurred) was 15 cm. in the short-day plants, but 45 cm. in the others. The great mass of roots at the working level of the long-day plants, together with their greater diameters and longer and thicker branches, was in marked contrast to that of the short-day plants. The lateral roots originating below 20 cm. depth were 12 cm. or less in length in the smaller plants; on the larger ones, the secondary rootlets on the bottom of the container were of similar length and development. Below the working level, lateral roots were sparse in the short-day container; there was practically none beyond 55 cm. depth. In the long-day container they were more abundant and of larger diameter than were those of the short-day plants between 15 and 55 cm. depth. Even the last 15 cm. of soil contained numerous rootlets.

Thus the root development of the short-day sunflowers corresponded in every way with that of very much younger plants than those of the long-day which had made a normal development.

Dahlia

The dahlias were about 5 inches tall and were developing a second pair of leaves when the one lot was subjected to the short-day. The two plants of each culture developed leaves at about the same rate but by the end of 15 days the long-day plants were twice as tall and the leaves of a darker green color. When taken off on June 17, the average length of stems was 71 and 26 cm. respectively and the diameter of the stems was almost twice as great in the taller plants. The larger plants had begun to branch and now had more and much larger leaves. The average relative leaf areas were 2,310 and 885 sq. cm. respectively (fig. 5).

The root system of the dahlia consisted of a number of main fibrous roots that arose from the base of the tuberous root. Some of these ran outward and upward, branching profusely to near the soil surface; and still others ran vertically downward. In addition, a few fibrous roots arose from the top of the tuberous root.

The number of roots arising from the base of the old, fleshy root was the same in both lots, varying individually from 10 to 39. They were better developed in the long-day plants where the largest roots were twice as thick, and the branches more numerous, larger, and longer. With a single exception, no roots occurred below 60 cm. on the short-day plants and the working level was 23 cm. The long-day plants extended their roots in considerable numbers quite to the bottom and sometimes along the floor of the container. The working level was nearly three times as great as that of the short-day lot and roots were much more abundant even in the deepest soil than below the 23 cm. level of the short-day plants. Moreover, the network of roots that extended above the bases of the tuberous roots was very much more pronounced in the soil of the long-day plants. Here also this network was found to continue to the working level at about 60 cm.

A lot of tuberous roots had developed from the base of the stems above the original propagule together with a few much-branched fibrous roots. The average number (35) was only slightly greater in the long-day plants where the fleshy roots were long and spindling (8.7 x 0.5 cm.) than in those of the short-day which were short and thick (5.4 x 1.6 cm.). The total volume of the latter (68 cc.) was over 2.5 times that of the long-day plants. While nearly all of the thickened but spindling roots ended without branching, the fleshy root continuations of the short, thick ones were branched, the laterals penetrating widely, and often to the working level.

ZIMMERMAN and HITCHCOCK (**21**) have shown that in certain varieties of dahlia, length of day determines the type of root system formed by cuttings. Heavy root storage is correlated with a short day and a fibrous root system with a long one.

RAGWEED

The ragweeds had a second pair of leaves at the beginning of the experiment. Within a week the long-day plants were twice as tall as those of the short-day, and, as in all other cases, the latter lacked the deep, dark-green color of the long-day lot. By June 27 when the experiment was concluded, the four long-day plants had made a vigorous vegetative growth and attained a height of 90 cm. but showed no signs of flowering. Those of the short-day were only 12 cm. tall and small inflorescences were beginning to appear. Average stem diameters were 10.6 and 4.1 mm. The leaves had three times the length and breadth in the larger plants and the dry weight of tops was 7.6 times greater in the long-day plants (fig. 6).

The root systems of the ragweeds showed almost as marked differences as the tops, those of the short-day plants being very poorly developed. The strong taproots of the larger plants were about 13 mm. in diameter; those of the smaller ones did not exceed 3.5 mm. Although the thread-like taproots of the latter extended to the bottom of the container and often ran 5 to 10 cm. along the bottom, they were poorly developed in comparison to the vigorous taproots of the larger plants, which undoubtedly would have extended two or three feet deeper.

