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Nutritional Factors in Plant Growth and Development - Paper Presented at the Fifty-Sixth Annual Meeting

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NUTRITIONAL FACTORS IN PLANT GROWTH AND DEVELOPMENT

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The large number of recent publications on the physiology of plant development reflects a widespread, contemporary interest in this subject. Researches in this area deal chiefly with the effects of specific growth substances and mineral nutrients on functional and structural ontogeny. The major contributions on the physiology of growth substances have already been conveniently assembled in certain excellent monographs (36, 53, 283, 339, 424) and reviews (37, 422, 192). Recent researches on nutrition in relation to plant development have not as yet been comprehensively reviewed. Data in this field as a whole are extremely diverse, especially as they relate to the nutritional cycle of biennial and perennial crops (20, 259, 411). In typical annuals, however, certain common relationships seem to characterize the mineral, carbohydrate and protein metabolism such that a number of generalizations can be made to aid an understanding of nutrition in relation to growth despite varietal differences (142, 228, 394).

Interest for many years has centered in the metabolic transformations characterizing the transition from vegetative to reproductive activity. Data of various authors working with annuals on this phase of nutrient metabolism permit some degree of correlation because plants have commonly been cultured under greenhouse conditions which circumvent the more extreme edaphic and meteorological variables inherent in field tests. Use of relatively large populations of annuals coupled with reasonably uniform cultural conditions also give the resulting data a fairly satisfactory degree of statistical validity. A review of research on the nutrition of annuals may thus serve to assemble a widely dispersed literature and perhaps also facilitate correlation of work in this area with that on phytohormones. Recent contributions on plant development indicate a reciprocal relationship between growth substances of the hormone type with the carbohydrate, protein and mineral components of plants (5, 16, 23, 116, 130, 204, 297, 399, 408).

Growth substances are known to influence enzyme activity (39, 261, 363) and thus bring about qualitative as well ac quantitative changes in organic synthates and metabolism (93, 131). The concentration of carbohydrate and nitrogenous components also varies

61

with the concentration of growth substances in various parts of
the plant (5, 141, 252, 253, 254, 366, 390, 431, 447). The forma-
tion of growth substances is not only dependent on a supply of
inorganic nutrients such as nitrogen (16) but growth substances
themselves also appear able to induce differences in the content of
inorganic nutrients (50, 136, 343). In fact since many of the ma-
jor growth responses have already been clearly correlated with
specific hormonal agents, discovery of the mechanism of interac-
tion of these substances with nutrients in achievement of the
plant's developmental potentialities constitutes a major problem in
the physiology of growth.

1. THE PROBLEMS OF PLANT DEVELOPMENT

Before proceeding with a discussion of the data on physiologi-
cal ontogeny, it may be helpful to outline certain attributes of
plant growth as these relate to experimental techniques and inter-
pretation of data. Studies on the physiology of plant development
are complicated by the fact that, at a given time, similar organs
of the growing plant are in varying stages of their developmental
sequence (12, 97, 229, 342). Unlike the animal, which commonly
matures as an entity, the typical plant consists of numerous, scat-
tered growing points in the form of apical and lateral meristems.
These essentially embryonic tissues give rise to a succession of
new organs in a progressive sequence of time. The resulting or-
gans exhibit quasi-independent growth (119) such that neither
comparable size and age of plants as whole nor of their separate
parts serve as sound criteria of development similarity (326, 355).
Briefly, the various parts of a growing plant may display simul-
taneously the entire range of development from youth to senes-
cence.

This variability arises in part from the fact that during growth
a single plant alters its own environment in such a way that
structures appearing in chronological sequence reflect a progres-
sive ecological succession with concomitant differences in meta-
bolism (29, 97, 200, 260). In leaves of species with an erect habit
there is commonly a vertical progression from mesomorphy of
mature lower leaves to comparative xeromorphy of mature upper
leaves on the same stem (19, 145, 245, 395, 416, 441). A rising
gradient of sap osmotic pressure seems to characterize the mature
internodes of the stem (92, 383, 395, 398) which is accentuated
by water shortage (145). Similarly vertical gradients of enzymes
(287) hormones (97, 424) and nutrients also occur in stems. Up-

per stems and leaves tend to be higher in nitrogen and protein content (10, 148, 200, 274, 362, 364, 397) though this gradient depends largely on the method of sampling (260, 274). Hydrolyzable reserve carbohydrates, on the other hand, tend to exhibit a higher concentration in basal leaves and stems (29, 200, 397). Mineral nutrient ions also commonly display vertical gradients of distribution (102), such that the concentrations of calcium, sulphur and magnesium tend to be greater at lower stem levels (10, 222, 264,311), while potassium and nitrogen are highest at upper levels (325). Despite these variations of its different portions, the vegetative parts of the plant as a whole gradually shift from a state of predominant anabolism in early life to one of increasing catabolism at maturity (21, 84). Due to such variations in composition and metabolism of various plant organs, methods of culture and analysis must be carefully adapted to experimental factors concerning which information is sought. The conditions of the environment during the entire growth cycle must be accurately known and methods of sampling for tissue analyses must be highly selective.

Correlation of plant response with environment is, however, beset with certain difficulties because plants are to a considerable degree the products of their past as well as of immediate environment as shown by studies of so-called "induced" phenomena (273). The obvious structural response to the specific morphogenic stimulus of light or temperature may, for example, often occur weeks or months after application or perception of such stimuli (143, 274). Thus, the environment under which a response makes its appearance may not necessarily be that which induced it, especially if the environment has changed appreciably during growth (12, 137, 246). Such delay between perception of and response to stimulus (after-effect) is especially evident in influences of the photoperiod upon flowering and in temperature responses of vernalized seeds. There is, for instance, considerable experimental evidence that conditions of moisture (315), temperature and light prevailing during formation of the embryo while still attached to the mother sporophyte may be more important to subsequent growth of seedlings than the physical factors of the environment prevailing during and after germination (115, 174, 180, 194, 199, 290, 443, 444). Though lying beyond the scope of this review, the recent theory of phasic development of plants seeks to correlate formative response with the external factors of temperature and light. It has been demonstrated that these factors may induce

qualitative shifts in metabolism and hence of development (428).
The direct effect of the environment may be upon enzymatic
systems and growth substances (358), but the grosser structural
changes following vernalization and photoperiodic induction to a
considerable degree depend upon the nutrient conditions of the
plant for their full expression. Such effects of physiological in-
duction often provide an explanation of the developmental differ-
ences frequently found among plants growing in currently com-
parable environments (108, 126, 234, 235, 239, 429).

Induced responses must, however, be clearly distinguished from
those which are non-induced. A brief exposure to a given environ-
mental stimulus may produce a permanent, qualitative transition
as in the case of flowering under influence of day length, or mere-
ly a quantitative response which is proportional to the duration
of the stimulus. The observation of Murneek (276) may be cited
as an example of the latter in which he has shown that elongation
in the flower stalk of *Rudbeckia* is proportional to the duration
of long day stimulus. Though stem elongation in this case is de-
pendent upon long day exposure, it ceases when plants are re-
turned to short day. Hence, growth of the flower stalk in *Rud-
beckia* is a non-induced phenomenon which stands in sharp con-
trast to the inductive effect of a brief exposure to long day on
flowering of the same plant (220).Certain photoperiodic responses
of vegetative structures such as bulbs and tubers of other plants
similarly appear to be of the non-induced type (332, 448).

