oxidase of corn embryos were measured during the early stages of germination. These metabolic indices at the 18-hour stage were compared with the germination percentage, tetrazolium test, vigor rating, and cold test of 31 lots of corn of varying viability. Loss of viability appeared to be closely associated with respiratory failure in most seeds. Malic dehydrogenase activity was more closely correlated with germination percentage and respiratory capacity than that of the other 2 enzymes, although considerable malic activity was retained in nonviable seeds. It is doubtful whether inactivation of these 3 enzymes was a major cause of loss of viability, but it appeared likely that dehydrogenase activity was more closely correlated with tetrazolium reduction than with germination percentage. Variations in respiratory metabolism did not explain the differences between germination percentage and cold test or vigor rating.

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GLUCOSE DISSIMILATION IN THE HIGHER PLANT. EFFECT OF AGE OF TISSUE[1,2]

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We have recently described a series of experiments (4) from which it was concluded that a sequence of glucose breakdown other than that of glycolysis by the Embden-Meyerhof-Parnas (E.M.P.) pathway plays a part in the respiration of several plant tissues. There were indications from this work that an alternative method of glucose dissimilation (Warburg-Dickens, Direct Oxidation pathway) was particularly prominent in the older aerial parts of plants and by contrast the respiration of a highly meristematic tissue (corn root tip) was shown to occur exclusively by the classical glycolysis sequence (5). In this paper we will present evidence, obtained from experiments with a wide variety of plant parts of different ages that in juvenile and undifferentiated tissues generally, the E.M.P. sequence is of major importance, but that as the tissue ages, the Direct Oxidation pathway comes to play an increasingly important role.

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Materials and Methods

The method used to evaluate the relative contributions of the E.M.P. sequence and the Direct Oxidation pathway has already been described (3, 7). It involves the measurement and comparison of radiochemical yield in the CO_2 produced by equal samples of tissue respiring glucose-1-C^{14} and glucose-6-C^{14} respectively. Usually, the amounts of tissue added to the flasks were such that in a 4 to 5 hr run not more than 20 % of the glucose had been respired and we were able to calculate the C_6/C_1 ratio (% yield of C^{14} from glucose-6-C^{14}/% yield of C^{14} from glucose-1-C^{14}) in the early stages of glucose dissimilation.

Plant Materials: Root tissues of corn (Wf9 × 38-11) and Castor bean (U.S. 74) seedlings were obtained by soaking the seed overnight in water and allowing it to germinate at 29° C. When the seedlings were 6 to 7 days old and the roots were 10 to 15 cm in length they were excised and washed and cut with a razor into segments of 1 cm from the tip backwards (table I).

Stem tissue of sunflower, tomato, *Bryophyllum* sp. and Coleus was taken from stock greenhouse plants and that of pea (Alaska) was from plants grown on sand in the greenhouse. Generally three pieces of the stem were analyzed. These sections are designated in table II as A: sections from internode near the apex. B: from an internode midway between the growing tip and ground level, and C: from the internode at the base of the stem. Leaf tissue from peas, castor bean, coffee and sunflower was used. The coffee leaves were from small seedlings about one year old and the plants which were described earlier provided the rest of the leaf material. Tissues of two different ages were usually compared (table III) by selecting A: young leaves near the apex which were still small and expanding, and B: fully expanded mature leaves from older nodes. The cotyledons and hypocotyl of germinating castor beans were also examined (table IV). The stage of development of the tissue which was analyzed is recorded in the table. Another type of undifferentiated tissue used in this study was Avena coleoptile (table V). The coleoptile sections were obtained in the following manner. Husked Avena seeds ("Victory" from Svalöf) of equal size were germinated on blotters in Petri dishes. After the blotters were moistened with water, the seeds were exposed to the red light of a 60-watt bulb for 4 hours at a temperature of 24 to 26° C. After a germination period of 72 hours in darkness, 23 to 25° C and a relative humidity of 85 %, the seedling possessed coleoptiles approximately 22 mm in length. The top 3 mm of

Table I

Evaluation of C_6/C_1 Ratio for Root Tissue

Plant	Segment	Glucose-6-C^{14}	Glucose-1-C^{14}	C_6/C_1*
		% Yield	*% Yield*	
Castor bean 7 days successive 1 cm segments	A (tip)	11.9	12.2	0.98 (0.98) **
	B	5.7	7.4	0.77
	C	6.3	9.8	0.64
	D	5.6	11.2	0.50
	E	7.8	13.8	0.56
Castor bean 6 days successive 2 cm segments	A (tip)	8.5	9.2	0.92 (0.94)
	B	5.5	8.4	0.66
	C	6.9	8.9	0.78
Corn 7 days successive 1 cm segments	A (tip)	20.3	16.4	1.24 (0.91, 1.12)
	B	20.7	19.4	1.06
	C	17.7	22.9	0.77
	D	18.6	23.6	0.79
	E	14.7	17.7	0.83

* C_6/C_1 = % radiochemical yield from glucose-6-C^{14}/% radiochemical yields from glucose-1-C^{14}.

