THE DEVELOPMENT OF BEAN SEEDS (PHASEOLUS VULGARIS L.)[1,2]

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Though the cell has been accepted as a biological unit since the time of Schleiden and Schwann, it has been ignored as the physiological unit. Numerous studies have been made on the physiology of fruits and seeds (6, 10, 19) and the embryology of many species has been described (15, 16), yet only a few attempts have been made to examine the biochemical changes on a *per cell basis*. It is unfortunate that so few cellular studies have been made, since they might indicate cell similarities that are not apparent at the organ level. The physiological investigations on the growth of plant cells that came to the author's attention include cowpea roots (22), corn roots (8, 11), onion roots (31), pea roots (2, 4), and apple fruit pulp (1, 20, 23); these papers are considered in the discussion of the results.

The aim of this investigation was to describe the development of bean seeds in cellular terms and to compare the per cell values obtained with those of other plant cells. To this end, the fresh weight, dry weight, nitrogen (N) content, phosphorus (P) content, and the rate of oxygen uptake were measured and cell counts were made on maturing bean seeds.

MATERIAL AND METHODS

Black Valentine bush beans (*Phaseolus vulgaris* L.) were planted 4 inches apart in rows 18 inches apart in greenhouse beds containing 0.5 foot of soil. Plantings were made at 2-week intervals so that a complete range of seeds could be collected in each harvest. The plants were watered daily and no artificial illumination was used. At the start of flowering, some 40 days after planting the seeds, the newly open flowers were individually labeled daily. Approximately a week later, the number of marked flowers, which were now small pods, was reduced to one per plant. Pods from different plantings, 11 or more days past the open flower stage, were collected every day or two. If the seeds in a pod were uniform, that is the fresh weight of the lightest bean was at least 2/3 that of the heaviest, one or two of the seeds in the pod were selected at random for further study.

Whenever the material sufficed, N, P, and respiratory measurements were made on the same single bean seed sample. As cell counts involved the destruction of the seeds, only fresh weight and respiratory measurements could be made on beans used for this purpose. Cell counts were made on the cotyledons alone. The reason for this was that, on the one hand, it would have been difficult to perform several chemical analyses on the youngest pairs of cotyledons encountered due to their small size; nor would it have been possible to obtain valid rates of oxygen uptake due to wounding in excision. On the other hand, the author was unable to properly macerate entire seeds for cell counts. The experimental design permitted one to obtain measurements on individual seeds rather than only average values.

Fresh weights were taken on the selected seeds within an hour after the pods were picked, immediately after opening the pods. Samples weighing less than 25 mg were measured on a Roller-Smith torsion balance to 0.01 mg; samples weighing more than 25 mg were measured on a similar balance accurate to 0.2 mg.

Respiratory measurements were made in a Warburg manometer at 25° C. After preliminary experiments, with intact bean seeds ranging in fresh weight from 20 to 600 mg, had indicated a respiratory quotient of unity by both the direct and the indirect method, all subsequent measurements were made on oxygen uptake alone in a CO_2-free atmosphere. In addition to the alkali, no further fluid was put into the vessels. All calculations were made including the water content of the seeds in the volume of the vessel occupied by liquid, and ignoring the volume occupied by the dry constituents. The error in measuring the oxygen uptake of a seed for an hour or longer was less than 5 %.

Dry weights were taken after the respiratory measurements, on seeds that were not macerated. The beans were dried for 24 hrs at 65 to 70° C, and weighed on torsion balances. Later the seeds were crushed in a device consisting of a block of brass with a 10-mm diameter, flat-bottomed hole into which fitted a short rod. After crushing, each seed was individually ground to a fine powder with a mortar and pestle for analysis.

Nitrogen was determined essentially after the method of Thompson and Morrison (30). To convert all reduced nitrogen to ammonium ion it was important to continue digestion with H_2SO_4 and H_2O_2 for 0.5 hr beyond clearing. The samples were neutralized using bromthymol blue as an internal indicator (one drop of 0.04 % weight/volume per tube); the yellow to blue change was used. This procedure is more convenient than the use of litmus paper as an outside indicator which Thompson and Morrison (30) advise, and no appreciable error is introduced. The error of this method is approximately 5 %.