Up to the present time it has been customary to consider the
growth cycle as comprising primarily a vegetative and reproduc-
tive phase. There has been a general tendency to regard flowering
(anthesis) as the beginning of the reproductive phase. A current
issue of great interest in physiological studies concerns the exact
point at which the most significant metabolic changes occur in the
transition from vegetative growth to flowering. Recent data indi-
cate that the period between inception of flower primordia and
bud formation rather than the period of anthesis in which fertil-
ization occurs is the better physiological criterion of and index to
the onset of reproduction (120, 216, 270, 320, 337, 356, 386, 449).
The tendency of the layman to designate the obvious appearance
of blossoms as the beginning of reproduction is understandable, yet
such a landmark is unsatisfactory from the physiological stand-
point. Though the differentiation of flower initials involves the
least conspicuous of the formative changes connected with flower-

ing, this stage is critical in development from the metabolic view-point. Appearance of floral primordia marks initiation of a qualitatively different type of metabolism. Many of the nutritional transitions hitherto correlated with flowering (anthesis or blossoming) actually occur much earlier, namely with origin of the flower parts (313, 331, 409). On a formative basis, flower inception characteristically also marks a transition in rate of vegetative development and elongation of the main axis or shoots of typical annuals (45, 202, 320, 393). Differences in pre-anthesis and post-anthesis physiology are also sufficiently marked to warrant these as sub-divisions of the flowering phase itself (216, 272, 320).

Further, the physiologist also finds it necessary to distinguish sharply between flowering and fruiting. The functional attributes of fruit formation differ as much from flowering as the latter differs from vegetative growth (103, 112, 220, 319). Fertilization is commonly accepted as the beginning of the fruiting phase even though pollination without gametic fusion is in many cases known to result in parthenocarpic fruits. Experimental parthenocarpy provides a convenient method of differentiating the physiology of fruit from that of seed formation.

The method of sampling and expression of data are also important (84, 86, 113, 181, 425). The constituents of the entire plant must be known in absolute amounts rather than in mere percentages in order to check the changes in total weights throughout the growth cycle (285, 289, 329, 410). A chronological record of rates of increase in separate portions of the plant provides a much clearer picture of metabolism, and these, when combined with leaf area and root volume, give a fairly clear picture of the metabolic efficiency of individual structures as well as of the plant as a whole (19). The point of the preceeding remark is perhaps best illustrated by the relation between mineral and organic constituents of the plant. Though salts continue to increase in absolute amounts throughout most of the plant's life, their percentages usually decrease because the rate of complex organic syntheses accelerates rapidly prior to maturation (73, 222, 302, 304, 309,). The record of absolute amounts of salts usually shows a progressive increase whereas percentages thereof often fall during growth of the plant. Though salt absorption eventually ceases during senescence, the percentage composition curve alone does not reveal this fact. A localized record of absolute amounts of specific inorganic ions makes compositional shifts immediately discernible in point of

time and place, data which are important aids in distinguishing cause and effect. Many helpful suggestions as to metabolic efficiency are obtained by expressing composition and syntheses in terms of unit leaf weight or area (19, 362). Such a record, for example, unmistakably reveals the vertical gradient of increasing leaf dry weight per unit of surface. Photoelectric areameters now provide a more convenient method of surface determination than the older tedious planimetric measurements (147, 197, 435). Measurements of aggregate absolute weight in a large number of plants helps to minimize sampling errors and avoids the inadequacies of percentage composition (84, 410). Continuous growth records promise to clarify many as yet obscure points on developmental physiology. To insure the best results, however, such experiments must be arranged with due regard to a sequential record of the environment and localized tissue analyses in terms of actual rather than mere percentage composition throughout the growth cycle.

Certain details of technique are imposed in studies of plant development, due to the fact that scattered growing points are the active loci of hormone secretion and formative change. Plant tissues of unlike secretory function are not usually organized in the form of separate glands as in animals but are usually closely interwoven structurally. This type of organization presents experimental difficulties and often renders gross physico-chemical tissue analyses inappropriate in studies of plant development. It necessitates such highly localized sampling that use of refined procedures of micro-analysis often become necessary (19, 84, 86, 285, 289, 326, 362). Recent developments in spectographic analysis (146), histochemistry and use of artificially activated isotopes have already provided the biologist with microtechniques of great value in analysis of small samples. Root analyses are also essential to a comprehensive grasp of the metabolic characteristics of the plants as a whole, an operation which is greatly facilitated by liquid and gravel cultures from which roots are readily retrievable. Such cultures provide a substrate far more uniform in composition and more amenable than soil to control of temperature, hydrion concentration, salts, water supply, microflora and other edaphic factors. Sand and gravel cultures apparently approximate the conditions of natural soils sufficiently to make the data of such studies of value in actual agronomic practice. Inclusion of data on root composition in recent studies on growth has brought to light a number of important top-root interrelationships.

In studies of development, attention focuses largely upon formative tissues, namely upon meristematic cells from which plant structures originate. It is the task of the physiologist to identify the metabolic factors which cause the morphological differences observable among cells arising from a common meristem (392). Since changes in metabolism of initially equipotential cells arising from a meristem must precede structural differentiation, the developmental physiologist is chiefly concerned with those protoplasmic changes which underlie the contrasted growth patterns of tissues. Such protoplasmic conditions must be precisely correlated with the environmental factors which bring them about in order that the investigator may understand the complete sequence of events and be able to check his interpretations. Existing contributions of plant anatomy and morphology have already implemented the structural phase of the developmental problem but more detailed studies on metabolism and specific morphogenic inductors are needed to bridge the remaining gaps in our knowledge of the relationships between environment and plant structure. In the ensuing review, attention is given to a number of papers which aim especially to correlate form and function with nutrition.

2.   WATER RELATIONSHIPS

Water content of rapidly enlarging seedlings rises to a maximum as soluble food reserves of the seed are translocated to the young shoot and root. In pot culture experiments in which the rate of water consumption can be compared with water content of tissues, it is evident that in the earlier phases of vegetative development water intake readily compensates transpiration since maximal tissue hydration occurs well before flowering (19, 216, 362). As the growing plant achieves independence by means of its own organic syntheses, rapid water absorption and protein formation become its predominant metabolic characteristics. They induce a high degree of succulence in newly formed tissues. As vegetative growth progresses and as carbohydrate components of the plant begin to increase, moisture content begins to decline slowly but progressively in all parts except young leaves and stem tips even under conditions of uniform availability of water in the substrate. At this time absorption of water and transpiration are approximately balanced even though an age factor manifests itself as a somewhat more rapid diminution of moisture in older as compared with younger leaves. Upper leaves maintain their moisture supply at the expense of lower leaves and roots, (75, 245). Re-

duction in moisture per unit dry weight characteristically pro-
gresses with the age of all vegetative parts even under conditions
of uniform water supply (19, 71, 92, 362, 402, 441). This dif-
ferential between old and younger leaves in degree of hydration
or percentage moisture is associated with the emergence of a
vertical gradient of increasing xermorphy as leaves mature. Fully
developed leaves at upper levels exhibit lower moisture content
per unit area and fresh weight (245), a fact which suggests that
the meristem from which they originate is also undergoing a shift
in water balance.

