

analysis which were used have been described previously (8).

The electrophoretic diagrams obtained from the anther extracts (Fig. 1) are complex and different for the four bud lengths. Four electrophoretically distinguishable components characterize the extracts, although only three components are detectable in any single-bud-length sample. The differences in the total area displacement of the electrophoretic patterns are relative to the concentration of protein in the samples. As shown in Fig. 2 (upper curve), there is a protein increase prior to mitosis, a decrease through and following mitosis, and a final value of only about one-fourth of the maximum.

Estimations of the actual amounts of protein represented by the individual electrophoretic components are shown in Fig. 2 (lower curve). Of the individual electrophoretic components, the fastest-moving one, *D*, shows the most spectacular change. This non-Gaussian component increases in amount during the premitotic period but is undetectable during mitosis and thereafter. Components *B* and *C* are present in greatest amount at mitosis despite a decrease in the total soluble protein at this time. Component *C* appears to be absent before mitosis, although it may merely be obscured by the large amount of component *D*. Component *B*, however, can be detected in all of the extracts. Component *A*, which is also present in all of the extracts, is unique in that it shows no conspicuous quantitative change.

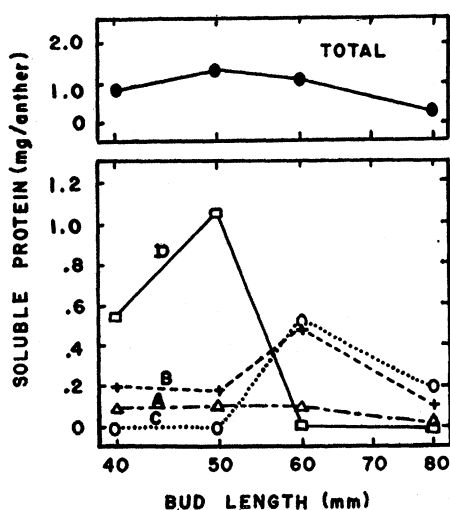


Fig. 2. Changes in the soluble proteins of *Lilium* anthers with increasing flower bud length. (Top) Total values obtained by Folin determination. (Bottom) Values for electrophoretic components based on proportion of the total pattern area represented by individual components. Average electrophoretic mobility (all values $\times 10^{-5}$ cm²v⁻¹sec⁻¹): component *A*, -2.5; *B*, -3.5; *C*, -4.8; and *D*, -6.1.

One may be tempted to speculate that component *D* may in some way be associated with chromosome duplication, since it occurs at very nearly the same bud length at which Foster and Stern (1, 2) have described large concentrations of soluble deoxynucleosides. One may further speculate that component *B* or component *C*, or both, which are in highest amount in buds of 60-mm length, may correspond to the spindle protein described by Mazia (9). These speculations are hazardous, however, in the absence of any characterization of the components beyond their electrophoretic mobilities. These preliminary studies are being followed by attempts to separate the components by means of cellulose ion-exchange columns. Such separation would make it possible to purify them for further chemical and physical characterization (10).

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21 June 1960

Boron and Sugar Translocation in Plants

An article entitled "Translocation of particles within plants" by J. W. Mitchell, I. R. Schneider, and H. G. Gauch (1) reviewed and discussed an important subject in plant physiology, and the citation of 71 references would suggest that the authors intended to present a critical review of the latest information on the subjects covered. One familiar with the literature on boron,

however, is struck by their omission of any reference to published data not in accord with the hypothesis they presented for the role of boron in sugar translocation.

Their discussion of this subject was limited to and centered about a hypothesis initially presented 7 years ago (2-5) suggesting that a major function of boron was in the translocation of sugar. They postulated (2, 3) that the sugar-borate complex may move from cell to cell or that boron as a constituent of the membrane forms a temporary union with sugar at these sites to effect its passage. They further considered boron-deficiency symptoms such as necrosis of apical buds and root tips to be in reality manifestations of sugar deficiency, in that lack of boron prevents the movement of required sugar to these loci of active growth.