Like the sunflower, this species gives rise to strong laterals in the surface 15 cm. of soil. In fact, these are so vigorous that they often equal the taproot in size and degree of branching. On the long-day plants they were frequently 4 mm. in diameter at their origin and many of them extended along the bottom of the container. In fact, they were larger throughout

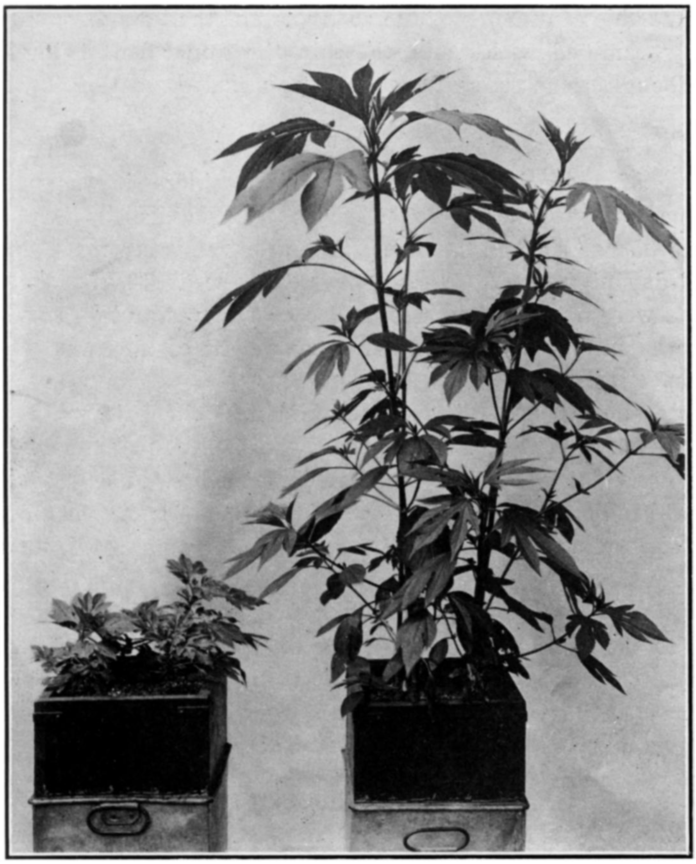

FIG. 6. Development of great ragweed at the end of six weeks. The tall plants have had daily about 15 hours of light.

than the taproots of the short-day plants. Major branches of the short-day plants were only one-fourth as large, being mere threads which did not extend beyond 40 to 60 cm. in depth. Laterals, however, were fairly profuse but mostly short and only occasionally of the third order. Laterals on the major branches of the long-day plants were very much more abundant, several times as long, and often rebranched to the fourth order. Even in the center of the container, the secondary branches were as large as any of the primary branches of the taproots of the short-day plants. Smaller branches from the two lots of taproots varied in about the same proportion as those described.

Only in the surface 15 cm. of soil in the short-day containers were roots fairly numerous; at greater depths they were sparse, consisting of the thread-like taproots and their short, scattered branches. Conversely, almost every cubic centimeter of the entire soil of the long-day container was thoroughly ramified with roots, those in the upper half being especially dense, although great mats of roots also occupied the bottom layers of soil.

Oats

Because of an accident to one of the containers, it was necessary to replant the oats on June 3. After it was well established, the plants were thinned to 35 per container. Final measurements were made on July 19. The short-day plants were 32 cm. tall and in the fifth-leaf stage, the long-day plants were 53 cm. high, each had 6 or 7 leaves and on some the panicles were beginning to appear. The dry weight of tops was 4.4 and 11.4 grams respectively.

Oats develops a fine, fibrous root system. The primary root system consists (usually) of the three seminal roots (*i.e.* the primary root and two almost equally large laterals) and their branches. The secondary root system, which develops later and constitutes the larger part of the root mass, consists of numerous adventitious roots that develop from the lower nodes of the stem.

Among the short-day plants only a few roots of the primary system extended to the bottom of the container but practically all of those of the long-day not only reached this depth but also ran 10 to 15 cm. along the floor of the container. The latter were also much more profusely furnished with longer branches. Roots of the secondary system did not penetrate beyond 13 cm. in the short-day container, but they reached twice this depth on the long-day plants. Moreover, actual count showed that they were about 4 times as numerous and their branches were longer and well clothed with laterals. Thus the roots of the short-day oats corresponded to a much earlier stage of development than that shown by the long-day plants.