There is frequent reference in the literature and substantial
agreement on the occurrence of marked alterations in internal water
balance during flowering (19, 89, 159, 160, 187, 191, 202, 225,
226, 258, 259, 292, 306, 350, 362). Sharp division of opinion
exists, however, as to the time of inception and duration of this
shift which clearly indicates a significant alteration in general
metabolism as well as a distinct transition from the previous
slow decline in moisture characteristic of earlier vegetative growth.
Some of the discrepancies on this point are attributable to methods
of analysis. Most investigators have relied on measurement of per-
centage moisture content of tissues sometimes at rather widely
separated intervals. Investigations in which daily water consump-
tion is accurately measured (89) show a transitory but profound
reduction in rate of water absorption in the period of flower bud
formation. It is abrupt in onset, occurring at the time of low
carbohydrate supply to the root. Water absorption rises again
with subsequent increase in root carbohydrates with an accom-
panying improvement in the top-root ratio but water balance does
not again achieve the previous levels of the vegetative phase.

A thorough investigation of water balance during growth of
wheat has recently been made by Bakhuyzen (19) who also re-
views the general literature on this subject. Though Bakhuyzen
associates marked alteration in water balance with flowering, he
states that "our data do not show at exactly what moment the
loss of water from leaves, stems and ears occurs, whether at stam-
ination or at fertilization of ovaries" of wheat grown under con-
stant conditions in a twenty four hour day. He correlates the
change in moisture with fertilization, yet his own data as well as
those of other workers indicate that inception of the shift in
moisture occurs prior to anthesis rather than at fertilization (45,
89, 125, 167, 356).

As flowering is approached, the moisture curve of lower leaves per unit area tends to shift in the direction of water loss in lower leaves while upper leaves may yet be gaining in unit moisture content (258, 259, 355). Lower leaves of wheat cease to gain in moisture as early as at the twentieth day, at which time floral primordia may already be found. This alteration in water content of lower leaves precedes anthesis by ten to fourteen days in wheat under optimal conditions of moisture supply. The change in gradient of the water curve in lower leaves of cereals and other plants is sometimes quite abrupt. The pre-flowering drop in moisture content is often associated with and hence a convenient index to the presence of flower primordia or young buds in many annuals (215, 216, 362, 355). On the basis of recent work, it thus appears that the initial change in the direction of lower moisture content is associated with inception of flower buds rather than with full anthesis (89, 167) as heretofore maintained by many authors.

Reduction in tissue moisture becomes more pronounced general-ly as flowering reaches its ascendency. This tendency results in a rise in osmotic pressure of tissue fluids due in part to concentra-tion of residual solutes. The increase in osmotic pressure is, how-ever, incapable of arresting the trend of progressive dehydration as shown by continuation of water loss in spite of very appreci-able increments in inorganic solute concentration in the sap at this time. We cannot escape the inference that forces other than os-motic pressure play an important role in internal water balance (19, 259, 295, 362, 406). Studies on drought and cold resistance have shown the importance of hydrophilic colloids to plant sur-vival under these adverse circumstances (106, 164, 398). The re-cent work of Smirnov (362) demonstrates that cell colloids are fully as important in regulation of moisture content under normal conditions of growth as they are in plant survival during drought and low temperature (340). His data show that normal vegeta-tive growth is characterized by high colloid and high moisture content of tissues, which with high nitrogen (protein) usually pro-duces a condition of considerable succulence in the actively grow-ing shoot.

The increase in transpiration and depressed rate of water entry entail a drop in moisture content of cells during flowering with a comparable increase in soluble salts of the cell sap. When the concentration of soluble salts exceeds certain critical values, as it does in older leaves, there is an abrupt diminution of hydrophilic

colloids accompanied by a further and commensurate drop in moisture content of these tissues. Smirnov (362) suggests that precipitation of a large portion of cell colloids at high salt concentrations is the probable underlying cause of the sudden, coincident reduction in moisture of older leaves (13, 222). It has been shown that highly hydrated protein gels are close to the precipitation point and sensitive to slight changes in hydrion and salt concentrations (13). Confirmation of Smirnov's interpretation is found in the fact that dried powders of young but fully developed leaves can regain hygroscopically almost all their original moisture when exposed to a humid atmosphere (190), whereas this is not true of old leaves high in salts. This high degree of hygroscopicity can hardly be attributed to the salts known to occur in plant tissues in view of the fact that hygroscopicity diminishes with the rise in electrolyte content of older leaves. Measurements of sap viscosity, surface tension and the hygroscopicity of dried tissues in a moist atmosphere are convenient indices of colloid content as they check well with direct measurements of tissue colloids. Hygroscopicity of dried leaf material and high colloid content are pronounced in young leaves, conditions which suggest a highly peptized state of hydrophile constituents in the intact condition (295). Smirnov's observations lead to the conclusion that increments in water retentivity of leaves due to osmotic pressures arising from water loss are more than offset by the salting out of hydrophile colloids. Inability of the latter to retain previously adsorbed water leads to a commensurate drop in tissue moisture.

The salting out of colloids by the rising concentration of electrolytes during drying seems to be in the nature of an exchange mechanism whereby previously adsorbed enzymes are liberated. Enzymes in the free form become hydrolytically active, initiating conversion of insoluble to soluble organic reserves (100). Hydrion changes during this period may also influence the course of enzyme action (132, 133). The salt effect observed during incipient drying thus involves initially the precipitation of organic colloids with a sharp reduction in their hydrophilic properties and retentivity of tissue moisture (17, 60, 125, 299, 313, 334, 348, 359, 365, 369). Subsequently, displacement of adsorbed enzymes by the rising concentration of electrolytes leads to hydrolysis of insoluble reserves. Hydrolysis of food reserves in older basal leaves is soon followed by translocation to upper and younger portions of the shoot as well as to reproductive structures. Loss of organic reserves from lower leaves seems to preclude the pos-

sibility of later restoration of organic synthesis and hence of water balance. Lower leaves consequently tend to become chlorotic, to dry and absciss. Upper leaves temporarily maintain their water and nutrient supply at the expense of those below (19, 75, 245).

As the result of accumulation of organic and inorganic solutes, a state of physiological dryness arises. Walter (415) suggests that hydrolyses by very virtue of their increase of osmotic pressures of the cell sap accentuate the effects of dehydration by creating a state of physiological dryness which accelerates the metabolic trends induced by original water losses. Briefly, the degree of effective tissue hydration can be lowered by gain in solutes without actual water loss. The resulting rise in osmotic pressures is, however, insufficient to restore normal water balance to judge from continuation of the drying process and increments in dry weight percentage throughout the phase of solute accumulation. Progressive drying leads eventually not only to an acceleration in hydrolysis of reserves but also to diminished formation of polysaccharides and proteins. There exists a great body of data sustaining the general thesis that reduction in tissue moisture operates to stimulate enzymatic hydrolyses and to impede condensation of soluble amino acids and monoses (3, 9, 22 49, 52, 65, 158, 169, 184, 255, 259, 287, 288, 307, 330, 344, 345, 359, 362, 365, 369, 404, 405, 415, 432, 436).

The condition of the plant in flower is one of water disbalance and general moisture insufficiency. Despite uniformity of water supply, the percentage moisture of tissues continues to fall. This fact in association with internal redistribution of water implies inadequacy of absorption by the root. Even before anthesis water loss is above the compensation level but it is further displaced by increases in transpirational surface of flowers in bloom. At this stage, the net assimilation rate (355, 392) of the plant as a whole undergoes a diminution parallel to the drop in tissue moisture (75, 76), a fact which indicates the importance of water in the developmental cycle (238). The rate of stem elongation also falls at this time (240) and development of the absciss layer in the young pedicel may become evident. Sap acidity changes also occur as water content of tissues diminishes. Acidity of tissue fluids first increases in lower leaves and eventually involves younger leaves at progressively higher levels (113). Bakhuyzen (18) states that the primary cause of death of an annual plant which has flowered is the great loss of water at the time of flowering which reduces the general assimilatory rate of the plant (240).

