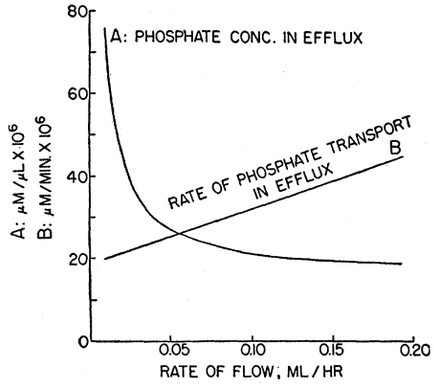

Fig. 1. Effect of longitudinal flow rate through the root on phosphate concentration found in efflux (*A*) and rate of phosphate transport by effluent stream (*B*). Graphs for apical corn root (*Zea mays* L.) segments from Smith (*5*).

μmole/ml yielded 20×10^{-6} μmole of phosphate per minute per root segment. The average C_1, rising from 0 to 0.076 as the solution flowed through the root was, therefore, 0.038 μmole/ml. Solving for k (Eq. 2) we obtain $k = 0.116 \times 10^{-6}$. With this value of k and the C_1 values read from curve *A* (Fig. 1) for different flow rates, the Q values were computed for each flow rate. These are given in Table 1 (on a per segment per minute basis) and demonstrate the very slight expected effect of the observed changes in C_1 on the diffusional transport of phosphate and also the hyperbolic character of Q as a function of flow rate. Diffusion into the flowing root stream, therefore, could not have been controlling the amount of phosphate recovered. One must conclude that phosphate was released into the flowing stream by a process that was proportional to some exponential function of the concentration in the flowing stream. Whether leakage or a more specifically controlled secretion of accumulated phosphate into the flowing stream was involved, this process and not diffusion through free space was the rate-limiting one for transport into the xylem.

Table 1. Theoretical effect of variations in C_1 on the amount of phosphate transported by diffusion across the root into the xylem.

Flow through root (ml/hr)	Phosphate theoretically transported (μmole/min per root segment)	Δ μmole/min / ml/hr
0.009	20.0	
		25
.025	20.4	
		4
.050	20.5	
		2
.100	20.6	
		0—
.194	20.6	

Now, what of the absolute magnitude of the diffusion process relative to the observed rate of solute transport? According to Eq. 1 and using a value for D of 10^{-5} cm^2 sec^{-1}, letting $r_o/r_1 = 5$ (actually the radius of the central cylinder is approximately one-third that of the root, so that the factor of 1/5 provides a safe margin), and letting $C_o - C_1 = 1$ μmole/ml (actually ranging in this case from 0.96 to 0.99), we find that a cylinder 3 cm long should take up 7020×10^{-6} μmole of phosphate per minute. However, diffusion occurs through only about 7 percent of the cross-sectional area of corn roots [the effective radial pathways for an apparent free space for corn roots of 15 percent (*4*)], and the diffusional path is tortuous (being about 1.5 times the distance along a radius), so that we must multiply the value for an ideal cylinder by the fraction 0.07/1.5 to determine diffusion into the root segment. We would, therefore, expect an uptake of about 350×10^{-6} μmole/min per root segment compared to observed uptakes of 20 to 40, or an order of magnitude greater than was actually observed. It has been shown that equilibration of free space in bean roots is in good agreement with the diffusion equation when a normal diffusion coefficient of about 10^{-5} cm^2 sec^{-1} is employed (*4*). The discrepancy in this case is large enough to suggest that the diffusion through free space is not the rate-limiting process in phosphate transport through the root.

Increased transpiration ordinarily causes an increased flow of water through the cortex. Smith's experiment is of particular interest because the technique employed allowed variation in the rate of flow through the xylem with little or no water-flow through the cortex. Instead, the movement of water through the xylem of the root was achieved independently of any movement of water or solution across the cortex. Regardless of the rate of water-flow through the root, diffusion alone, with essentially no mass flow, was responsible for the phosphate transport across the cortex to the central cylinder. This diffusion of course occurred, but diffusion was apparently stopped at some barrier, which then interposed its own concentration-sensitive mechanism for the release of phosphate into the stream of water moving through the vascular tissues. If Smith's results are not conclusive proof (a very rare commodity in any case) of the existence of a barrier to free diffusion in the root, they are at least very strong evidence for such a barrier.