Cosmos

One lot of cosmos was placed under short-day illumination upon the appearance of the first leaves. Paler color and retarded growth were clearly evident a week later and by June 27 when the short-day plants were in full bloom, differences in vegetative growth were marked (fig. 7). The seven short-day plants averaged 35 cm. tall, with a stem diameter of only 2.5 mm. The other seven were 50 cm. high and the stems were 6 mm. thick. The dry weight of the stems, in the same sequence, was 1.4 and 10.0 grams, and that of the leaves 0.6 and 9.6 grams.

Cosmos has a taproot which penetrates deeply, and develops numerous strong laterals in the surface soil. The deeper portion of the taproot is well branched but the branches are relatively short.

Fig. 7. Cosmos about 60 days old. Those receiving daily light for only 6 hours are in bloom. Two of the 7 plants from each container were cut and placed in the jars for photographing.

The main roots of the larger plants were 3 mm. in diameter, and except for the limited depth of soil would probably have extended to depths of 1.25 meters or more. The fine taproots of the smaller plants were no larger near their origin, than those of the larger ones at 80 cm. in depth. They were scarcely 75 cm. long. On the short-day plants 10 to 12 laterals barely 1 mm. thick arose in the surface 10 cm. of soil. The longest extended only 24 cm. and most of them were much shorter. Many of the main laterals were unbranched, others had branches a cm. or less in length. The long-day plants had approximately three times as many strong laterals, some originating at 15 cm. depth. These had twice the diameter and three times the number of laterals as those of the short-day. Moreover, the laterals were 1 to 5 cm. long and frequently rebranched. Branches from the taproot were sparse and short below 35 cm. depth on the short-day plants.

But on the larger plants even at 50 cm. depth they were fairly abundant and some were 10 cm. long. The larger taproots branched throughout their length. The short, fine taproots of the smaller plants, the smaller number and limited extent of the branches, and the smaller number of branch orders all indicated an arrested development which corresponded in general with the lesser development of the tops.

Carbohydrate determinations

The preceding data show that in every case the development of the absorbing system was clearly correlated with the transpiring surface. This was true for the long-day plants, *viz.*, clover, iris, and oats, which require long days for successful flowering and fruiting, as well as for cosmos, ragweed, and dahlia which come into blossom normally only when short days occur. The sunflower, which is not materially influenced in time of flowering by the length of day, at least in medium-high latitudes, likewise showed a clear correlation between development of root and shoot.

Where, as in this experiment, all conditions except that of length of day are favorable for growth, it would seem that development of both tops and roots would be directly correlated with the rate of food manufacture. This is clearly indicated by a series of measurements on the rate of carbohydrate manufacture in several of the species.

In these experiments, the photosynthetic activity is based on total carbohydrate content and upon increase in carbohydrate content of leaves after insolation, this being measured as reducing sugars. The photosynthetic activity was determined by the picric acid colorimetric method as modified by Long (**10, 11**).[1]

Photosynthetic determinations were made on the leaves of sunflower, radish, and dahlia on June 13 and 15; of the ragweed on June 13, 15, and 26; and of the red clover on June 26 and 27. All except June 27 were bright sunny days. Samples of the plants growing under long-day exposure were secured at daylight, 9:00 A. M., 4:00 P. M., and sunset. Those from plants under the short-day were taken at 9:00 A. M. and 4:00 P. M. In all instances, care was taken to secure samples from fully grown leaves of approximately the same age, that were shaded as little as possible.

Table I gives the actual amount of sugar per square centimeter in each sample, the relative amounts in the long- and short-day plants at 4:00 P. M., the increase in sugar content during the entire period of illumination, and the actual and relative increases between 9:00 A. M. and 4:00 P. M. for both sets of plants.

[1] These data are from unpublished work by Miss Theodora Klose, to whom a detailed outline of the method was furnished by Doctor Long.