** The values in parentheses are from individual experiments carried out on separate occasions.

Table II

Evaluation of C_6/C_1 Ratio for Stem Tissue

Plant	Segment	Glucose-6-C^{14}	Glucose-1-C^{14}	C_6/C_1
		% Yield	*% Yield*	
Tomato about 3 months	A	34.0	51.2	0.66
	B	24.3	52.0	0.47
	C	21.4	48.8	0.44
Coleus about 3 months	A	4.7	7.6	0.62
	B	7.5	14.5	0.52
	C	4.9	9.4	0.52
Pea 18 days	A	1.2	2.5	0.48
	B	1.1	2.8	0.39
	C	0.74	2.6	0.28
Pea 23 days	A	3.8	7.6	0.50
	B	5.6	12.3	0.46
	C	3.3	9.3	0.35
Pea 23 days	A	5.1	11.1	0.46
	C	4.2	9.9	0.42
Sunflower about 2 months	A	1.1	0.95	1.15
	C	1.4	0.99	0.71
Bryophyllum about 7 months	A	2.7	3.6	0.75
	B	6.1	8.5	0.72
	C	11.7	15.7	0.75

Table III

Evaluation of C_6/C_1 Ratio for Leaf Tissue

Plant	Segment	Glucose-6-C^{14}	Glucose-1-C^{14}	C_6/C_1
		% Yield	*% Yield*	
Castor bean	A	3.1	5.1	0.61
	B	1.4	2.9	0.48
Pea 21 days	A	3.1	7.4	0.42
	B	2.0	6.3	0.32
Pea 24 days	A	5.4	9.7	0.56
	AB	4.9	10.0	0.49
	B	3.4	8.7	0.39
Coffee	A	2.8	9.0	0.31
	B	1.2	4.7	0.25
Sunflower about 2 months	A	6.6	9.3	0.66
	B	2.6	4.8	0.55

the coleoptile was discarded and the next 10-mm section was used.

MANOMETRIC EXPERIMENTS: The general procedure was to cut the experimental material with a razor into sections or pieces about 1 mm in thickness. This step was omitted in the experiments with roots; these were washed in several changes of distilled water, dried lightly, and weighed into equal samples of 0.5 to 3.0 gm fresh weight. In most of these experiments four such samples of tissue were placed in the main compartments of Warburg vessels of 100 ml capacity. In addition to the tissue, the main compartment contained 30 micromoles of phosphate buffer at pH 5.0 in a volume of 2.5 to 4.0 ml of water. To two of the four vessels equal amounts (usually 10 to 30 micromoles) of glucose-1-C^{14} of known activity (7 to 30 millimicrocuries) were added while the others received the same amounts of glucose-6-C^{14}. The glucose was added immediately prior to attaching the vessels to the manometers. The vessels were shaken at 25 or 30° C for a period of 4 to 5 hours, dark conditions being provided where necessary. The atmosphere in the flask was air and the center well carried 0.2 ml 20 % KOH to absorb the respired CO_2.

MEASUREMENTS OF RADIOACTIVITY: At the end of the experiments the KOH–K_2CO_3 was removed and converted to $BaCO_3$, which was then washed and dried and assayed for radioactivity. In all the experiments C^{14} was determined by assaying $BaCO_3$.

RESULTS

In each experiment, the radiochemical yield in the respired CO_2 from each glucose sample was evaluated and this was then expressed as a percentage of the total radioactivity supplied in the original glucose. From these data, the C_6/C_1 ratio is calculated. The C_6/C_1 ratio represents the maximum fraction of glucose being metabolized by the E.M.P. pathway (7), and thus the minimum contribution of other pathways metabolizing glucose is represented by the fraction $1 - \frac{C_6}{C_1}$.

