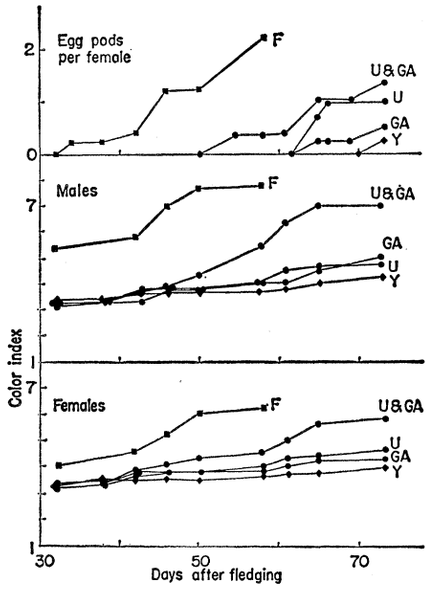

Fig. 3. Egg laying and color change in groups of desert locusts fed for 38 days after fledging on yellow, senescent leaves of *Brassica* spp. and then treated as described in Fig. 1. Records for locusts from the same batch but fed on green leaves are also shown (*F*).

affected. Locusts treated with a dietary supplement of gibberellin A_3 (about 1 μg per locust per day), administered with a diet of yellow leaves from the time of fledging, matured at the same rate as those fed on green vegetation; but when gibberellin A_3 was given to locusts fed on green leaves, it had no noticeable effect, or even retarded maturation. Locusts fed on yellow vegetation and receiving an external dose of 1 μl of eugenol (applied as a microdrop on the ventral surface of the thorax), 7 days after fledging, also showed the color change of approaching maturity as early as those fed on green leaves, and they started laying eggs on the same day. Unlike gibberellin A_3, eugenol hastens both the color change and the time of oviposition in animals fed a green diet (*1*). In other words, gibberellin A_3 only hastens maturity in animals fed the senescent vegetation presumed to be low in natural gibberellin, while eugenol is able to trigger the onset of reproductive capacity whether the locusts are feeding on green or on senescent vegetation.

In further experiments we have fed animals for 5 weeks after fledging on senescent *Brassica* and then either supplemented the diet with gibberellin A_3 (about 1 μg per locust per day) or applied a single external dose of eugenol, or the two in combination. After about 2 weeks the treated animals began to change color, and a week later oviposition started (Fig. 3). Under these conditions the two substances seem to be synergistic.

Marshall (*7*), writing of the breeding seasons of vertebrates in general and of birds in particular, states: "If animals that populated the equatorial regions, or special areas (e.g. arid regions) often far away from the equator, did not, in fact, adopt diverse regulatory and 'timing' devices they could not have survived. . . . They abandoned their traditional response to photostimulation (those that already possessed such a response) and came to obey more appropriate stimuli that would ensure that their young would be produced at the period most propitious for their survival." What is true of vertebrates is true of organisms generally in this context and, in particular, is true of locusts.

We would suggest that a diet low in gibberellin and essential oils, such as the desert locusts have in the dry season when they are feeding on old and withered vegetation, delays the attainment of sexual maturity, and delays the color changes which accompany it. At the onset of the rains, bud-burst in the aromatic desert shrubs provides a trigger, in the form of vegetation rich in gibberellin and eugenol and other monoterpenoids, which suffices to initiate sexual maturation and subsequent breeding (*1*). In this way breeding of the desert locust is geared to the rains.

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References and Notes

1. D. B. Carlisle, P. E. Ellis, E. Betts, *J. Insect Physiol.*, in press.
2. D. B. Carlisle, D. J. Osborne, P. E. Ellis, J. E. Moorhouse, *Nature* **200**, 1230 (1963).
3. K. Shoji, F. T. Addicott, W. A. Swets, *Plant Physiol.* **26**, 189 (1951); E. C. Humphries and A. W. Wheeler, in *Regulateurs Naturels de la Croissance Vegetale* (Editions du Centre National de la Recherche Scientifique, Paris, 1964), No. 123, pp. 505–515.
4. D. J. Osborne, *J. Sci. Food Agr.* **16**, 1 (1965).
5. R. A. Fletcher and D. J. Osborne, *Nature*, in press.
6. R. H. Dadd, *J. Insect Physiol.* **6**, 126 (1961).
7. A. J. Marshall, in *Biology and Comparative Physiology of Birds* (Academic Press, New York, 1961), vol. 2, p. 307.