TABLE I

PHOTOSYNTHETIC ACTIVITY OF LONG- AND SHORT-DAY PLANTS

			Sunflower				Radish				Clover			
			June 13		June 15		June 13		June 15		June 26		June 27	
			Actual	Relative	Actual	Relative	Actual	Relative	Actual	Relative	Actual	Relative	Actual	Relative
			mg.	*per cent.*	*mg.*	*per cent.*	*mg.*	*per cent.*	*mg.*	*per cent.*	*mg.*	*per cent.*	*mg.*	*per cent.*
Sugar per sq. cm.	Long day	Daylight	0.704		0.640		0.704		0.640		0.768		0.640	
		9 A. M.	0.832		0.640		0.704		0.640		0.768		0.768	
		4 P. M.	1.152	100	1.088	100	0.896	100	1.024	100	2.368	100	1.408	100
		Sunset	0.896		0.960		0.896		0.960		1.024		1.024	
	Short day	9 A. M.	0.640		0.640		0.704		0.640		0.384		0.423	
		4 P. M.	0.768	67	0.896	82	0.768	86	0.960	94	0.872	37	0.646	46
Increase per sq. cm.	During entire day	Long day	0.448		0.448		0.192		0.384		1.600		0.768	
		Short day	0.128		0.256		0.064		0.320		0.488		0.223	
	Between 9 A. M.–4 P. M.	Long day	0.320	100	0.448	100	0.192	100	0.384	100	1.600	100	0.640	100
		Short day	0.128	40	0.256	57	0.064	33	0.320	83	0.488	31	0.223	35

TABLE I.—(*Concluded*)

			Ragweed						Dahlia			
			June 13		June 15		June 26		June 13		June 15	
			Actual	Relative	Actual	Relative	Actual	Relative	Actual	Relative	Actual	Relative
			mg.	*per cent.*	*mg.*	*per cent.*	*mg.*	*per cent.*	*mg.*	*per cent.*	*mg.*	*per cent.*
Sugar per sq. cm.	Long day	Daylight	0.768		0.640		0.512		1.024		0.768	
		9 A. M.	0.640		0.640		0.704		0.896		0.768	
		4 P. M.	1.024	100	1.088	100	0.992	100	1.152	100	1.280	100
		Sunset	1.088		1.024		0.896		1.024		1.280	
	Short day	9 A. M.	0.704		0.640		0.576		0.768		0.640	
		4 P. M.	1.152	113	1.152	106	0.896	90	1.024	89	1.152	90
Increase per sq. cm.	During entire day	Long day	0.448		0.448		0.480		0.256		0.512	
		Short day	0.448		0.512		0.320		0.256		0.512	
	Between 9 A. M.–4 P. M.	Long day	0.384	100	0.448	100	0.288	100	0.256	100	0.512	100
		Short day	0.448	117	0.512	114	0.320	111	0.256	100	0.512	100

An examination of the table shows that on both June 13 and 15 the daily rate of increase in sugar in the sunflower was considerably higher in the long-day plants, and also that greater amounts of sugar per unit area occurred in the plants having the longer illumination.

Photosynthetic tests of the radish show, as in the sunflower, a much higher rate of daily increase in sugar content and also larger amounts of sugar per sq. cm. The differences are somewhat less on June 15, probably owing to differences in the place of selecting samples or in environment, but the decrease is consistent in the two species.

The red clover gave not only the greatest increase in photosynthate of any of the plants tested but also the greatest differences between the long- and short-day plants. Table I shows a much higher rate of increase in sugar content between 9:00 A. M. and 4:00 P. M., as well as during the entire period of illumination of the two lots of plants. The smaller amounts of photosynthate on June 27 are due to the fact that this was a cloudy day.

In contrast to the behavior of the three preceding species, ragweed and dahlia under long daily illumination gave no higher rates and, in fact, often lower ones, than those under 7-hour daily periods of light. The photosynthetic tests on the ragweed on June 13 showed a slightly higher rate of increase in the short-day plants between 9:00 A. M. and 4:00 P. M. The total daily increase during the entire period of illumination is, however, the same. The actual amounts of sugar at 4:00 P. M. are greater in the short-day plants than in those of the long-day. The tests on June 15 are essentially the same except that the total daily increase is greater in the short-day plants instead of being equal in the two sets as on June 13. On June 26 the rate of increase between 9:00 A. M. and 4:00 P. M. still remained higher in the short-day than in the long-day plants; contrary to the previous results, however, the total increase during the entire period of illumination of the long-day plants was greater than the increase during the 7-hour period of illumination of the short-day plants. The actual amount of sugar at 4:00 P. M., moreover, was greater in the former. The short-day plants were beginning to flower which, no doubt, resulted in rapid use of the photosynthate and perhaps accounts for the lower actual amount of sugar in these plants at this time. The rate of increase remained higher throughout in the short-day plants.

As regards the dahlia, table I shows a slightly higher amount of sugar at 4:00 P. M. in the leaves of the long-day plants than in those of the short-day. The rate of increase, however, between 9:00 A. M. and 4:00 P. M. is the same in the two sets of plants. The increase during the 7-hour period of light of the short-day is equal to the increase of the long-day plants during their entire period of illumination.