It would appear, however, that there are a number of other factors which contribute to the ultimate decline of typical annuals, important among which are the radical changes in internal distribution of nutrients (70, 240, 265, 266, 267, 268, 275, 362), modifications in structure of vascular tissues (75, 76, 314, 333, 360, 386, 388, 434), and reduction in the rate of absorption by the root. The unfavorable water balance in the flower phase is temporary but of such magnitude as to be critical (19) as shown by the known sensitivity of plants to slight alterations in external water supply at this stage (64, 338, 372). Alternations in internal moisture, osmotic pressures, and distribution of nutrients are the most conspicuous metabolic phenomena associated with the shift from the vegetative to the reproductive state (332, 333), yet this does not necessarily imply that they are the primary causes of reproduction (270). Flower-forming substances such as florigen and probably carotinoids play a more direct role than nutrients in the initiation of this important developmental shift (53, 85, 117, 211, 212, 213, 215, 216, 248, 269, 271, 272, 277, 280, 335, 401, 408).

The early fruiting or post-fertilization phase is characterized by a temporary restoration of water and nutrient balance due to a renewal of anabolic processes. It has been suggested that the intensity of the anabolic impulse determines whether or not the plant can overcome and survive the heavy nutrient demands of developing fruits (278). In annuals, however, the renewal of absorption and synthesis is transitory, soon giving way in vegetative parts to a final reduction in water and nutrients which terminates in senescense and death.

3. MINERAL NUTRIENTS

In so far as the present review is primarily an attempt to outline the major shifts in nutrient balance during the normal growth cycle of common annuals, no attempt is made to discuss either the specific physiological role of individual nutrient ions or the pathology of mineral malnutrition. The bibliography of the vast literature on the effects of variable nutrition has been assembled by Niklas and Hock (286). Older works on mineral nutrition have been summarized in the classical monographs by Czapek (73), Honcamp (156), Kleberger (185), and Wolff (437). We have good current and critical reviews of this subject in the Annual Reviews of Biochemistry (125, 149, 354, 367, 375), in Fortschritte

der Botanik (312), and in other publications (41, 127, 135, 151, 236, 353, 361).

The mechanism of salt absorption has for many years been a subject of debate among physiologists. The earlier concept that transpiration played the major role in root absorption (109, 341) was vigorously challenged by results of numerous experiments in which no correlation could be found between the two processes (249). Hoagland and his associates have recently adduced evidence which reconciles many of the earlier apparent discrepancies The California workers present a convincing array of experimental data on the role of aerobic respiration of the root in the absorption of inorganic nutrients (152, 375, 376). They have been abundantly sustained by other workers in the thesis that salt absorption is directly dependent upon aerobic respiration of the root system (7, 8, 38, 46, 55, 59, 63, 144, 152, 164, 166, 223, 224, 225, 226, 285, 303, 312, 316, 379, 381, 385). These observations correlate well with the known benefits of soil aeration in plant growth (4, 7, 8, 57, 58, 68, 101, 186, 208, 209, 210, 249, 384, 419).

The experimental verification of the absorption of inorganic materials as a function of root respiration to a large degree improves our understanding of the plant's ability to accumulate inorganic ions against an internal concentration gradient, a process which obviously requires a sustained source of available energy. Particular significance attaches to experiments on salt absorption by excised roots and other tissues which are entirely free from the transpiration factor. Use of such materials not only permits excellent control of experimental conditions but also accurate measurement of respiratory and absorption rates. The close correlation between respiration and initial salt intake fully justifies the conclusion of a cause and effect relationship between the two processes (48, 373, 374, 377, 378, 382). Hoagland (150) points out that though initial salt absorption is not a function of transpiration, the latter process over a long period of time may be indirectly effective in so far as salts may be moved from root to shoot by the transpiration stream thereby presumably facilitating additional absorption. Neither does Hoagland overlook the role of transpiration in regulating the concentration and aeration of the soil solution in the immediate vicinity of the root system or rhizosphere.

The maintenance of aerobic respiration in the actively absorbing root is normally dependent upon a carbohydrate as well as upon

oxygen supply and it would be expected that any factor interfering with the flow of these materials to the root would tend to
diminish nutrient intake (70). There is now an appreciable amount
of evidence showing that fluctuations in rate of absorption by
roots during the course of plant development are ascribable to the
alterations in oxygen and carbohydrate supply. The root is dependent upon the shoot for its carbohydrates. When these are low
in roots there is not only a reduction in rate of absorption (70)
but also a relative decrease in rate of root growth, such as is often
found in plants under conditions of high nitrogen supply. During
rapid expansion of the shoot under normal conditions of growth,
it commonly appears to pre-ëmpt the major portion of the carbohydrates thus leaving the root with an inadequate supply. Fluctuations in top-root ratios at various stages of growth indicate
that these two portions of the plant do not develop commensurately. Slow root enlargement and absorption are coincident with a
preanthesis stage of low root carbohydrates (89). The carbon dioxide tension in the soil is known to rise as the result of root
respiration and there is evidence that this diminishes absorption
through changes in root permeability which involve resistance to
water movement from epidermis and cortex to the xylem (198).
Thus part of the beneficial effect of soil aeration is attributable
to removal of carbon dioxide (193, 218, 385) even though accumulation of this gas is less critical than shortage of soil oxygen
(285). Further Brewig (43, 44) reports certain significant effects
of the transpiring shoot upon root permeability. His data indicate
a diminution in root permeability with reduction in rate of transpiration. As a result, root permeability and water absorption tend
to vary directly with transpiration. He is of the opinion that the
roots of the intact plant are much more permeable than excised root
systems. Hoagland (150) also stresses the need for more information on the effects of metabolism and reproduction in the shoot on
the activity of root cells (33, 56, 140, 421). The work of Steward
(374) indicates the necessity of an oxygen supply for salt retention as well as for absorption (19). The fact that soil aeration
sometimes proves ineffective (177) or even injurious (208, 209)
indicates, however, that factors other than respiration may play
an important part in water and salt absorption (26, 104, 249,
384). Ulrich (400) has recently demonstrated an interesting case
of buffer action in the root by means of organic acid formation.
When roots absorbed cations in excess of anions carboxylic acid
increased but acids disappeared if anion absorption predominated.

Under favorable growing conditions subsequent to germination, the phase of rapid vegetative enlargement in typical annuals is characterized by progressive increments in absolute amounts of inorganic elements, carbohydrates and proteins. As the increase in organic synthates accelerates, the proportion of ash on a percentage basis begins to fall even though absolute amounts of the latter may continue to rise until well toward maturity (301). Plants often tend to absorb the major portion of their total mineral supply in very early life (21, 426) and early absorption is in general in excess of current needs when the external supply is favorable. In early vegetative stages under conditions of constant supply, nitrogen, potassium and phosphorus commonly increase faster than calcium, iron, magnesium and sulphur due in part to the relative immobility of the latter group of elements within the plant (11, 28, 54, 134, 222, 321, 328, 329). With increasing age, the percentage of calcium and nitrogen tends to fall somewhat more rapidly than other elements in typical annuals such as sunflower (329), barley (289), and wheat (42, 250). It is interesting to note that when nitrogen is available both as nitrate and ammonium salts the latter may be absorbed more rapidly in early development of small grains whereas the rate of nitrate intake may reach its peak at flowering (370).