Phosphorus was determined by the method of King (14). Digestion with perchloric acid and H_2O_2

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was continued 10 min past clearing as shorter periods did not liberate maximal amounts of phosphate. (It is of interest to note that as the seeds matured, the percentage of phosphorus not released by digesting merely to clearing increased from about 10 to 40.) The error of this method is less than 5 %.

Cell counts were made using a modification of the method of Brown and Rickless (3). The seed coat and epicotyl were removed from a bean seed to be macerated and the cotyledons were infiltrated by means of a water pump with an 0.8 *N* HNO_3 solution containing 7.5 % weight/volume chromic acid; to avoid foaming a drop of caprylic alcohol was added before infiltration. The cotyledons remained in this solution from 12 to 48 hrs depending on the fresh weight of the seeds; for example, cotyledons from seeds weighing 25 mg were treated for 12 hrs, 100 mg for 30 hrs, and 200 mg or heavier for 48 hrs. Cotyledons from seeds weighing over 400 mg were very difficult to macerate and required repeated and prolonged infiltration. Afterwards, the macerated cotyledons were shaken violently in a stoppered tube for 2 min to separate the cells; the excess acid was neutralized with sodium bisulfite; a drop of 1 % fast green added to stain the cells; and water added to make a volume suitable for counting with a hemocytometer, that is about 300 to 200 cells in a volume of 1.6 mm^3. Four separate samples were counted from each pair of cotyledons; the lowest count was usually at least 2/3 as great as the highest. The results reported are based on the average of each set of four counts.

Results and Discussion

The data obtained were very variable. This heterogeneity is largely a consequence of a lack of a physiological age index; such indexes have been reported for vegetative Xanthium plants (9) and lily flower buds (7) but not for bean seeds. During the first 10 days past flowering, while the pods were elongating, the weight of the individual seeds could be estimated from the length of the pods. Later the respiratory activity and the percentage of water in the seeds were correlated. But for neither period was a strict relationship found, and all attempts to find even a crude age index for the entire period studied failed. Therefore the data have been presented directly against time.

The data on the dry weight, nitrogen content, phosphorus content, fresh weight, and the rate of oxygen uptake of individual seeds at different stages of development were obtained in the Spring of 1954 and are presented in figures 1 to 5. The points in these and other graphs present mean values; the vertical lines their 95 % confidence intervals, calculated using Student's *t* test (32). By a numerical procedure (18), the smooth trend lines were obtained. It must be remembered that the smoothed curves were derived from single measurements on many individual seeds. Such data can yield distribution curves at different stages, but do not suffice for growth curves. Quick changes that may occur in the growth process of an individual will appear to be gradual when based on smooth averages (26). As great variability was found at all stages of seed development, no great weight should be attached to the exact numerical values obtained. Remembering the limitations of the data, one can nevertheless obtain some insight into the processes occurring during bean seed development.

During the first 3 weeks past flowering, the dry weight (fig 1), N (fig 2), and P (fig 3) per seed increased slowly. At the end of this period their respective values were only about 1/6 of those finally reached. In the following 2 weeks they increased greatly. Twenty-four days after flowering, they achieved their maximum rates: 22 mg dry wt/day, 0.75 mg N/day, and 0.08 mg P/day. Older seeds continued to grow at a steadily decreasing rate; till at maturity, approximately 6 weeks after flowering, they measured 353 mg dry weight, 12.5 mg N, and 1.4 mg P. While the dry weight, N, and P of the developing seeds increased together, the percentage composition did change (table I). Twelve days after flowering, the seeds contained 6.5 % N and 1.1 % P on a dry weight basis; 20 days later, the figures had fallen to half these values. The fresh weight per seed (fig 4) paralleled the other growth parameters initially; 24 days after flowering it also reached its maximum rate of increase, 65 mg/day. While the rate then declined rapidly, the fresh weight continued to gain till 36 days after flowering a maximum of 714 mg was reached. In older seeds the fresh weight itself decreased as the seeds dried. As the beans matured, the ratio of dry wt/fresh wt per bean increased—at first steadily, but with greater maturity of the seeds more rapidly. The data indicated that growth of the seeds ceased concomitantly with their loss in fresh weight (fig 7).