In interpreting these results it must be kept in mind that the rate of increase in these tests represents the balance between the process of photosynthesis on the one hand and those of respiration, translocation, and growth on the other. Hence, the higher rate obtained under certain conditions is not necessarily due to a higher rate of manufacture of materials under these conditions but may result in part from a slower rate of respiration, or removal, or growth.

GARNER and ALLARD have found that there are different optimal light periods for maximum vegetative growth, for sexual reproduction, and for tuberization, each of which varies with the species. The photosynthetic data given above seem to indicate that those plants, such as the radish and clover, whose optimal light period for reproduction lies above 12 hours (long-day plants) are more active photosynthetically or less active in removing or using the product under long-day illumination than under a 7-hour daily light exposure.

The growth data show that there was a rapidly increasing leaf area for photosynthesis and increased water loss in the clover, radish, and sunflower under long-day illumination. Notwithstanding the rapidity of growth and accompanying high rate of respiration for the necessary release of energy, the leaves of these plants showed the highest rate of increase in carbohydrates under equal periods of illumination. In addition, the extra hours of illumination resulted in an additional amount of food for increased growth. The demands for an ever increasing supply of water to replace that lost by transpiration, together with abundant materials for growth, resulted in every case in a root system the extent of which correlated well with the development of the tops. Under the short-day illumination less food was manufactured, growth of tops was retarded, and the root system was correspondingly abbreviated.

It seems that the dahlia and ragweed when grown under a long daily period of illumination, use the entire product of photosynthesis in promoting vegetative growth, the balance between the transpiring and absorbing system being well maintained. Under short-day illumination the dahlia accumulates a much greater relative amount of material in its fleshy roots. As pointed out by GARNER and ALLARD (**4**), this accumulation obviously indicates an excess of carbohydrates over current consumption. This surplus of carbohydrates is not due to increased photosynthetic activity but rather to the inability of the plant to utilize the carbohydrate, whether it be present in relatively large or small quantity. Since this portion of the food is not utilized by the growing plant, the result is a decreased extent of both root system and above-ground parts. The case of the ragweed is not quite so clear. It is a well established physiological fact, however, that respiration is high during the period of anthesis and much of the photosynthate furnished by the meager leaf area was undoubtedly used in supplying energy for this process. This interpretation is in agreement with that of GARNER and ALLARD (**4**) who conclude "that the duration of the daily illumination period not only influences the quantity of photosynthetic material formed but also may determine the use which the plant can make of this material."

NIGHTINGALE (**15**a) has shown that radish, salvia, buckwheat, and soy beans were limited in the synthesis of nitrates to other forms of nitrogen by a 7-hour day. Associated with relatively little assimilation of nitrates was an accumulation of carbohydrates within these plants when they were subjected to short-day illumination. Carbohydrates accumulated in the short-day plants, presumably because there was relatively little utilization of them in the synthesis of nitrates to other forms of nitrogen.

Summary

The relative development of roots and tops of eight species of plants grown under 7-hour and 15-hour daily illumination respectively, was determined. The plants were grown for about 7 weeks in soil in containers 30 x 30 x 80 cm. in size, which permitted of rather normal root development.

Red clover, radish, iris, and oats, all long-day plants as regards flowering, developed large tops and proportionately extensive root systems when subjected to the 15-hour day. Under short-day illumination the growth of both tops and roots was greatly retarded and approximately to the same degree. Their development was similar to that of the long-day plants when the latter were only 3.5 weeks old.

Sunflower, whose time of flowering is less modified by the length of day, developed in a manner similar to the preceding species.

Dahlia, the great ragweed, and cosmos are short-day plants. They attained their greatest size and greatest root development under the 15-hour day. Under short-day illumination the dwarfed tops were furnished with a correspondingly meager absorbing system, although more food was accumulated in the short-day dahlia. Thus in all cases development of the root systems was in direct correlation with the development of tops.

The effect of length of daily illumination upon photosynthetic activity showed that red clover, radish, and sunflower are either more active in photosynthesis or less active in removing or using the product under long-day illumination than they are under a 7-hour day. Great ragweed and dahlia were found to be more or less equally active photosynthetically under the two light periods, or less active in removal or use of the products under short-day illumination.

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