Numerous investigators (6-12) have questioned this view, and most of the published evidence has not substantiated the hypothesis of Gauch and Dugger (2). Boron-deficient stem apices and root tips, for example, are not sugar-deficient (6, 7), nor do sugar applications to terminal regions alleviate boron deficiency symptoms (5, 6, 9, 10, 13). Skok (11) has critically reviewed this subject and has shown (10) that boron may have an apparent but entirely indirect effect on sugar translocation. His experiments suggest that the boron effect is related to cellular activity and growth rather than directly to the formation of a boron-sugar complex. Materials, including sugar, move from leaves to such metabolically active regions as growing tips (12). When growth is decreased by lack of boron, movement of sugar to these areas is decreased and the addition of boron might be expected to raise the metabolic rate toward the normal, which in turn results in an increased movement of sugar into these regions. This indirect relationship was demonstrated by measuring the movement of C¹⁴-labeled sugar applied to the lower leaves of normal boron-sufficient plants, boron-deficient plants, and normal boron-sufficient plants with their terminal buds excised. The removal of the bud, the actively growing region, reduced the translocation of the applied sugar into the apical part of such plants to 57 percent of that observed in boron-sufficient plants; this was even a greater reduction than that observed in the boron-deficient plants.

I have obtained similar evidence substantiating an indirect relationship between boron and sugar translocation in experiments in which the translocation of C¹⁴-labeled sucrose was studied in boron-deficient sunflower plants with and without H₃BO₃ added directly to

the terminal bud (14). A significantly greater amount of sucrose was translocated to the terminal portions of plants to which boron had been applied to the terminal buds; in most experiments, however, no difference was found between the two series in the sugar translocated to the roots.

It is certain that many and perhaps most of the details regarding the exact role(s) of boron in plant growth are yet to be uncovered. The final accepted role(s) for this element can only be assigned when all reported data become integrated. Investigators who ignore data only defeat this accomplishment and do an injustice to the general reader not specifically involved or interested in this research area but only desirous of remaining abreast of the subject.

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With regard to the criticisms of our recent article entitled "Translocation of particles within plants," we feel that McIlrath may have misunderstood the intent of the article. As we understand it, this series of articles was designed to give the nonspecialist in the field a general presentation of various subjects, together with some typical problems involved. Limitations in space and in the number of citations dictate that the many subjects which are touched on shall be handled without a presentation and discussion of all ideas on the subject and without reference to all the literature which impinges on the topic. We reject the assumption that the 71 references would indicate that we were covering the subject exhaustively, since admittedly hundreds of papers would have been pertinent to so broad a topic as this one which ranged from ions through macromolecules.

With regard to our failing to discuss the various roles of boron, and particularly the evidence which has been interpreted as not supporting the Gauch-Dugger hypothesis, we felt that such a discussion would have been irrelevant to the theme of our article. Each of the three sections (ions, molecules, and macromolecules) was illustrated with a typical piece of research; we chose examples from our own researches about which we were naturally best informed and for which we had illustrative material. For that reason we cited neither the many researches which support the boron concept nor those which did not.

Although a discussion of the pros and cons of the Gauch-Dugger concept would have been irrelevant, the question of evidence against that concept has been raised by McIlrath and thus deserves comment. The junior author (Gauch) assumes responsibility for evaluating this question and does not accept the evidence against the Gauch-Dugger hypothesis presented by McIlrath and his co-workers and that of certain of the papers cited by McIlrath. He recognizes this difference of opinion as honest and healthy for science. Unfortunately it is impossible to present in this space his objections to McIlrath's experimental procedures and to the use of boron-sufficient plants showing boron-toxicity symptoms [W. J. McIlrath and B. F. Palser, *Botan. Gaz.* **118**, 49 (1956); B. F. Palser and W. J. McIlrath, *Botan. Gaz.* **118**, 53 (1956)] as the controls by which the performance of boron-deficient plants was evaluated and the validity of the Gauch-Dugger concept was questioned. Lastly, for the sake of the record and for the nonspecialist, it should be added that there are recent papers which support the Gauch-Dugger hypothesis.

We regret that the intent of the article and our handling of it caused misunderstanding. We trust that we have hereby clarified our intent and that we have explained why we handled this admittedly broad topic the way we did.

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