TABLE IV

EVALUATION OF C_6/C_1 RATIO OF THE COTYLEDONS AND HYPOCOTYL OF GERMINATING CASTOR BEAN

TISSUE	STAGE	GLUCOSE-6-C^{14}	GLUCOSE-1-C^{14}	C_6/C_1
		% Yield	*% Yield*	
Cotyledons	4 days	7.6	9.9	0.77
	5 days	13.6	16.8	0.81
	6 days	6.3	11.6	0.54
	7 days	1.8	3.2	0.56
	8 days	2.6	4.9	0.53
Hypocotyl	2 cm (5 days)	8.5	12.0	0.71
	5 cm	5.1	7.9	0.64
	12 cm	3.1	5.3	0.59
	13 cm	4.0	6.4	0.62
	20 cm (8 days)	4.7	8.5	0.56

TABLE V

EVALUATION OF C_6/C_1 RATIO FOR AVENA COLEOPTILE AND EFFECT OF INDOLEACETIC ACID ON THE RATIO

GLUCOSE	MμC ADDED	% RECOVERED	μM O_2 UPTAKE	C_6/C_1
-6-	27.7	2.77	17.0	1.13
-1-	36.9	2.45	16.0	
	IAA added (2.4 mg/liter in cup)			
-1-	27.7	3.91	22.6	1.02
-6-	36.9	3.82	19.1	

Each Warburg vessel contained 18 coleoptiles of 10 mm length. After 6 hrs, control coleoptiles 12.4 mm, IAA coleoptiles 16.6 mm.

The following points are clear from the data shown in tables I to V.

a. Leaves and shoots in general show lower values for the ratio than the root tissues examined.

b. With few exceptions the ratio does not remain constant as a given plant organ ages.

c. The change in the ratio is always in the same direction, i.e., the younger tissues show higher values than their older counterparts.

d. Roots have values close to unity in the meristematic regions near the tip, but in successively older segments, the values decline rather sharply to a plateau.

e. A similar trend is obvious in the other plant parts examined but the youngest tissues which it was practicable to use frequently showed values considerably less than one.

f. The addition of indoleacetic acid to oat coleoptiles increases the consumption of glucose, but the C_6/C_1 ratio remained close to unity.

DISCUSSION

The data presented in this paper are consistent with the concept that as embryonic areas differentiate during growth, the carbohydrate metabolism undergoes a qualitative change. It appears that, while embryonic tissues respire glucose exclusively via the E.M.P. sequence,[3] the Direct Oxidation pathway makes an increasing contribution as growth and differentiation occur.

There is already evidence which, by itself, is not conclusive but which suggests that the E.M.P. sequence is particularly vigorous in meristematic tissues and that the respiratory and fermentative ability of plant cells may alter during growth. For example, Phillips (16) reported a decline in the ability of barley seedlings to accumulate alcohol under nitrogen as they grew from the 4-day to the 10-day stage, and Ruhland and Ramshorn (18) have shown that even under aerobic conditions ethyl alcohol may accumulate in young roots of *Vicia faba*, particularly in the meristematic regions. Decreases in respiratory quotient (RQ), reflecting similar changes in the contribu-

[3] We have also examined corn coleoptiles and mesocotyls which yielded ratios of 1.15 and 0.98 respectively.

tion of aerobic fermentation, may occur during plant development. Thus Merry and Goddard (15) for barley and Meeuse for peas (14) and Ruhland and Ramshorn (18) for cambia and root tips of several plants have reported RQ's considerably greater than 1 in young tisues while in the corresponding mature tissues values of near unity were the norm.

Changes in the amount of certain respiratory enzymes during the life cycle of the plant might also be considered as evidence of a changing respiratory pattern. In the pea plant alcohol and formic dehydrogenase activity decreases as germination proceeds and after six days these enzymes are virtually absent. When the pea plant reaches maturity these enzymes reappear (8).

It is clear that the relative concentrations of critical enzymes of the alternative sequences might determine the extent to which each participates in the respiration of a given tissue. Thus in the pea root the appearance of the Warburg-Dickens pathway may be related to the disappearance of aldolase, a similar situation having already been reported for the heterofermentative lactic acid bacteria *Leuconostoc mesenteroides* (9). It was the increasing evidence of the occurrence of enzymes of the Direct Oxidation pathway and the demonstration of partial reactions of this sequence in plant extracts (1, 2, 10) which prompted our investigation showing that it contributes to the respiratory breakdown of glucose (4). The interesting possibility that the non-participation of this pathway in embryonic tissues may be due to the absence of the enzyme systems is at present under investigation. However, differences in the relative amounts of the enzymes concerned may not be the universal explanation, since it sems unlikely that non-limiting amounts of the enzymes of both pathways may occur in some cells. In these cases the cause of the shunting of glucose-6-phosphate from one route to the other is unknown, although it is apparent in the case of yeast that oxygen exerts an influence on the pathway of glucose metabolism. In these cells, the E.M.P. pathway is used exclusively under anaerobic conditions (12) while in the presence of oxygen, part of the glucose is respired by the Warburg-Dickens sequence (3). A lack of oxygen may conceivably cause the same condition in "young" plant tissue. However, Ruhland and Ramshorn (18) have reported that even in the presence of 100 % oxygen, aerobic fermentation is not suppressed in some young tissue and there is no reason to believe that there is a hindrance to the entrance of oxygen into the cells of such tissue which disappears in maturation.