Table I

Composition of Maturing Bean Seeds

Days after flowering	Percentages		
	N/dry wt	P/dry wt	Dry wt/fresh wt
12	6.5	1.1	15
22	4.5	0.7	24
32	3.5	0.4	40
42	3.5	0.4	59

The rate of oxygen uptake per seed (fig 5) was correlated with the rate of dry weight, N, and P increase, but not with their absolute values. Two weeks after flowering the rate of oxygen uptake was only 30 mm^3/hr, a week later it was 170 mm^3/hr, and 26 days after flowering a maximum of 235 mm^3/hr was reached. Seeds older than 26 days past flowering respired progressively less, till in the mature seeds no oxygen uptake could be found. Such low respiratory rates as have been reported in the literature for mature seeds, 0.37 to 0.007 mm^3 O_2 hr^{-1} gm dry wt^{-1}

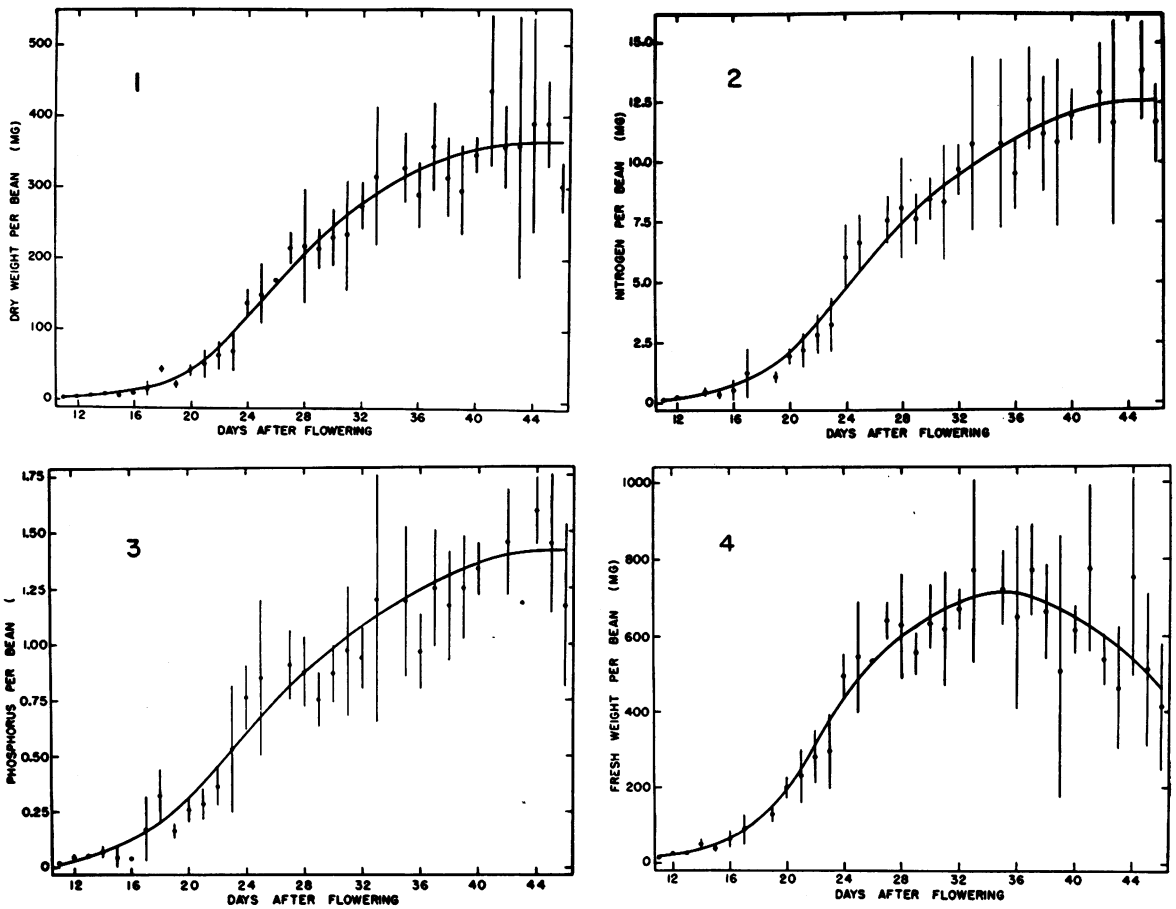

FIG. 1. Time course of the dry wt per bean seed. Curve based on 272 seeds.
FIG. 2. Time course of the nitrogen content per bean seed. Curve based on 238 seeds.
FIG. 3. Time course of the phosphorus content per bean seed. Curve based on 225 seeds.
FIG. 4. Time course of the fresh wt per bean seed. Curve based on 275 seeds.

(17), would not have been detected in the present study.

A plot of the oxygen uptake per mg dry weight against the percentage of dry matter in the seeds (fig 6) presents a curve similar to those reported by previous workers (24, 25). The highest respiratory rates were found for the youngest material studied; increasingly lower rates were found for older seeds; there were no indications of a climacteric rise. The form of this curve resembles those for the relative rates of increase, $dX/(X \cdot dT)$, in terms of dry weight, N, and P.