Note added in proof: In a personal communication to one of us (L.B.), Smith affirmed belief in a barrier to free diffusion in the root, correcting an erroneous impression to the contrary given by his paper (*5*). The present analysis of Smith's data remains useful in refuting those who may still believe in a continuous free-space system leading into the conducting tissues of the plant.

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26 January 1961

Soil Mineralogy as Factor in Spread of Fusarium Wilt of Banana

Abstract. A correlation is established between the spread of *Fusarium* wilt of banana and soil mineralogy. Montmorillonoid-type clay minerals occur in all soils in which disease spread is slow, but, with the exception of two soils, this group of minerals is absent in soils in which it is rapid.

Fusarium wilt of banana, commonly called Panama disease, is caused by the soil-borne, root-infecting fungus, *Fusarium oxysporum* f. *cubense* (E.F.S.) Snyd. and Hans. The disease was first noted in Central America about 1900 and continues to be one of the main problems in the commercial production of wilt-susceptible banana varieties. The observation that the spread of the disease is not uniform in all soils resulted in the concept that soils differ in their "resistance" or "susceptibility" to the fungus (*1*). Early investigators classified banana soils as susceptible, semiresistant, or resistant (*1*), but current usage has modified these terms to short, intermediate, and long life, respectively. The effective banana-producing life of soils is determined by the rate of spread of the disease throughout a plantation and, from an economic point of view, is based on the length of time required for more than 50 percent of the plants there to show disease. Wilt-susceptible bananas can generally be produced on short-

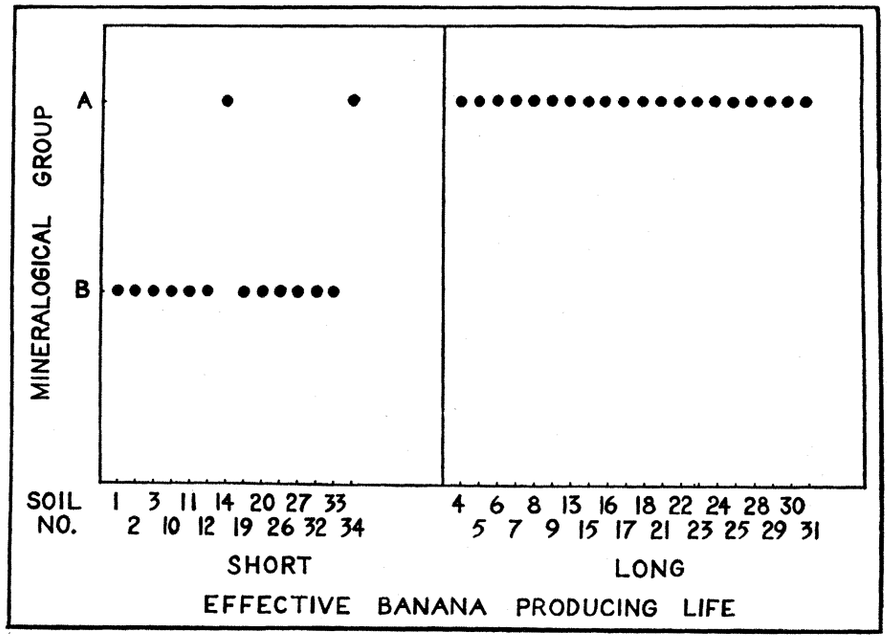

Fig. 1. Correlation between the effective banana-producing life of soils and soil mineralogy. Mineralogical group A contains montmorillonoid-type clay minerals, and group B does not.

life soils for 3 to 10 years, on intermediate-life soils for 10 to 20 years, and on long-life soils for more than 20 years. Some long-life soils have been in continuous banana cultivation for more than 70 years.

Not only is it of great economic importance to be able to predict accurately the potential life of soils, as large expenditures are required to convert virgin lands into plantations, but elucidation of mechanisms responsible for soil life may lead to methods for control of the disease in areas where it is now present. Potential banana lands in Central America are surveyed by a few individuals highly experienced in banana production and in evaluating banana soils.