29 April 1965

Roots as Organs of Assimilation of Sulfate

Abstract. *Roots of the field pea (*Pisum arvense *L.) can reduce a small proportion of the sulfate that they absorb from the external medium. Some of this reduced sulphur is transported to the shoot as methionine and, to a lesser extent, as cysteine and glutathione.*

Remarkably little is known about the metabolism of sulfate in the higher plant. In certain species free sulfate is reported to be the only form of sulfur transported from roots (*1*). In others, organic compounds of sulfur are regular constituents of bleeding sap or fluids extracted from the xylem (*2*, *3*), and this has been claimed as evidence that roots may act as important sites for metabolism of sulfate (*2*). However, in the absence of proof of synthesis in the roots, it is not clear whether the appearance of organic sulfur in the xylem really reflects sulfate assimilation, or whether it signifies a breakdown of root protein or even a circulation of substances originally synthesized in the shoot system.

There is general agreement that in all plants photosynthesizing leaves function as the main centers for reduction of sulfate (*4*). Nevertheless, it is also evident that nonphotosynthetic tissues may incorporate sulfate-sulfur into organic compounds. The activity of roots in this respect is proved beyond doubt in cultures of excised roots where, with the exception of traces of the sulfur-containing B vitamins, all sulfur is normally supplied in the form of sulfate. In excised roots, incorporation of sulfate-sulfur into sulfur-containing amino acids has been recorded by using radioactive sulfate (*5*). The experiment described here provides evidence that roots of the field pea (*Pisum arvense* L.) contain an active system for reducing incoming sulfate and that certain of the products of assimilation become available for transport to the shoot.

The roots of sulfur-sufficient, nodulated plants were supplied with radioactive sulfate, and at specified intervals afterward the shoots of 20 plants were removed and bleeding sap collected from the root stumps (*6*). The distribution of S^{35} in the sap and in the water-soluble and protein fractions of the shoot and root was examined for each harvest of plants (*7*).

Free sulfate accounted for more than 90 percent of the radioactivity of all

Table 1. Specific activity of various sulfur-containing compounds obtained from roots, bleeding sap, and shoots after feeding $S^{35}O_4^{--}$ to the roots of nodulated plants of field pea. (Specific activities are expressed as counts per minute per microgram of sulfur.)

Compound	Hours after supplying $S^{35}O_4^{--}$		
	1	24	48
Roots			
Protein methionine	81.8	222	294
Protein cysteine	111	201	208
Free methionine	12.7	33.4	199
*Bleeding sap**			
Free methionine	1710	1159	428
Free glutathione			(10.1)
Free cysteine		(6)	
Shoots			
Protein methionine		242	472
Protein cysteine		307	644
Free methionine		(10.2)	31.6

* From 0.19 to 0.36 percent of the total S^{35} of the sap was recovered in the organic compounds, methionine, glutathione, and cysteine. These together constitute less than 2 percent of the total nitrogen of the bleeding sap and represent a concentration of 2 to 8 μg of sulfur per milliliter. Cysteine is present in smaller amounts than glutathione and methionine.

samples. Total radioactivity of the shoot increased throughout the 2 days of the experiment, while that of roots and sap decreased. Organic compounds of sulfur were labeled in the sap and roots within 1 hour, but in shoots not until after 4 hours. The specific activities of certain organic compounds of the root, shoot, and sap were determined by combining data from an amino acid analyzer with measurements of the radioactivity of relevant fractions of eluate from the analyzer made with a liquid scintillation counter. The data are presented in Table 1. After 1 hour, sulfur-containing amino acids were labeled in the protein and water-soluble fractions of the root, and methionine of high specific activity was recovered from the sap. At this time the S^{35} had not exchanged with organic compounds of sulfur in the shoot, so that the labeling of cysteine (cystine) and methionine of the root must have been implemented by its own reductase system.