Bakhuyzen (19) points out that fertilization with inorganic salts apparently does not raise the rate of photosynthesis per unit leaf area but that the beneficial effects of fertilization result from leaf area increase (98, 123, 196). The gain in potash, phosphorus, and sulphur evidently parallels protein formation on the one hand while on the other, calcium and magnesium increases are associated with photosynthesis and dry weight gain (19).

Differentiation and growth of floral structures apparently induce a systemic change in metabolism (6), evidenced in part as a reduction rate of water and salt absorption by the roots as already noted (38, 70, 125, 243, 312, 314, 329). Recent studies of respiration in relation to salt and water absorption suggest that lowered intake is attributable to impaired root respiration (59, 170, 303). Subsidence in the rate of root respiration is most commonly due to a progressive reduction of free oxygen and accumulation of carbon dioxide in the soil atmosphere (198, 296). Under such conditions, anaerobic respiration may be initiated but it is evidently not conducive to water or nutrient absorption (152, 224). Prolonged root anaerobiosis may in certain instances even

result in formation of cortical air spaces due to tissue necrosis (237). The factor of diminished permeability of root tissues also becomes important at the time of flowering (30, 43, 44, 15, 198, 222, 383).

The percentage drop in salt content usually noted in roots prior to and during early anthesis is not wholly ascribable to increase of organic materials but represents an actual diminution in rate of salt entry. Determinations of inorganic nutrients per unit dry weight rather than percentage salt content are necessary for the immediate detection of this change in root activity (121, 410). The root at this time lapses into a state of retarded absorption of both salts and water thus accentuating tissue dehydration throughout the plant (89). Several investigators have observed that salt intake up to the time of flowering is approximately commensurate with rate of supply but that it then begins to fall off (70, 86). As the fall in water content of roots and flowering tops becomes more pronounced, there occurs a marked redistribution of salts throughout the entire plant (387). Entire shoots commence to lose an appreciable proportion of their nutrient reserves to the roots (51, 82, 83) while at the same time salts also tend to accumulate at floral loci. At this stage of growth, roots appear to be active competitors of the flower buds for the labile nutrients of the shoot despite the relatively high respiratory intensity in floral tissues (25, 195). The flowering phase in some instances is marked by a transitory excretion of inorganic nutrients which can be resorbed during the phase of renewed growth subsequent to flowering (51).

The method of sectional sampling and sequential analysis at various stages of growth, in such a manner that a comprehensive balance sheet may be maintained at all times of net assimilative gains, discloses that with the onset of reverse translocation in the reproductive phase roots become the competitors of young fruits for the soluble reserves flowing outward from the leaves (51, 60, 67). Quantitative analysis, however, shows that the sum of specific elements accumulated in the fruits plus the residues thereof in the foilage usually does not balance out to the original total of the vegetative shoot (60, 83, 250). The discrepancy has, often without actual proof, been attributed to loss by leaching and accumulation in roots. In experiments including periodic root analyses, two major trends become evident; namely, actual translocation of organic and inorganic nutrients from the shoot to the root during repro-

duction, and the eventual excretion by the root into the substrate of appreciable quantities of potassium, nitrogen and sometimes of phosphorus (2, 87, 153, 159, 160, 161, 163, 172, 175, 233, 301, 430). Reserve translocation of electrolytes precedes that of organic reserves (83).

In the early stage of fruit formation immediately following fertilization, there is frequently a temporary restoration of moisture and nutrient balance due to rise in water and salt absorption by the root and renewal of organic syntheses in upper leaves. Reference has frequently been made in agronomic literature to the efficacy of fertilizer placement and soil aeration just preceding or during the flowering phase (14, 15, 24, 69, 77, 79, 80, 88, 91, 94, 99, 114, 118, 176, 178, 217, 279, 281, 293, 300, 328, 329, 336, 337, 346, 445). The favorable response to such treatment is evidently ascribable to the transitory improvement of absorption and synthesis shortly after fertilization. It appears, however, that the developing fruits appropriate the major portion of the new material because translocation continues to be oriented primarily to reproductive rather than to vegetative structures. Leaves obtain little if any of the additional nitrogen as shown by experiments in which nutrient distribution is accurately followed by determination of absolute amounts in various parts of the plant at this time (19). Fruits function as nutrient sinks to such a high degree that as they continue their growth, they absorb not only the current organic and inorganic food supply but rob vegetative parts of protoplasmic constituents beyond the limits of survival. Eventually reverse or downward translocation becomes evident as the aggregate concentration of inorganic nutrients of the entire shoot falls distinctly below that of the early fruiting phase (83, 84, 250, 410). Reverse or downward translocation of potassium, nitrogen and phosphorus from shoot to root with appreciable excretion to the soil during maturation phases has been reported in a great variety of plants (82, 86, 107, 187, 210, 213, 215, 216, 277, 410). Downward transport and root excretion of nutrients has already been reviewed elsewhere by the author (210).

The nutrient relationships of developing seeds and fruits though in some respects similar to vegetative parts are nevertheless different from those of vegetative organs. Fruit enlargement is characterized by an early, rapid intake of water and nitrogen which often subsides abruptly (11, 40, 95, 139, 189, 201, 203, 205, 219, 221, 231, 249, 274, 290, 446). Under conditions of favorable sup-

ply, the mineral components of dry fruits and of seeds in general appear to vary independently of the reserves available to them from vegetative parts (226, 267). Seeds are known to be high in nitrogen, phosphorus, magnesium and potassium (31, 244, 251, 440) but comparatively low in calcium and sulphur (11, 27, 222, 347), while fruits are relatively high in potassium, calcium and phosphorus (73) as compared with vegetative organs. Fruits evidently can serve as a local nitrogen source for developing seeds (60). Vegetative parts tend to be fairly high in organic sulphur and phosphorus. Seeds and fruits on the other hand are higher in inorganic phosphorus and sulphur (188, 264). Fertilizer placement during the reproductive phase tends to increase the nitrogen, phosphorus and potassium but not the calcium content of developing ovules (241, 407, 418). Despite obvious size increments, early stages of fruit and seed development are often accompanied by temporary loss in actual dry weight which may represent not only loss of carbohydrates as a result of respiration (247), but some actual excretion of mineral elements (161).

4. PROTEINS AND CARBOHYDRATES
A. Vegetative Stage

The initial vegetative phase of growth is distinctly anabolic with a high rate of organic syntheses and absorption of mineral nutrients (202, 250, 289). The actively growing plant is high in water and nitrogen with protein and protoplasmic syntheses as the dominant nutritional feature at this stage (42, 188, 274). If dry weight and nitrogen increments during early growth are plotted graphically, the nitrogen curve commonly rises more steeply than that for dry weight, reflecting an increase in percentage of nitrogen on a dry weight basis (19, 157, 206, 242, 329, 412, 413). Nitrogen increments precede dry weight gains during the phase of most rapid enlargement, a relationship which suggests the importance of nitrogen for the production of new tissues (19, 412, 413). The rapid rise in percentage nitrogen in early growth is a common phenomenon and it has been termed "Vorauseilen des Stickstoffes" by German workers (19). High nitrogen content is associated with high moisture content and succulence of tissues (19, 29, 89, 200, 257, 260). The percentage nitrogen drops with maturity of older leaves and the appearance of upper, younger xeromorphic foliage (19).