The cell count data, obtained in the Fall of 1953 and the Spring of 1954, are presented in figure 8. Though the seeds matured at different rates in the two periods, the counts from both groups were comparable when the fresh weights of the seeds were used for an age axis. On this account and in order to include data from seeds of unknown age, the trend curve in figure 8 was derived by smoothing the mean number of cotyledon cells of seeds having smiliar fresh weights; a secondary axis indicates the approximate age. The number of cotyledon cells per seed increased rapidly from 360,000 twelve days after flowering to 2,400,000 twenty days after flowering. Few cell divisions occurred in cotyledons older than three weeks after flowering; at this time the dry weight of the bean seeds was less than 1/6 of that finally reached. In apples (1, 20), cucurbits (27, 28), and tomatoes (12) cell division also ceases long before the growth of the fruit stops.

Though in the current study an increase in the cotyledon cells per seed from 360,000 to 2,600,000 was observed, this represents less than 3 cell generations (fig 9). In peas (5) fertilization occurs 12 to 24 hrs after the flower opens and in Lima beans (29) a day or two before the flower opens. If one assumes that the bean ovule is fertilized on the day that the flower opens and that all embryo cells divide at an equal rate, then it follows that since 18.5 cell generations have occurred by the 12th day after flowering, the average rate of cell division was a mitotic cycle every 15.5 hrs. Such a value is similar to those reported for pea root cells (2) and corn root cells (8), namely 15