Until it was demonstrated that cells also contain enzymes capable of oxidizing pentose derivatives produced in the initial reactions of glucose-6-phosphate oxidation and that the Direct Oxidation pathway may, as a result, account for the complete oxidation of sugar the major significance which was attached to this sequence was a a probable route to the pentoses in vivo, the pentoses being required in the formation of ribosenucleic acid (11). It is interesting in this regard that we have been unable to detect the occurrence of the Direct Oxidation pathway in the meristematic tissues of root tips in which the utilization of pentose in such reactions might be expected to be at a maximum. Bernstein has reported a similar condition in the young chick (6). It would appear that a C_3—C_2 condensation mechanism is the major route of pentose synthesis in growing tissue. In this reaction, the C_2-component is probably transferred by transketolase from fructose-6-phosphate to glyceraldehyde-3-phosphate (C_3 piece) to yield pentose phosphate.

It has often been suggested that auxin may influence carbohydrate metabolism, and that indoleacetic acid increases the rate of oxygen uptake in coleoptiles has been verified by many investigators. In the present study, we have reconfirmed the stimulation by auxin of glucose respiration of Avena coleoptiles but found that the hormone did not affect the pathway of glucose respiration, the coleoptiles having respired the glucose in both cases exclusively via the E.M.P. pathway.

Summary

The purpose of this investigation was to study whether the developmental age of a plant tissue had any effect on the pathway of respiratory metabolism of exogenous glucose. Through the use of a method involving the measurement of the rate of glucose-1-C^{14} and glucose-6-C^{14} oxidation by the plant tissue (stem, root, leaf, cotyledon, hypocotyl, coleoptile) it was found that while immature tissue respired glucose either exclusively or to a large extent via the Embden-Meyerhof-Parnas glycolytic sequence the participation of the Direct Oxidation pathway was increasingly pronounced as the tissues aged and differentiated, and in many mature tissues it accounted for at least 50 % of the respiration. In short term experiments in which auxin stimulated the growth of coleoptile segments, there was no effect on the pathway of glucose dissimilation.

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EFFECT OF CERTAIN METABOLIC INHIBITORS ON TRANSLOCATION OF P^{32} IN BEAN PLANTS[1,2]

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In previous studies of the movement of solutes through phloem tissue, it has been found possible to influence the rate and direction of solute movement. In most investigations the direction of movement of certain tracers (viruses, growth substances, radioactive isotopes, etc.) was found to occur in the same direction as (by inference) the movement of organic solutes (1, 5, 8). Treatments such as subjecting the cells to temperatures of 0 to 10° and 30 to 40° C (see references in 10, 11) and also non-lethal concentrations of certain metabolic inhibitors (4), have been found to be inhibitory. More severe treatments which resulted in death of the cells were reported to have stopped the movement (11). In all of these studies it is questionable whether the observed change in solute movement resulted from an effect of the treatment on the transport mechanism per se as suggested by Curtis (4) or from an indirect effect, e.g., an alteration in the permeability of the medium through which the movement occurred, as suggested by Crafts (3). There can be little doubt, however, that these treatments influenced the metabolism of the cells through which the movement occurred, yet the role of the cytoplasm remains obscure. On the basis of all these studies, a more detailed investigation of the relationship between phloem transport and metabolism of the cells through which the movement occurs appears to be warranted. It would be of paramount importance to isolate the phases of metabolism most closely associated with the transport mechanism. From such data it might be possible to infer the role of cytoplasm relative to the movement of substances through the tissue.

The basic technique utilized in these studies was to apply a P^{32} solution to one primary leaf blade of a bean plant and subsequently measure the amount of the material which had moved through the petiole of the treated leaf and into the stem. Various chemicals which have been reported to influence certain phases of plant metabolism were injected into the treated leaf petioles.

METHODS AND MATERIALS

Bean plants (*Phaseolus vulgaris* var. Black Valentine) approximately 1.5 to 2 weeks old, were used in all of the experiments in this investigation. The plants had grown individually in one-quart Mason jars which were painted black on the outside and filled with a supplemented four-salt culture solution of the following composition: 0.0017 M KNO_3, 0.0017 M KH_2PO_4, 0.0026 M $Ca(NO_3)_2$, 0.0017 M $MgSO_4$, 2.2

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[2] Paper No. 575 from the Department of Botany and Plant Pathology, the Ohio State University, Columbus 10, Ohio. Additional details and tabular data are included in a dissertation of the same title, The Ohio State University Library, 1954.
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