The data suggest that the processes leading to a release of organic sulfur to the xylem are separate from the general metabolism of the root. Thus, the specific activity of the methionine of the sap is always many times greater than that of either the soluble phase or the protein of the root. Furthermore, the total S^{35} label recovered in methionine of the sap decreased over the 2 days of the experiment, while that of the body of the root increased. These findings suggest that the methionine released to the sap is produced in tissues and cellular compartments adjacent to the xylem, and that its synthesis is closely connected with the transport of sulfate across the root. At the same time, release of organic compounds of sulfur to the xylem is clearly a selective process, since although many compounds of sulfur are present in the soluble phase of the root, only a few of these carry sulfur to the shoot system.

Out of every thousand atoms of S^{35} leaving the root only two to four atoms were bound to organic compounds (Table 1). Judging from rates of bleeding of roots, this contribution of organic sulfur must be of little significance to the nutrition of the whole shoot system, and it certainly cannot be held responsible for the large increases in the labeling of shoot protein which took place throughout the experiment. However, when radioactive sulfate is supplied externally to the root only one element of the complex of transport activities within the whole plant is revealed. For instance, it fails to determine whether circulation of free sulfate occurs between phloem and xylem pathways and, if such a circulation does occur, whether it is accompanied by further reduction in the roots or translocation of organic sulfur from the shoots. Similarly, it provides no explanation as to why S^{35} exchanged readily with the cysteine and glutathione of the roots, but only extremely slowly with these same compounds in the bleeding sap.

Essentially similar results were obtained when $S^{35}O_4^{--}$ was supplied to roots of field pea, with nitrate being used as a source of nitrogen. The assimilation of sulfate can therefore be considered as an integral part of the normal metabolism of the root rather than a specialized activity of the root nodules. Parallel studies of the synthesis of organic compounds of nitrogen in the field pea have shown that both nodulated roots and roots relying on nitrate function effectively in synthesizing certain of the amides and amino acids required for protein synthesis and the establishment of soluble reserves of nitrogen in the shoot (*7*, *8*). It would be interesting to see how these functions of the root are related to the metabolism of sulfate.

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References and Notes

1. G. Reuter and H. Wolffgang, *Flora* **142**, 146 (1954); N. E. Tolbert and H. Wiebe, *Plant Physiol.* **30**, 499 (1955).
2. D. Féjer, *Acta. Biol. Acad. Sci. Hung.* **9**, 159 (1959).
3. E. G. Bollard, *Ann. Rev. Plant Physiol.* **11**, 141 (1960).
4. M. D. Thomas, *Encyclopedia of Plant Physiology* (Springer, Berlin, 1958), vol. 9; B. B. Biswas and S. P. Sen, *Indian J. Plant Physiol.* **2**, 1 (1959); L. G. Wilson, *Ann. Rev. Plant Physiol.* **13**, 201 (1962).
5. J. L. Liverman and J. B. Ragland, *Plant Physiol.* **31**, vii (1956).
6. J. S. Pate, *Plant Soil* **17**, 333 (1962).
7. ———, J. Walker, W. Wallace, *Ann. Bot.*, in press.
8. J. S. Pate and W. Wallace, *ibid.* **28**, 83 (1964).
9. I thank Prof. D. J. Carr (Queen's University, Belfast) for his advice and interest. This study was supported by a grant from the Agricultural Research Council.

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Adaptive Enzyme Synthesis: Its Inhibition as a Possible Analogue of Immunological Tolerance

Abstract. *Substrate induction of tryptophan pyrrolase in the liver of rats is inhibited by prior treatment of very young rats with tryptophan. This inhibition seems analogous to immunological tolerance, which can be produced by prior treatment with the antigen. The findings provide support for an analogy between mechanisms of adaptive enzyme synthesis and those involved in adaptive immunity.*

The phenomena of immunological paralysis (*1*) and immunological tolerance (*2*) have been difficult to account for in current theories of antibody formation. A completely satisfactory hypothesis has not been proposed, and this necessitates further investigations into the mechanism of the induction of paralysis and tolerance. Both situations of unresponsiveness can be specifically induced by excess of antigen, and early life is the period during which animals are most susceptible to the induction of the unresponsiveness.

Immunological tolerance similar to immunological responsiveness is a property of a population of lymphoid and reticular cells which constitute the immunological system. This population consists of different cell types, and their relations to each other are only partly known. The changes in this cell population which constantly occur in response to contact with antigens severely complicate the study of the intracellular processes that lead to antibody production or unresponsiveness.

Since the required condition of a stable cell population could not be