

duration, and order of succession of responses could be obtained from the records.

Increased deprivation time results in a greater number of completed feeding responses, a shortened duration of feeding responses, and a decrease in the ratio of initiated to completed feeding responses (Table 1, A, B). But neither the number of initiations nor the total time spent feeding is reliably increased by deprivation.

These effects on feeding behavior are reversed in the course of the feeding session, as the fish become satiated: the frequency of completions decreases, response duration becomes longer, and there are more initiations per completion. The time spent feeding and the frequency of initiations increase at the beginning of the feeding session, remain at high values, and then fall off slightly at the end of the hour.

Hunger shows its effects on the predominance of completions over initiations, not on the predominance of feeding behavior over nonfeeding behavior.

In the conflict sessions (Table 1, C), the total time spent feeding is below normal values, and more markedly so for increasing shock intensities. But the ratio of initiations to completions is lower than normal, and the duration of feeding responses is below normal. These latter two effects are not changed by increasing shock intensities.

Nonfeeding behavior has become more predominant in the conflict sessions, but when feeding behavior is shown it is like that of very hungry fish (6). As a result, over half the fish performed more completed feeding responses than normally under conditions of low shock, with some fish scoring as much as 40 percent over normal values.

As the feeding session progresses, the usual satiation changes occur and deviations from normal feeding scores are less marked. For example, the initiated to completed response ratio is below normal throughout the session, but reliably below normal only for the session as a whole or for the first 15 minutes of the session (4).

The effects of thwarting (Table 1, D) resemble those of conflict in that the fish may perform more or fewer completed feeding responses than normally. But now total time spent feeding and the frequency of initiations have increased, whereas the initiation to completion ratio is higher than normal.

It is noteworthy that the usual differences in feeding behavior for the three deprivation conditions have disappeared in the tests that follow thwarting.

The effects of thwarting and of conflict must be specified in terms of meas-

ures that indicate the predominance of the observed pattern of behavior over its alternatives and the predominance of high and low intensity forms of the behavior pattern. A model linking these two aspects of motivated behavior has been described (7, 8).

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6. The conflict study shows how cessation of feeding occurs. In the course of normal feeding sessions, only increases in time spent feeding were reliable. Though interruptions of feeding involving returns to the living area are few at the end of the session, these are of a reliably longer duration and extend further away from the food area. In the stickleback's normal environment this should increase the likelihood of exposure to stimuli that evoke behavior incompatible with feeding and thus end feeding activities.
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8. The experiments on which this report is based were performed at the Oxford University Department of Zoology. Grateful acknowledgment is made to Dr. N. Tinbergen for his encouragement and helpful criticisms. The research was carried out while I was in receipt of a Miss Abbott's School Alumnae Fellowship, offered by Brown University, and of an intermediate and terminal predoctoral grant, awarded by the National Science Foundation.

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Changes in Soluble Proteins of Developing Lily Anther

Abstract. The extract of soluble proteins from *Lilium* anthers is characterized by four electrophoretic components. Three of the components show quantitative differences markedly correlated with the synchronized division of the microspores contained within the anthers. One of the components increases in amount before mitosis and disappears at mitosis; two of the components have peak values at the time of mitosis and decrease thereafter; a fourth component remains relatively constant in amount throughout.

In recent years it has become increasingly apparent that many of the major steps of chromosome synthesis take place before the visible events of mitosis. In particular, one may cite the synthesis of deoxyribonucleic acid (1-4) and of nuclear histones (3, 5). The anthers of *Lilium* are favorable material for investigating relationships of this sort since mitosis of the microspores within the anthers is highly synchronized and precisely correlated with the length of the developing flower bud (6). Foster and Stern (1), for instance, have shown striking changes in the quantity

of soluble deoxyribosides in the anthers, which are correlated with bud length and hence with the mitotic process. The work reported here is a preliminary study by analytical electrophoresis to determine the behavior of the phosphate buffer-soluble fraction of anthers prior to and during mitosis.

Anthers were collected from flower buds of *Lilium longiflorum* cv. 'Croft' of specified lengths and placed in a freezer until samples of sufficient size were obtained. The bud lengths studied were 40 and 50 mm (before mitosis), 60 mm (during mitosis), and 80 mm (after mitosis). A single sample consisted of the anthers from 10 to 15 buds which were within 1.0 mm of the desired length. Each sample was extracted, with the aid of glass homogenizers, in the cold, in a 0.1 ionic-strength phosphate buffer of pH 7.0 (7). Extracts were centrifuged at about 4000g for 0.5 hour, and the supernatants were dialyzed for 18 hours against three changes of buffer. After ultraviolet estimation of the protein concentration, the dark-colored extracts were diluted with buffer to approximately 12 mg/ml to facilitate electrophoretic analysis, and aliquots of these diluted samples were analyzed for protein concentration by the Folin method. The instrument for electrophoresis and the methods of

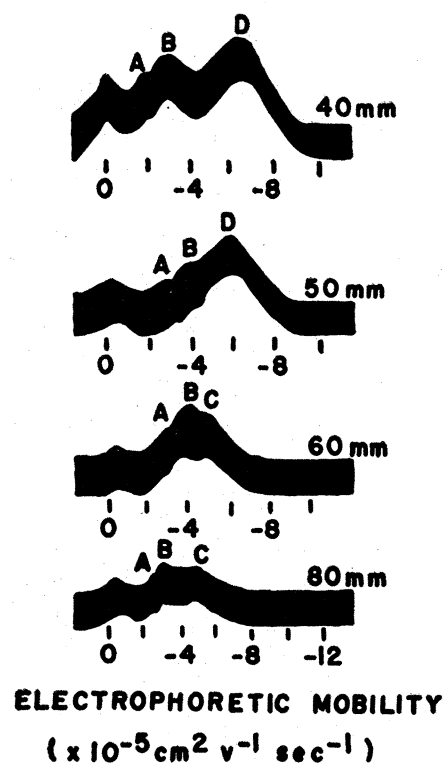


Fig. 1. Descending electrophoresis patterns, at pH 7.0, of phosphate buffer-soluble proteins extracted from *Lilium* anthers. Potential gradients were 6.9, 6.8, 7.0, and 6.7 v/cm for the 40-, 50-, 60-, and 80-mm samples, respectively.

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.

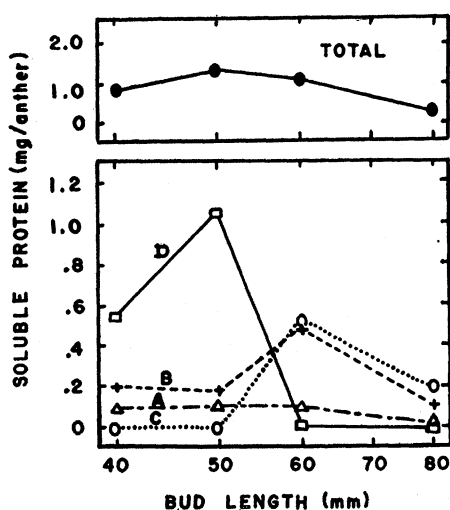


Fig. 2. Changes in the soluble proteins of *Lilium* anthers with increasing flower bud length. (Top) Total values obtained by Folin determination. (Bottom) Values for electrophoretic components based on proportion of the total pattern area represented by individual components. Average electrophoretic 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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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