Reference has already been made to the existence of a rising gradient of percentage nitrogen in the progression from basal to

upper stems and leaves (10, 29, 105, 274), a statement which may at first seem in conflict with the well known increase in xeromorphy of the higher portions of the shoot. High nitrogen percentages of upper portions of the shoot are found when young tissues of this region are included in analyses. When comparisons are made only between fully developed basal and upper leaves, however, the latter have a lower moisture and nitrogen content per unit dry weight (19, 260, 362). We have here an instance of the necessity of comparing physiologically similar structures if erroneous inferences are to be avoided. These relationships explain the possibility of diminishing succulence of upper leaves despite the commonly observed rising gradient of nitrogen concentration in the progression from basal to upper stems and leaves.

During the vegetative phase of growth, there is an intimate connection between carbohydrates and protein synthesis. Not only are carbohydrates and nitrogen used in the synthesis of proteins, but a portion of the soluble monoses evidently provide the respiratory energy necessary for the chemical reduction of nitrates as an antecedent to protein formation. In fact in young plants, the supply of soluble sugars appears largely to condition the rate of protein synthesis (261, 262, 263, 362, 442). Obviously also the availability of oxygen is essential to the respiratory oxidation of a portion of the carbohydrates but is usually not a limiting factor in early growth as it is later. Mothes (261, 263) has shown that all conditions, such as light, photosynthesis, and open stomata, which tend to raise internal oxygen tension favor protein formation. Conversely, protein hydrolysis is accelerated by a low internal oxygen supply, and by low water content in later development as already mentioned in the preceding section on mineral nutrients.

Thus photosynthesis as a source both of carbohydrates and oxygen is closely bound up with nitrate reduction and protein synthesis. It may also be recalled that aerobic respiration in the root is essential to intake of nitrates and other inorganic ions. When the supply of carbohydrates in the root is low, nitrogen absorption and consequently protein formation in the plant are both retarded. During the later phases of active vegetative growth, the plant rapidly accumulates carbohydrate and appears to become relatively less efficient in protein than in carbohydrate elaboration (19) as shown by a rise in the carbon-nitrogen ratio (148). Due apparently to the great carbohydrate demand during expansion of

the shoot, a progressively smaller portion of the carbohydrate supply reaches the root in the course of vegetative development such that the root often, if not characteristically, reaches a critically low carbohydrate supply just prior to flowering (89, 215, 216, 399). Reduction in absorptive activity of the root occurs at this time as shown by a pronounced but transitory diminution of water and salt intake (89).

The conspicuous stages in the nutrition of the vegetative plant thus comprise an initial anabolic phase in which intake of inorganic nutrients and synthesis of proteins is rapid. In the second phase, the accumulation of carbohydrates is rapid while the rate of protein synthesis gradually subsides. As flowering is approached a third or catabolic phase becomes evident in which hydrolyses of reserves begin to overbalance syntheses, and a general internal redistribution of nutrients is initiated. Though conditions of environment and nutrient supply to a considerable degree determine the exact time of the shift from predominantly anabolic to catabolic activity, the transition is characteristically associated with flowering and it is commonly initiated prior to anthesis (89).

4(b)   The Flowering Stage

As previously stated, the onset of flowering is associated with a systemic change in water and mineral nutrient balance. An equally profound redistribution of organic synthates accompanies the change in inorganic nutrients at this time. Root carbohydrates, especially soluble sugars, evidently become low enough to impair salt and water absorption to such an extent that neither water nor nitrogen intake by roots appears to cover the requirements of the shoot (19, 61, 89, 187, 230, 294). Continued transpiration consequently entails progressive reduction in moisture content which in turn impairs gas exchange and initiates hydrolysis of organic reserves (260, 362). At this stage nearly three fourths of the total carbohydrate reserve of leaves may be in the soluble state which is about triple the sugar content of foliage in the vegetative phase (74, 367). Foliar respiration also falls despite the increase in soluble sugars. There is then a drop in general assimilative efficiency (19, 47, 89, 433) of the plant as a whole.

As hydrolysis of food reserves continues, leaves are gradually depleted of their organic and inorganic nutrients. These flow into the stem and accumulate in appreciable amounts at floral loci. Depletion of foliar nutrients, organic and inorganic, and reverse

translocation thereof during flowering are coincident with a general subsidence in the respiratory rate of vegetative organs (35, 65, 122, 439) especially of leaves which fall to a very low respiratory level during anthesis (362). The rate of nutrient depletion accelerates as respiratory activity falls, a correlation which suggests that respiratory energy is essential to nutrient retention (19). This concept correlates with the role already ascribed to respiration in the absorption of water and salts by roots as well as with the acceleration of absorption by soil aeration (55, 57, 58, 63, 165, 208, 209). Older leaves have lower rates of respiration and evidently are lower in oxidases (284, 362). They do not regain much protein nitrogen even under adequate supply (259). Due to loss of power to synthesize proteins, senescent leaves accumulate acid amides and ammonia (285, 362). Mothes (259), however, stresses the necessity of distinguishing between the respiratory responses of young and old leaves. He points out that respiration falls more rapidly in older leaves as drying progresses.

High respiratory losses of carbohydrates during flowering are often the cause of a reduction in rate of dry weight gain and depression of protein synthesis in the plant as a whole (19, 171, 368). Decline in the rate of respiration to a considerable degree results from the impaired gas exchange accompanying progressive reduction in water content of vegetative tissues during the reproductive phase (34, 247, 417). Floral structures, on the other hand, have a high respiratory rate, a condition which may underlie accumulation of water and solutes at reproductive loci during reverse translocation (25, 195, 414). Such functional transitions precede and later continue *pari passu* with the morphological development of flower and fruit. Floral loci also become centers of auxin formation. The presence of auxins apparently favors carbohydrate accumulation (5, 390, 424).

Reduction in rate of protein synthesis has a two-fold origin, namely reduction in free internal oxygen due to subsidence in the rate of photosynthesis and reduction in respiration due to impaired entry of atmospheric oxygen associated with progressive tissue dehydration. Mothes (263) has shown the dependence of protein synthesis upon internal oxygen tension, and a reduction in rate of synthesis commensurate with decline in photosynthesis. Smirnov's data (362), in turn, show a correlation between the rates of respiration and protein synthesis in sunflower and tobacco (90, 121, 125, 128). It is consequently probable that photosynthetic oxygen favors protein formation by acceleration of

aerobic oxidation of carbohydrates. Smirnov points out that in the early life of annuals, protein synthesis parallels and hence is presumably dependent upon the concentration of monose sugars. During reproduction, however, protein production ceases to be proportional to the soluble sugar content but instead parallels the foliar respiratory rate (327, 380). Thus in the vegetative phases carbohydrate supply is the controlling factor in protein synthesis while oxygen supply becomes regulatory in the reproductive phase. Smirnov adduces quantitative data in support of his contention that respiratory energy is essential to protein formation during reproduction. He points out that the common commercial practice of decapitating or "topping" tobacco plants to remove the inflorescence prevents the sharp drop in foliar rate of respiration and protein synthesis ordinarily encountered during flowering of intact plants. Exfloration and removal of fruits in tomato and cotton, like topping in tobacco, reinitiates nitrogen and water absorption (70, 266, 267, 359). There is considerable interaction among plant parts during this stage as shown by the fact that defoliation and exfloration materially alter the course of enzyme action (32, 305, 359, 362). Further evidence for the correctness of Smirnov's interpretations is found in the differences in the amounts of carboxylic acids which distinguish intact and decapitated plants. The former are high and the latter low in specific organic acids, a contrast reflecting differences in mode of respiration.