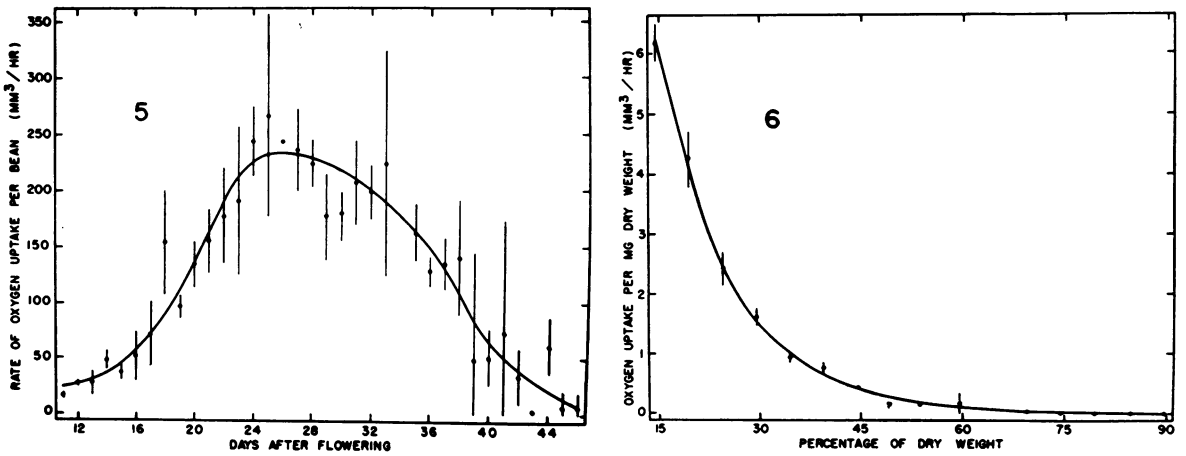

FIG. 5. Time course of the rate of oxygen uptake per bean seed. Curve based on 274 seeds.

FIG. 6. Relation between the rate of oxygen uptake per mg dry wt and the percentage of dry wt per seed. Curve based on 264 seeds.

and 14 hrs. (The latter value was obtained as the average for the distal 2 mm of the corn root; 16,000 cells are produced per hour by 223,000 cells.)

The percentage of a seed's dry weight due to its cotyledons is shown in figure 10. At nearly all stages of seed development the embryo consisted almost entirely of cotyledons; the epicotyl was never more than 2 % of the embryo's dry weight. The cotyledons grew much faster than the seed coats. In the smallest seeds studied, having a dry weight slightly over 2 mg, the seed coats accounted for 95 % of the dry weight of the entire seeds; but in mature seeds the seed coats accounted for only 10 %. The relation of the dry weight of the cotyledons to that of the seed coat can be expressed by the allometric formula (13): $y = bx^k$, where y is the dry weight of the seed coat and x, the dry weight of the two cotyledons of a seed; inspection of the appropriate plot indicated b to have a value of 0.55 and k, of 0.38. Despite the criticisms that can be made of such a formula (21), it nevertheless expresses the data concisely.

An approximation of the dry weight, N content, P content, fresh weight, and rate of oxygen uptake of the average cotyledon cell was made from the following information: (a) the values for the average bean seed at various stages of development, (b) the proportion of a seed's dry weight due to the cotyledons, and (c) the number of cotyledon cells at a given stage of seed development. An assumption made was that the seeds were uniform; i.e., on a dry weight basis the contents and the respiratory rates of the seed coat and embryo of a given bean were the same. This assumption is crucial for the youngest seeds studied since these consist predominantly of seed coat. As the epicotyl never represented more than 2 % of a seed's dry weight, its chemical composition and rate of oxygen uptake probably did not greatly influence the per seed values. It appears likely that in an immature seed, the composition and respiratory activity of the cotyledons and the seed coat do not differ much since both are composed of embryonic cells. In increasingly mature seeds, differences may well exist and increase: but as the seeds mature, the seed coats, constituting a decreasing fraction of the beans (fig 10), influence the per bean seed values less and less. Conversely, the cotyledons represent an increasing fraction of the seeds as these mature, and the composition and the respiratory activity

TABLE II

RANGE OF VALUES FOR THE AVERAGE CELL DURING DEVELOPMENT. THE SMALLER OF A PAIR OF FIGURES REFERS TO AN EMBRYONIC CELL; THE LARGER, TO A MORE MATURE ONE

CELL ORIGIN	DRY WT	FRESH WT	N	P	O_2/HR
	10^{-6} mg	10^{-6} mg	10^{-6} mg	10^{-6} mg	10^{-6} mm³
Bean seed	2–123	11–250	0.08–4.4	0.01–0.50	12–78
Apple fruit (1, 20, 23)	5–1300	30–6000	0.2 –3.6	.....	7–90
Cowpea root (22)	0.7–5	3–90	0.05–0.30	0.01–0.04	.....
Corn root (8, 11)	1–8	8–125	0.15–0.36	.....	9–48
Pea root (4)	0.5–7	10–170	0.02–0.34 *	.....	10–60
Onion root (31)	.....	.....	0.05–0.30 **	.....	6–50

* Protein nitrogen.

