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Mineral Nutrients in Relation to Flower Development: PROFESSOR W. F. LOEHWING 517
Petroleum and National Defense: DR. GUSTAV EGLOFF 520
Scientific Events:
University College, London; Damage to Scientific Institutions in London; Emergency Courses to Train Engineers and Technicians; The Hospital of the Medical College of Virginia; The Meeting of Mathematicians at Baton Rouge; Award of the Medals of the American Society of Mechanical Engineers 522
Scientific Notes and News 525
Discussion:
Dental Research at the National Bureau of Standards: DR. GEO. C. PAFFENBARGER. *Control of Prickly Pear in Australia:* DR. FRANCIS RAMALEY. *The Dens and Behavior of the Desert Tortoise:* PROFESSOR A. M. WOODBURY and ROSS HARDY. *Electric Fences that Repel Deer:* J. G. BURR. *J. Peter Lesley and Joseph Lesley:* DR. LAWRENCE WHITCOMB 527
Quotations:
The British Scientific Advisory Committee. The Future of Polish Science 530
Scientific Books:
Recent Publications of the British Museum (Natural History): PROFESSOR T. D. A. COCKERELL. *Aquatic Plants:* PROFESSOR ROBERT B. WYLIE 531
Reports:
The Cotton Root-rot Tour and Conference of 1940: DR. WALTER N. EZEKIEL 533
Special Articles:
A Quantitative, Absolute Method for the Estimation of Complement (Alexin): PROFESSOR MICHAEL HEIDELBERGER. *Arthritis of Mice:* DR. ALBERT B. SABIN and DR. JOEL WARREN. *Phosphate Acceptors in "Respiratory Phosphorylation" in Muscle Tissue:* DR. W. A. BELITZER and K. S. GOLOVSKAYA 534
Scientific Apparatus and Laboratory Methods:
A Simple Method for Recording Electrocorticograms in Animals without Opening the Skull: PROFESSOR HUDSON HOAGLAND. *An Inexpensive Mouse Cage:* PROFESSOR E. WILBUR COOK, JR. 537
Science News 10

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MINERAL NUTRIENTS IN RELATION TO FLOWER DEVELOPMENT[1]

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FOR several years, the writer and his associates have investigated the role of mineral nutrients in relation to reproduction and sex expression in higher plants. From these and numerous other investigations, it is evident that the most profound metabolic and structural changes of the plant's entire life originate in the brief period between the origin of floral primordia and full bloom (Loehwing, 1938–39). Hence a detailed study, correlating chemical composition with histological structure in this particular phase of development, appeared to offer exceptional promise of valuable results, not only as to the functions of mineral nutrients in flowering but also as to their specific role in general developmental physiology.

Though interest in these investigations has centered primarily in the physiology of flowering, physiological studies obviously could not be confined to this phase alone. Only a continuous and detailed chronological inventory of the progress of events in root and shoot, from the vegetative, flowering and fruiting phase provides the requisite interpretative data. Because the most significant changes of the flowering phase are highly localized (Borthwick and Parker, 1939) the usual mass analyses of entire tops have to be supplemented with separate, sequential physico-chemical study of all formatively active zones of growth. For interpretative purposes, these data must be expressed in absolute amounts of the individual constituents as well as in the traditional terms of percentage composition. Determination of salts by actual weight is essential because of the fact that the relatively greater rate of carbohydrate and protein accumulation in plants tends to mask the critical changes in actual amounts of mineral matter. A progressively diminish-

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[1] Address of the retiring president of the American Society of Plant Physiologists, Columbus, Ohio, December 28, 1939.

ing percentage of salt constituents may, for example, represent an actual gain in total amounts thereof. The divergence between percentage and absolute weight of salts is, in fact, the usual case in the growing plant. Salt content actually rises in the vegetative plant but appears in the data as a progressively lower percentage of the entire dry weight. During the reproductive phase, on the other hand, diminishing percentages of salts may frequently reflect reduction in total amounts, as becomes apparent from data discussed herein. Omission of such actual weights from many otherwise thorough studies in the literature of mineral nutrition has greatly diminished their interpretative value.