As diastatic action of starch is accelerated by incipient drying of the tissues, there is at first an accumulation of sucrose (362). As dehydration becomes more pronounced, starch hydrolysis yields increasing amounts of glucose. The starch-sucrose reaction is reversible, starch synthesis predominating when water balance is favorable but there is no reconversion of glucose to starch with moisture restoration (158). Schulze (348) reports formation of a protease activator in *Phaseolus* and *Nicotiana* at the time of flowering which is either inactivated or eliminated during the fruiting stage. Though a post-floral restoration of water balance occurs as a result of renewed carbohydrate and protein synthesis, neither they nor the moisture content rise to the pre-floral level. Other active enzymatic constituents of the flowering phase may undergo similar modifications and thus contribute to the temporarily improved water balance commonly observed in the early fruiting phase.

In addition to the foregoing functional factors influencing the water economy of the flowering shoot, there also occurs a complicating structural modification in the conductive elements (207, 241, 360, 427). The work of several investigators (183, 333, 434) reveals a subsidence in cambial activity which originates in vicinity of the floral buds and commonly extends progressively outward therefrom toward the base of the stem (318, 360). Phloem formation especially seems to be reduced and when this results in a small pedicel, fruit setting is impaired (64). This resultant impairment of conduction appears to retard the redistribution of nutrients during the period of reverse translocation. Poor mobility of calcium and inadequacy of movement thereof from leaves to reproductive loci, may also impair flower and fruit formation (222). Struckmeyer (386) finds that plants in flower, when restored to a vegetative photoperiod, recommence normal cambial activity and growth (434). Evidence of circulatory difficulties (75, 76) and inadequacy of nutrient supply in the flowering phase is found in the studies on drought sensitivity. Several investigators have found plants more susceptible to permanent injury from water shortage during flowering than at any other growth phase, a functional response which evidently results from vascular inadequacy or failure of the type reported in histological researches (338, 372).

In summary it may be stated that vegetative development is marked by rapid absorption of salts and water, rapid accumulation of carbohydrates and proteins. The respiratory and net assimilatory rates are high. During flowering, there is initiated a general trend toward reduction in water content (322, 323), respiration (362), photosynthesis (368) and rate of protein formation (260) in vegetative structures. There follows a profound hydrolysis of food reserves and a general redistribution of soluble, organic and inorganic nutrients (313, 351). At the expense of leaves and stems, foods accumulate in flower buds as their respiratory rate rises (25). Structural modifications of the stem and reduction in the absorptive activity of roots commonly leave the flowering shoot temporarily at a critically low water level. The plant is especially susceptible to drought injury at this time (338, 372), thereafter either failing to resume growth or undergoing permanent structural modification despite subsequent restoration of moisture. The systemic redistribution of nutrients and alterations in anabolic efficiency of the plant are sequential to disturbed water balance characterizing the flowering stage.

Certain nutritional changes involved in blossoming or anthesis of floral organs themselves are equally rapid but of a localized nature. Food reserves previously mobilized in the perianth and accessory floral structures are commonly translocated to the sex organs with surprising rapidity just prior to anthesis (66, 213, 214, 256, 310, 349). In terms of the floral tissues *per se,* the morphological and nutritional transformations of anthesis are very profound (291) but in terms of immediate metabolic effects on the plant these changes are local rather than systemic (66, 256, 291, 310). The nutritional aspects of typical floral gynoecia and androecia have already been discussed elsewhere (111, 168, 182, 211, 213, 214, 357, 420). Far-reaching systemic stimulation, however, results from the processes of fertilization and the ensuing grand period of fruit enlargement (278, 362).

4(c) Fruiting Phase

In a discussion of nutrition in relation to plant development, it is convenient to distinguish flower and fruit formation even though their separation may at first appear both artificial and arbitrary in light of the natural sequence of the processes (120). It may be argued that the phenomena of fruit formation are largely a progression of the processes initiated at flowering. Formatively, however, the pistil prior to pollination and fertilization usually lapses into a condition of relative stasis which commonly culminates in flower abscission in the absence of pollination. Pollination alone, however, often retards flower abscission and may stimulate rapid parthenocarpic growth of the ovary. To this the physiological stimulus of pollination is normally added that of fertilization of the ovules. Thereafter ovary and ovule enlargement is often extremely rapid due to food and water intake. The general resurgence of metabolic activity which occurs subsequent to sexual union is sufficiently profound to justify a distinction between the physiology of flowering and fruiting, particularly from the standpoint of nutrition (266, 267, 272, 362).

Fertilization of flowers serves as a systemic stimulus to renewed absorptive and anabolic activity (78, 96, 241, 278, 348, 362, 420). The root system undergoes enlargement and exhibits accelerated absorption of salts and water, frequently reabsorbing a portion if not all of the nitrogen and potassium previously excreted during flowering (51, 82, 86). After flowering, young leaves renew protein synthesis (258, 259). Transpiration subsides, respiration rises and there ensues temporarily a better water balance in all

tissues. From a nutritional standpoint, the early phases of fruiting somewhat resemble those of the vegetative phase (368). Though not yet fully understood, the initiation of the vegetative cycle in developing ovules may serve as a stimulus to renewal of such activity in adjacent tissues (348). The growing ovule itself exhibits a vegetative metabolism temporarily of a parasitic character and at the expense of reserves within the parent sporophytae (19). Restoration of moisture in tissue in early fruiting phases is associated with improved respiration and renewed synthesis of proteins and higher saccharides largely by condensation of soluble products (3, 9, 158, 160, 202, 255, 404).

Developing ovaries function as centers of nutrient deposition due apparently to their high respiratory metabolism. During the phase of their most rapid enlargement, young fruits preempt incoming inorganic nutrients largely to the exclusion of vegetative parts of the shoot. In fact, in heavily fruiting types such as the tomato and cotton, the current rate of supply through the root system appears inadequate, resulting in a heavy demand upon the nutrient reserves of the vegetative organs to sustain fruit growth. The depletion of leaves especially at the base of the shoot may attain starvation levels, resulting eventually in their death and abscission before fruits have achieved maturity (266, 267). Chibnall (60) has shown the failure of pod formation in the absence of asparagine. After the major increments in fruit size have occurred, carbohydrate influx is rapid (71, 72). Fruit respiration tends to fall as enlargement subsides, followed in fleshy fruits by the color changes of the fully ripe fruit (129, 352).