** Values recalculated from figure 5 in Wanner's paper (31).

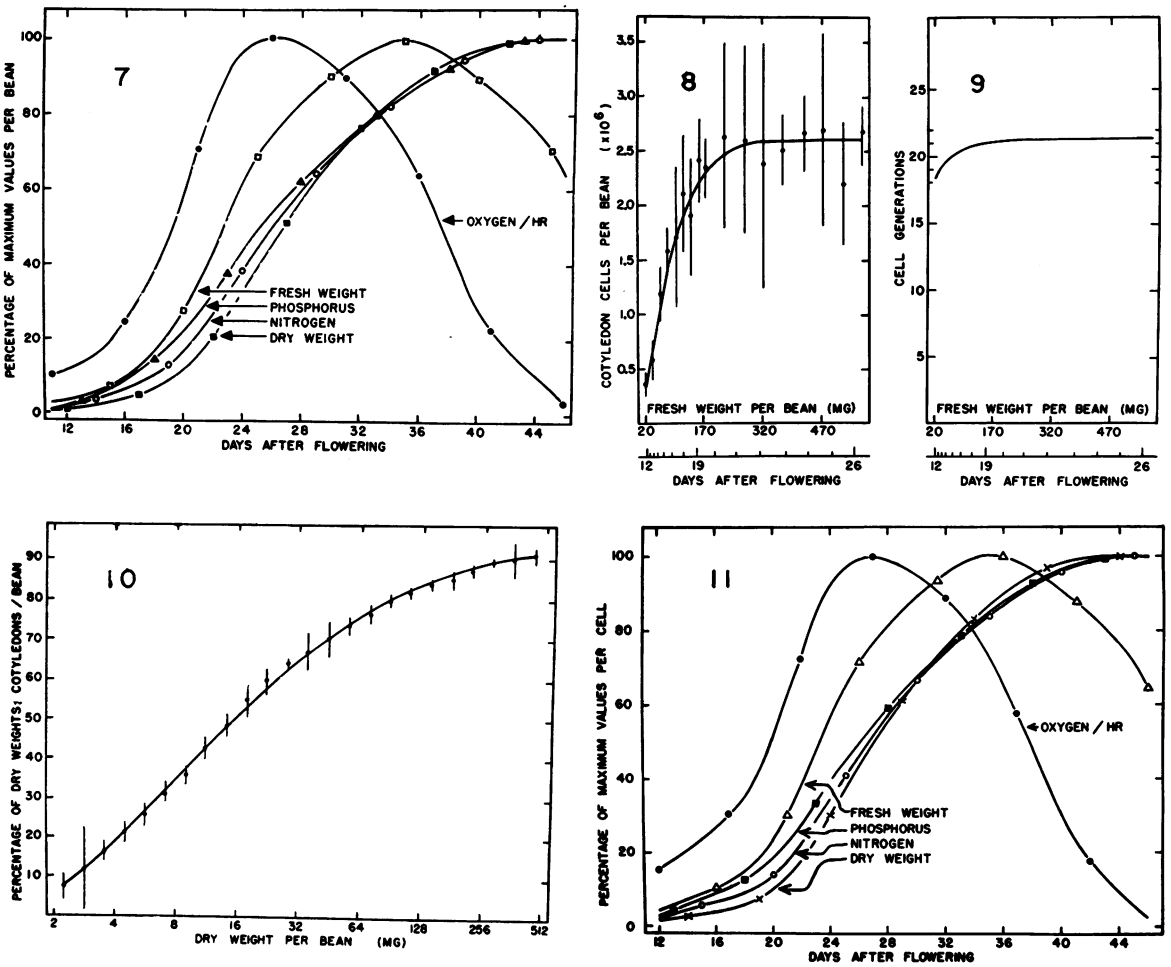

FIG. 7. Time course of the dry wt, fresh wt, N, P, and rate of oxygen uptake per bean seed. Maximum values, set at 100: dry wt 353 mg, fresh wt 714 mg, N 12.5 mg, P 1.4 mg, oxygen uptake 235 mm^3/hr.