With reference to the analysis of small amounts of tissue, it may be pointed out that earlier handicaps in this connection have, in considerable measure, been removed by recent perfection of micro-analytical and histo-chemical procedures. These micro-methods not only permit analysis of the minute amounts of meristematic and floral tissues available to the physiologist but also greatly expedite analysis generally. Micro-analyses of localized areas facilitate correlation of such data with histological sections prepared from the same tissues. As a final technical detail, pot cultures of known weight in coarse sand or silica gravel permit a continuous check on growth and transpiration, and also facilitate recovery of the root system.

During the course of the experiments in a controlled greenhouse environment, certain major trends soon become evident in hemp, beans and other herbaceous annuals studied. Rapid intake of potassium and phosphorus characterizes the period of seedling growth, but are overtaken by nitrogen absorption prior to initiation of floral primordia (Demidenko and Popov, 1937). Under conditions of adequate nutrient supply, the first obvious indication of flower inception is a rather abrupt and progressive increase in the rate of transpiration, readily detectable by the amount of water necessary to maintain the cultures at approximately constant weight. Despite the transitory rise in rate of absorption, tissue analyses at this stage show that plants actually undergo a change in water balance in the direction of lower water content and higher percentage dry weight. Water loss definitely exceeds rate of supply and a trend toward progressive dryness of tops is initiated (Bakhuyzen, 1937; Gouwentak, 1929; Mothes, 1931; Smirnov, 1928). The trend toward tissue dehydration, once started, is ordinarily continuous for several weeks and sometimes even to ultimate maturity. It is interesting to note that this increase in transpiration and change in water balance frequently precedes the appearance of visible floral structures.

Reduction in water supply entails a proportional change in solute concentration of all tissue fluids (Bakhuyzen, 1937). A rise in osmotic pressure of press sap is readily demonstrable but owes its origin not only to increased concentration of mineral nutrients but also to a rather sharp rise of soluble nitrogen and carbohydrates in the sap. The change in water balance thus appears to induce hydrolysis of insoluble protein and polysaccharide reserves, a metabolic transition generally known to presage early structural modification. Rise in rate of transpiration and the subsequent hydrolysis of insoluble carbohydrates originates in restricted areas of which the shoot apices are the initial foci. Increase in tissue dry weight spreads from these apical regions to adjacent leaves. Rapidly transpiring leaves thus deplete the water supply of contiguous tissues of lower osmotic pressure. Normal translocation upward is deflected from apical zones, and salts commence to accumulate in axillary loci. Dehydration is progressive in leaves and stem until entire shoots are involved.

In the roots, the change is not immediately one of altered water balance but rather a reduction in rate of salt intake, as becomes evident from successive determinations of the total mineral matter (Potapov, 1938). The percentage drop in salt content usually noted in roots at this stage is not wholly ascribable to the rapid increase of organic materials but represents in part an actual diminution in rate of salt entry. Determinations of actual salt content rather than its percentages are extremely helpful in the immediate detection of this change in root activity. Eventually, as flowering approaches its ascendency, the water content of the root system also becomes depleted and it then parallels the progressive drying of the shoots. The root at this time lapses into a state of retarded absorption of both salts and water which tends to accentuate tissue dehydration generally throughout the plant. Other investigators have also previously 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 (Crowthers, 1934; Deleano, 1936).

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. Entire shoots commence to lose an appreciable proportion of their nutrient reserves (Burd, 1919; Deleano, 1936) while at the same time residual salts tend to accumulate at floral loci. Nutrient depletion of vegetative organs and later even of accessory floral parts leads to an ultimate concentration of salts in developing stamens and pistils (Combes, 1938). Relative proportions of the different ions in the stem as a whole are also materially altered. Nitrogen and phosphorus accumulate at reproductive centers in part at the expense of shoot apices.

It is interesting to note that the number of floral primordia initiated is usually correlated with the amount of nitrogen and phosphorus in adjacent tissues (Biddulph, 1935; Cameron and Appleman, 1934; Grainger, 1938; Haas, 1935; Polster, 1938). Localized nutrient reserves thus appear especially important in early phases of flower development. In short, at the time of flowering all the nutrients, organic and inorganic, are in a state of extreme flux, which appears to be a mobilization of food reserves preparatory to the later utilization of certain compounds at reproductive centers. Similar responses with reference to concentration of organic reserves in developing fruits have been reported by other investigators (Murneek, 1932–37; Kraus and Kraybill, 1918) but actual mobilization seems to commence well in advance of fruiting proper (Bakhuyzen, 1937).