Pearsall (298) has shown that stem elongation may cease temporarily during flowering and again during fruit enlargement due to food demands of these structures. Absorptive activity of the root subsides even in a favorable substrate as the carbohydrate supply from the shoot diminishes in the course of fruit growth (70, 298). Subsequently growth of roots and apical meristems also ceases as reserves are preempted by fruits (70, 240). The ensuing moisture and protein shortages appear more critical than curtailment of electrolytes in causing the senescence and ultimate death of the plant. Luxury consumption of salts can tide the plant over longer periods of electrolyte than of water shortage. The unremitting continuance of transpiration precludes accumulation of any appreciable water reserves in annuals. When nutrient and water relations of biennials, perennials and succulents are compared with those of annuals, the survival capacity of the former

group during periods of enforced drought appears to depend pre-
dominantly upon superior regulation of water economy by avoid-
ance of that degree of desiccation which prevents resumption of
normal metabolism with renewal of water supply. Annuals are
unable to avail themselves of water even when available due to
absorptive failure of the roots after the nutrient demands of en-
larging fruits become persistent and exceed certain critical magni-
tudes. Leaves lose the power of direct protein synthesis and the
ability to reform proteins from proteolytic residues even in the
presence of carbohydrates (257). Loss of potassium has also been
stressed as a specific factor capable of inducing foliar senescense
(173). There ensues a sudden and final upturn in percentage dry
weight of shoot tissues which soon begin to manifest symptoms of
senescence as their moisture content falls to progressively lower
levels. The terminal stages of vegetative parts are characterized
by leaching of appreciable quantities of root electrolytes into the
substrate and extreme desiccation of the shoot despite some ab-
sorption of water from fruits prior to completion of the absciss
layer in the pedicles (240).

Desiccation of fruits entails increased resistance to gas exchange
with attendant alterations in respiration which shifts appreciably
from aerobic to anaerobic (247, 417) with production of volatile
hydrocarbons (40) in certain fleshy types. Tissue dehydration
and lowered respiration appear to underlie subsidence of nutrient
absorption of maturing fruits, an effect which is evidently also
accentuated by mechanical obstacles to translocation resulting
from cambial failure (386, 388). Pope (315) reports an ingenious
experiment in which he shows that if desiccation of the developing
barley kernel is prevented, no dormancy occurs and that it is
possible to obtain seedling transplants in fifteen to twenty days
after pollination.

One of the most outstanding contrasts between the maturation
of vegetative structures and seeds is the difference in response to
diminution of moisture. Loss of moisture in vegetative parts results
in hydrolysis of organic synthates while the same condition induces
condensation thereof in seeds (232, 285, 324) as shown by the
rapid conversion of amino acids to proteins (391) and of sugars
to starch. Young fruits and seeds are high in non-protein nitrogen
which is rapidly synthesized into proteins which accumulate in
the form of insoluble reserves. Proteolytic activity subsides dur-
ing maturation of seeds apparently due in part to increasing re-
sistance of the proteins to enzyme hydrolysis (317). It is appar-

ently the formation of hydrophilic polysaccharids and proteins with considerable bound water during maturation which protects seeds and fruits against an excessive water loss comparable to that sustained by leaves and stems and thus insures survival of the reproductive structures (352). Kidd (179) points out that arrested development of the maturing seed and even delayed germination of the moist seed are due to an inhibitory partial pressure of carbon dioxide in embryo tissues which induces a state of narcosis. Carbon dioxide narcosis of seeds depresses metabolism to a state of dormancy but without destructive injury such that when moisture and oxygen are restored, the developmental processes are renewed in germination (179).

5. SUMMARY

On a nutritional basis, the post-germinative developmental cycle of typical annuals may be conveniently subdivided into four different periods. The first comprises the high absorptive-high anabolic vegetative phase of rapid water and salt intake, rapid organic syntheses, maximal water content, and generally high respiratory level. Formatively this first phase represents the expansion or enlargement of vegetative primordia. The second or flowering phase represents an alteration in metabolism which entails structural differentiation. Functionally it is a period of lowered metabolism. Compared with the anabolic phase, respiration, absorption, water content, and organic syntheses are all lower in all vegetative parts. Reverse translocation of organic and inorganic syntheses takes place from leaves and stems to flowers, fruits and roots. Formatively, this phase comprises differentiation of flower primordia, enlargement of flower buds and anthesis. The third phase is one of temporarily renewed absorption and anabolism. Formatively it is the period of early fruit development. This merges gradually into the fourth or maturation phase in which seeds and fruits ripen while vegetative organs senesce and eventually die as a result of nutrient depletion and desiccation.

The initial systemic alteration in nutrition following the typically anabolic metabolism of early vegetative growth is correlated with a paucity of root carbohydrates and a resultant diminution in absorption. A cycle of progressive tissue dehydration and translocation of reserves ensues. Though developing seeds and fruits by virtue of their higher oxidation potentials form the chief centers of nutrient accumulation, roots seem to compete with them for an appreciable portion of the soluble reserves in the early fruiting

phase. The final senescence of stems and leaves is attributable to loss of water and food reserves following subsidence in respiratory activity of these structures. The food and water demand of fruits especially in heavily fruiting species exceeds the absorptive capacity of the root system which may also be largely drained of its reserves by nutrient excretion during maturation. The condition is one of inadequacy of food absorption and translocation in later stages of reproduction which is accentuated by failure of the cambium to continue production of new vascular elements. Assimilative powers of vegetative parts are lost as gas exchange is progressively impaired and oxidation potential reduced in the course of shoot dehydration.

The foregoing discussion represents an attempt to trace the major events in the nutritional ontogeny of typical herbaceous annuals but as stated in the introduction, it is not intended to convey the impression that these nutritional factors are the prime or causative agents in shaping the structural ontogeny of the plant. Under ordinary conditions of nutrition, light (138) and temperature prevailing during early growth have much to do with the number of vegetative primordia laid down and hence also with the number of leaves and nodes eventually formed by the plant (124, 371). Nutrients available during this vegetative (or vernalization phase (273) as the nomenclature of the phasic development concept designates this temperature-sensitive stage) do, however, determine the size of the vegetative organs developed under stimulus of temperature (336).

With reference to flowering, it may similarly be said that the photoperiod in conjunction with temperature rather than food determines the date and number of flower primordia (1, 53, 248). In this case also, however, the available nutrients may determine the course of growth and maturation of the reproductive organs (23, 24, 42, 155, 282, 308). In fact, on the basis of recent experiments it seems that photoperiodic induction itself may not occur in the absence of a source of carbondioxide for photosynthesis during the induction period (297). Food eventually determines the number of flowers which develop as well as the number and size of fruits which are set and mature. Considerations of the latter sort underlie the practice of repeated or late fertilizer placement since it is known that readily assimilable phosphorus and nitrogen, for example, applied in the early flowering phase may increase the number of fertile flowers and the yield of fruit. Went (423) reports the need for low night temperatures as an essential factor

in setting of tomato fruits (32). Mineral deficiencies during growth may, of course, impede or prevent differentiation or development of structural primordia even under proper stimulus of temperature and photoperiod (162, 396). Inadequate nitrogen in early growth, for instance, results in smaller plants and fewer if any flowers as compared with ample nitrogen supply. Under such conditions of malnutrition the plant is incapable of normal response to light and temperature.

The primary internal response of the plant to the known morphogenic factors of the environment is probably in the production of specific growth substances and these may consequently be considered the factors which determine the developmental or qualitative phases of its ontogeny. Certain highly localized redox systems also play a part in structural differentiation (403). The quantitative expression of these phases, on the other hand, is a function of the food supply. Stated in another way, the developmental potentialities of the plant are implemented by its organic and inorganic nutrients. Under conditions of nutrient deficiency the plant may not be capable of the normal developmental response to morphogenic factors of the environment, or if it is, it may yet be incapable of causing the growth of primordia which have been differentiated. In the light of recent evidence (12, 246, 275), it appears as if nutrients must give way to growth substances or hormones as the basic factors in *development* and differentiation though they retain their primary position as factors underlying *growth* in the sense of elongation and increase in size.

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108   IOWA ACADEMY OF SCIENCE   [Vol. 49

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