FIG. 8. Relation between the fresh wt and the number of cotyledon cells per bean seed. Curve based on 97 seeds. Secondary age axis is approximate.

FIG. 9. Relation between the fresh wt per bean seed and the number of cell generations that have occurred since fertilization. Secondary age axis is approximate.

FIG. 10. Relation between the dry wt per bean seed and the ratio of the dry wt of the cotyledons to that of the entire seed. Curve based on 353 seeds.

FIG. 11. Time course of the dry wt, fresh wt, N, P, and rate of oxygen uptake of the average cotyledon cell. Maximum values, set at 100: dry wt 123×10^{-6} mg, fresh wt 240×10^{-6} mg, N 4.4×10^{-6} mg, P 0.5×10^{-6} mg, oxygen uptake 78×10^{-6} mm^3/hr.

of the cotyledons increasingly determine the per seed values. Therefore the assumption that the contents and respiratory activity of the seed coat and the cotyledons in a given bean were the same became increasingly unnecessary as the seeds matured.

It must be stressed that the average cotyledon cell is merely a concept: the size of the cotyledon cells in a given bean seed varied greatly, especially in the more mature stages. Thus the values obtained are at best approximations.

The shapes of the growth curves for the average cotyledon cell (fig 11) are much like those for the average seed (fig 7). The dry weight, N content, P content, and fresh weight increased gradually during the first 3 weeks after flowering. Twelve days after flowering the average cell measured 1.8×10^{-6} mg dry weight, 0.08×10^{-6} mg N, 0.013×10^{-6} mg P, and 11×10^{-6} mg fresh wt. After cell division had ceased in the cotyledons about 3 weeks after flowering, the cells grew rapidly, achieving their maximal growth rates 24 days after flowering. The rates then decreased. About 36 days after flowering the cell fresh weight started to decline, and only small dry weight, N, and P gains were made later. At maturity the

average cotyledon cell had a dry weight of 123×10^{-6} mg, and contained 4.4×10^{-6} mg N and 0.5×10^{-6} mg P.

Respiration on a per cell basis increased approximately as the rate of growth increased. Twelve days after flowering the rate of oxygen uptake of the average cotyledon cell was 12×10^{-6} mm^3/hr; 8 days later it was 40×10^{-6} mm^3/hr; and 26 days after flowering a maximum rate of 78×10^{-6} mm^3/hr was reached. On a dry weight basis (fig 6), though not on a per cell basis (fig 11), young dividing cells were found to have a more rapid oxygen uptake than more mature, rapidly enlarging cells. This correlates with the fact that even though the greatest growth was made after cell division had ceased, the relative growth rate, $dX/(X \cdot dT)$, was greatest for the youngest material studied and decreased with advancing age.

A comparison of the per cell values of bean seeds with those of apple fruits, cowpea roots, pea roots, corn roots, and onion roots (table 2) shows that meristematic cells of various origins are much more alike than more mature cells. While an average apple cell weighs 200 times as much as a mature root cell and 10 times as much as a mature bean cotyledon cell, at the youngest stages studied less than a factor of 10 separates their dry weights. A parallel situation exists in terms of nitrogen. By contrast, the rates of oxygen uptake of growing plant cells were all similar. (It should be noted that a root cell passes from the meristematic state to maturity within a day; a bean cotyledon cell requires more than a month; and an apple fruit cell, several months. The growth rates of root cells, both relative and absolute, were much greater than those of the apple and bean, even though the latter acquired the greater final size. Sinnott, studying the growth of cucurbit fruits, concluded that final size is not so much related to the rate of growth as it is to the duration of growth (27, 28).)