To judge from the universality and profundity of other changes which promptly follow, the original shift in internal water balance is by far the most significant event in the entire nutritional picture. Uniformity and magnitude of the drop in water content make it a reliable index to the onset of flowering. Shift in water balance, indeed, appears to resemble a trigger action which unleashes extensive subsequent changes in metabolism of roots as well as shoots.

The increase in osmotic pressure of tissue fluids in the tops gradually extends to the roots and is attributable in part to the translocation there of salts from the tops as reproduction progresses. Though there is a rise in *percentage* of salts in the root and a rise of salt concentration in root sap, the *absolute amount* of inorganic ions is usually less on a true weight basis. These facts lead, then, to the obvious conclusion that the salt content of the entire plant is often less during the reproductive than during the previous vegetative stage. This implies excretion of nutrients from root to soil (Ackromeiko, 1932–36; Bakhuyzen, 1937; Burd, 1919; Loehwing, 1937; E. C. Miller, 1939). The phenomenon of nutrient excretion is especially evident in plants grown at high nutrient levels (Luttkus and Boetticher, 1939). But even in plants under conditions of inadequate feeding there is also evidence of similar accumulation of salts in the roots at the expense of tops. The element particularly involved in excretion is potassium with lesser amounts of nitrogen and phosphorus (Deleano, 1936; Ackromeiko, 1936). The speed and apparent ease with which potassium moves from tops of high to roots of lower osmotic pressure during the period of disturbed water balance, suggests a poising function of potassium in avoidance of injurious extremes of both osmotic pressure and nutrient disbalance among the mineral salts in the aggregate.

The metabolic readjustment to this increase in solute concentration of tissue fluids is extremely far-reaching. For example, plants at this stage are very conspicuously sensitive to drought, a fact noted by other workers in a wide variety of plants (Saskin, 1938; Bakhuyzen, 1937; Stevanovskii, 1936; Maximov, 1929). Drought sensitivity during flowering is presumably interpretable as a definite increase in foliar permeability. If behavior of this sort is demonstrable in experimental plants under conditions of uniform water supply, the effects of water disbalance at the flowering stage must be even more pronounced in crops under the natural field conditions of water scarcity during midsummer. The entire literature on mineral nutrition is replete with evidence of water shortage during the flowering phase of crop plants, and it is difficult indeed to understand that its physiological significance has not been generally recognized.

The functional as apart from the formative aspects of flowering, then, seem to involve the following sequence of events, namely, increased transpiration and its resultant upset of internal water balance in the shoot; osmotic and solute increments of the sap; and finally redistribution of nutrient elements throughout the entire plant, often involving some elimination of salts from the root.

With reference to mineral nutrients, the net effect of these changes during flowering would be to make the shoot, temporarily at least, largely dependent upon its own residual supply of salts rather than upon any rapid upward flow thereof from the roots (Crowthers, 1934). The assumption of what amounts to a partial, functional separation of root and shoot derives support not only from the above described changes in nutrient distribution and drought sensitivity but also from the vascular alterations known to be associated with flowering. The important researches of Roberts (1939) and associates (Struckmeyer, 1938; Wilton, 1936) on reduction in cambial activity and the resultant restriction in phloem clearly indicate that the flowering plant confronts serious problems in translocation (Gill, 1933; Liehr, 1927; Whyte, 1929). Wisconsin investigators (Roberts, 1939) report that locally applied low temperatures in the form of a girdle about the stem also act as an effective means of flower production, an observation which adduces additional evidence that reproduction is correlated with modified translocation. Similar reproductive responses have been induced by general low temperature treatment (Thompson, 1936–38) and by constrictions about stems (Roberts, 1939). Further corroboration of the conclusion that impaired conduction disposes to flowering is found in the recent painstaking work of Borman (1939) on the rooting of flowering cuttings. He finds, for instance, that cuttings of *Mirabilis viridis* taken in full bloom continue to flower until they take root, after which they initiate vegetative growth. Some of Borman's other data on rooting of cuttings also suggest a connection between flowering and restricted transport of nutrients.

