

that is being carried out by the epidermal cells in all parts of the body. During these eight days the five pairs of long chromosomes exhibit a well defined and constant pattern of puffing which has been described by Whitten in *Chromosoma* (26, 215; 1969). The process includes the appearance of a large number of Balbiani rings and in several cases puffed regions appear to "move along" the chromosomes, as though there were sequential activity of adjacent genetic loci. On the basis of timing it has been possible to suggest processes with which specific puffs may be concerned.

Finally, Goldberg, Whitten and Gilbert (*J. Insect Physiol.*, 15, 409; 1969) have attempted recently to relate the changes in soluble proteins in the foot-pad with puffing activity. Some clear-cut correlations have been obtained, one interesting feature being that the changes in soluble proteins are not correlated with changes in the circulating haemolymph, so that they must be local products the function of which should be reflected in the foot-pad nuclei. The most dramatic puffing activity is seen during days 5 and 6 of the pupal stage and it is immediately after this that several new protein bands appear. Results obtained so far are of sufficient interest to suggest that this system should prove to be a rich mine of information about the activation of gene sites.

ENZYMOLGY

Isoenzymes and Subunits

GONE are the days when it was imagined that each enzyme is a unique and indivisible protein entity. The one gene-one enzyme postulate does not, of course, imply that there cannot be more than one form of an enzyme and in fact isoenzymes—the products of different genomes—are now known to be common. Enzymes vary, moreover, according to the organ—and organism—from which they are derived, so that if isoenzyme diversity is encountered too, the number of distinct proteins exhibiting a given enzymatic activity becomes legion. Such diversity does, however, yield dividends, for a comparison of primary sequences (or even of peptide "fingerprints") will often reveal invariable features which are presumably those most closely concerned with catalytic or other functions. Such an approach may be more laborious and less sophisticated than X-ray diffraction, proton magnetic resonance or chemical modification, but the findings are no less worthy for all that.

In the same way that sequence analysis reveals that the primary structure of an enzyme is not unique (even though those of the crucial sites of activity are), a study of behaviour in dissociating solvents proves that very many enzymes have quaternary structure. In other words, the molecule may be composed of subunits—several polypeptide fragments that go to make up the whole. This has long been known for haemoglobin, myosin and many other proteins, and an increasing number of enzymes are now being dissociated.

Horecker's group at the Albert Einstein College of Medicine have just published the results of such work on rabbit liver fructose-1,6-diphosphate aldolase (R. W. Gracy, A. G. Lacko and B. L. Horecker, *J. Biol. Chem.*, 244, 3913; 1969). They developed a new procedure

for purification and were able to prepare a much more homogeneous enzyme than has been possible hitherto. Its molecular weight was 158,000, but when treated with guanidinium hydrochloride or sodium dodecyl sulphate four monomers with a molecular weight of about 39,000 were produced. This confirms previous chemical and physical data which assigned to aldolase a tetrameric structure of the form $\alpha_2\beta_2$. The fact that dissociation and reconstitution of the enzyme do not lead to the formation of new hybrid species such as α_4 or β_4 indicates, moreover, that the mode of combination of the fragments is subject to restrictions (D. E. Morse and B. L. Horecker, *Advances in Enzymology*, 31, 125; 1968).

Ever since the work of Gerhart and Pardee on aspartyl transcarbamylase it has been evident that quaternary aspects of enzyme structure are not without relevance to reaction mechanisms, questions of allostery, and so on. Kaplan's group at Brandeis University (H. D. Kaloustian, F. E. Stolzenbach, J. Everse and N. O. Kaplan, *J. Biol. Chem.*, 244, 2891 and 2902; 1969) have just published a report which interprets certain curious changes in the catalytic activity of lactate dehydrogenase during purification in terms of a model invoking subunit interactions. Their enzyme (from lobster muscle) has a unique susceptibility to product-induced modulations in activity. NADH, a product of the forward reaction, is a positive modulator of this reaction at low reaction rates, and an inhibitor at high reaction rates. After considering various possible mechanisms of product activation, Kaplan *et al.* propose a model which is rather different from the classical Monod-Wyman-Changeux model, or those based on Koshland's hypothesis. NAD⁺ and NADH are thought to occupy the same sites in the protein, and it is suggested that the binding of the reduced nucleotide to one or more of the four binding sites (this enzyme, too, is tetrameric) causes a structural change facilitating the binding of the oxidized form to another available site. This, they say, accounts for the anomalous kinetics. X-ray data on dogfish muscle lactate dehydrogenase are quoted to support this view: intramolecular rearrangements seem to occur when NAD⁺ or NADH diffuses into the enzyme crystals.

It would be a truism to assert that enzymology is no longer the exclusive province of the kineticist, but that it must be seen in the context of all other studies on protein structure. Enzymologists must count themselves one with those who work on haemoglobin (which indeed has been called an "honorary" enzyme), the immunoglobulins, the muscle proteins, membrane proteins, and many more.

GEOTROPISM

Light triggers Perception

from our Plant Physiology Correspondent

A BASIC similarity in the growth responses of roots or shoots disturbed from their normal orientation with respect to gravity has been shown by several investigations in recent years. One half of the organ is induced to grow faster than the other half. This lateral difference in growth rate causes the geotropic curvature, typically upwards in shoots and downwards in roots. The preceding stages in the geotropic response, per-