Despite their differences, cells of various origins have their similarities: the maximum rate of cell division and the rate of oxygen uptake per cell are comparable. It remains for further studies to determine whether or not this generality holds for other growing plant cells.

Summary

The development of bean seeds has been described on a cellular and organ basis in terms of dry weight, nitrogen content, phosphorus content, fresh weight, and rate of oxygen uptake. A comparison of the per cell values of various plants indicates that while the cells differ in size and content, their rates of oxygen uptake are comparable.

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INFLUENCE OF NIGHT TEMPERATURE AND NITROGEN NUTRITION ON THE GROWTH, SUCROSE ACCUMULATION AND LEAF MINERALS OF SUGAR BEET PLANTS[1]

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The storage roots of sugar beet plants grown in controlled climate facilities have been found to be lower in sucrose content than those normally grown under field conditions (10). When sugar beet plants were grown at 23° C under fluorescent light with an intensity of 840 fc and photoperiods of 8 hours, the storage roots contained only 3.3 % sucrose and weighed less than one-twentieth of those grown in sunlight for the same time period and air temperature. By increasing the day length in sunlight from 8 hours to a normal day of 12 to 14 hours the sucrose content of beet roots increased from 8.2 % to an average value of 9.3 %. The storage roots of the plants in the longer days doubled in size while the tops increased in size slightly. For plants in 8 hours of sunlight, decreasing night temperature from 30 to 2° C increased the sucrose content of the beet roots from 7.2 to 11.9 %, while decreasing day temperatures from 26 to 23° C increased the sucrose concentration only slightly (10). This overall failure of beet roots to accumulate sucrose at the expense of top and storage root growth is not a matter of age, since plants kept continuously in a greenhouse for natural day lengths with days at 23° C and nights at 17° C and with ample supplies of water and nutrients reached a maximum sucrose concentration of only 8.0 to 9.3 % early in the growth cycle of the plant (11). Thereafter the sucrose concentrations remained within this range until fall and winter when the values decreased to 3.9 %. The low sucrose values in winter were attributable to the short days and low light intensities which prevail during this season (11).

Whereas changes in climatic factors and in age of the beet plant have failed to produce beets above 12 % in sucrose, deficiencies in nitrogen have increased the sucrose concentrations of beets to values as high as 14 to 16 % (6). These increases, while spectacular, are still below the 16 to 20 % frequently observed in commercial fields. As a means of getting beets as high as those found in the field, a logical step to take experimentally is to study the combined effects of night temperature and nitrogen deficiency on the sucrose concentration and the quantity of sucrose stored within the root. These effects, including those upon growth and the leaf mineral content of the plant, are reported in the present paper.

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PROCEDURE

Beta vulgaris seed of the variety GW 304, treated with the fungicide Phygon XL at the rate of 1 %, was planted in vermiculite no. 2 grade on February 21, 1952, at a depth of 1.9 cm, in pots 25 cm in diameter and 30 cm deep. Each pot was provided with 4 holes at the bottom, which permitted the drainage of modified Hoagland's solution (3) added in excess daily. The seedlings from the seed balls, planted 10 to a pot, emerged on February 26, 1952. These were thinned at the 2-leaf stage to one plant per seed ball on March 12. On March 21, at the 5-leaf stage the plants were thinned to 4 plants per pot and finally, on March 28 at the 7- to 8-leaf stage, to 2 plants per pot. During this time and until August 12, 1952, the pots, 4 to a truck (51 cm × 51 cm), were kept for natural day lengths in a greenhouse maintained at 23° C from 8 A.M. to 4 P.M. and at 17° C from 4 P.M. to 8 A.M. Each week the trucks were rerandomized in order to reduce to a minimum the positional variability of the plants. Also, at weekly