Any stimulus which renews vascular development, rapid absorption and mass flow of nutrients re-initiates vegetative growth. This is shown in experiments on rejuvenation by reversal of the photoperiod. Plants in blossom can usually be induced to renew growth by shifting to a vegetative photoperiod. Within two days after such alteration in the light period, there occurs a drop in transpiration, followed by increased intake of water and vegetative proliferation at stem apices.

Mobilization of organic and inorganic feed reserves in the manner described has previously been associated by other investigators (Murneek, 1925–37) with the process of fruit development. In the speaker's opinion, there is no actual discrepancy in the two points of view, nor is there any doubt about the intense food demands of enlarging fruits in heavily fruited species. Our own data merely indicate that mobilization of reserves *begins* with flower formation rather than with fruiting. This is apparently preparation for the immediate and large respiratory demands of flowering itself as well as for the heavier nutrient demands of fruit enlargement. High rates of respiration during the flowering phase temporarily deplete carbohydrate reserves, yet this very fact makes the concentration of salts at floral loci especially noticeable. On the experimental side, it is easy to miss nutrient changes which originate during flower inception because this phase is brief and soon overshadowed by events of the fruiting phase.

It is interesting to observe that as fruiting attains ascendency, there again occurs a gradual rise in rate of water absorption and the entire picture of water relations is one of better balance. Transpiration gradually subsides with onset of fruiting but ordinarily does not fall to the vegetative level. Simultaneous with the improved water balance of the fruiting phase, the flow of inorganic nutrients from root to top is accelerated. From the nutrient standpoint, conditions in the fruiting plant somewhat resemble those of the original vegetative phase except that fruits instead of vegetative structures now serve as centers of deposition. Fruit development may, in fact, be the actual inception of vegetative nutrition by the young embryos which merely employ the old sporophyte instead of the soil as a substrate.

There still remains, of course, the problem of nutrients in relation to sexual differentiation; namely, as to the factors responsible for differentiation of pistils and stamens. In this connection mineral nutrients are probably less specific in their influence than certain morphogenic inductors, like the so-called flowering hormones (Cailachian, 1937; Kiesel and Pachewitsch, 1938; Riede, 1937; Savelli, 1937) which may be a carotinoid (Murneek, 1934). But certain inorganic ions are not without effect even in this connection, as evidenced from our data on sex differentiation in dioecious forms. High nitrogen supply results in a pure stand of pistillate hemp plants, while low nitrogen produces entirely staminate plants (Tibeau, 1936). The results are not attributable to selective mortality.

Physiological studies on sex expression in hermaphroditic species are more difficult than in dioecious forms because of the close proximity of the two sex organs. This complicates disentanglement of the staminate and pistillate processes which precede the actual appearance of the sex parts themselves. Combes (1936) has recently shown that accessory floral parts supply mineral nutrients first to the developing stamen and later to the pistil (Mason and Phillis, 1936). High nitrogen content is in general associated with pistil differentiation in both dioecious and monoecious species (Howlett, 1936; Loehwing, 1933; Tibeau, 1936) while low soluble ash favors stamen inception (Stanfield, 1937).

In summary, the sequence of physiological events antecedent to and concurrent with flowering comprises, first, the change in internal water balance, followed in turn by altered translocation and redistribution of nutrients. Precise knowledge of the pattern of salt distribution aids in identification of phosphorus and nitrogen as the inorganic ions most closely associated with early phases of the transition from the vegetative to the reproductive phase. Amino compounds seem to be especially specific in their effects on sex processes, and studies are now under way to identify them and determine the precise role of commonly occurring amino acids.

PETROLEUM AND NATIONAL DEFENSE[1]

By Dr. GUSTAV EGLOFF

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THE United States has the largest and most efficient army of fully trained petroleum hydrocarbons of any nation in the world or any combination of nations, available for immediate service to meet any need, either peacetime or in the national defense.

With 61 per cent. of the world's total oil production occurring within this country, American technology has developed the world's most effective and, in

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[1] Address delivered at Purdue University, October 31, 1940.