Although the criteria originally used in these surveys were, for the most part, subjective, attempts have been made to correlate soil life with soil characteristics in order to obtain more accurate predictions (*1*). Of the many soil characteristics investigated (for example, texture, *p*H, total soluble salts, cation exchange capacity, available phosphorus, calcium, magnesium, and potassium, organic matter, and drainage), only the level of available potassium (*2*) showed a relatively good correlation with soil life (*1, 3*). The long-life soils were usually high in available potassium, containing from 200 to 1000 parts per million, and the short-life soils contained from 30 to 200 parts per million. The level of available soil potassium has been implicated in a number of plant diseases, but no adequate explanations have been provided for this apparent relationship. Increasing the potassium content of short-life soils to that of long-life soils has consistently failed to extend the effective banana-producing life.

Because many soil characteristics depend upon the type and weathering sequence of the parent material, they may reflect only the type of clay minerals present in the soils. Inasmuch as clays have been shown to be involved in several microbial activities in soil, such as decomposition of organic matter (*4*), nitrification (*5*), nitrogen fixation (*6*), and adsorption of microbial products (*7*), they may also be important in the life of soils.

To determine whether effective banana-producing life is correlated with differences in the type of clay minerals, 34 soils were obtained from Honduras, Costa Rica, Panama, and Guatemala from banana plantations having different disease histories. These samples were analyzed mineralogically by differential thermal, x-ray diffraction, total potash, glycol retention, cation exchange capacity, and petrographic analyses. X-ray diffraction was the best method of analysis, because some soil factors, such as high levels of organic matter or $CaCO_3$, interfered with interpretation of the thermograms. Petrographic analysis was restricted to the 100- to 250-μ sand fraction and provided only an indirect index of the types of clay present. The other analyses were conducted to confirm the results obtained with the x-ray and differential thermal analyses.

With the exception of two soils, effective banana-producing life was correlated with types of clay minerals present in the soils (Fig. 1). There was no correlation between any of the other soil properties examined and disease history. Montmorillonoid-type clay minerals, present in all the long- and intermediate-life soils, were completely absent in the short-life soils, with the exception of soils 14 and 34. Preliminary attempts to separate intermediate- from long-life soils on a mineralogical basis were not successful, nor was there any correlation established between soil life and relative concentrations of clay minerals other than montmorillonoids.

The disease histories of the two short-life soils that contained montmorillonoid-type minerals are not well established. Soil 14, although located in an area surrounded by typically long-life soils, is formed from alluvium derived from two rivers, one of which deposits long-life sediments and one which deposits short-life sediments. The life of plantations on this mixed alluvium is, therefore, variable, and the sample used for mineralogical analysis may have been collected from a localized zone of long-life sediment. Soil 34 gave only a weak indication of the presence of montmorillonoids, and the disease history of the sample site is poorly defined. A good correlation between x-ray, differential thermal, and petrographic analyses was obtained with 15 soils analyzed by all three methods.

Concurrent with further studies to verify the correlation between the type of clay mineral and life of the soils, possible mechanisms responsible for the correlation are being investigated. Although emphasis is being directed primarily toward presumed clay-microbe interactions, possible clay-host relationships are also being considered.

The results obtained to date indicate that the potential banana-producing life of soils may be predicted on the basis of their clay mineralogy (*8*). It is hoped that this report will stimulate other investigations into possible relationships between soil-borne plant pathogens and soil mineralogy.

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16 January 1961

Operant Behavior during Sleep

Abstract. Operant-conditioning techniques were employed to produce organized behavior during sleep as defined by the electroencephalographic record. Patterned responding was found in so-called "light" and "deeper" electroencephalograph stages as well as in the awake record. Results suggest that the use of the electroencephalographic record as a reliable indicator of the sleep-awakefulness continuum be re-examined.

The numerous investigations of the role of the reticular formation (*1*), and single-unit responses (*2*), in the modification of on-going behavior have led to several speculations about how the central nervous system subserves sleep. Of equal interest has been the problem that operative functions normally thought to be characteristic of waking behavior alone are present also in the sleep state—functions such as discriminative responses (*3*), integrative behavior, and control of on-going activity. The problem appears to be in the inadequacy of traditional behavioral and physiological indices to define a state of sleep. This report shows that complex behavior can be produced while physiological indicators, such as the electroencephalographic record, signal what has been defined as "deep sleep."

The experiments were done on five subjects ranging in age from 17 through 28 years. The subjects were tested weekly. The normal routine was for subjects to report to the laboratory on the night preceding the testing night. Suitable activities were provided during the intervening period, and the testing session was begun as closely as possible to each subject's normal bedtime hour. All subjects were thus deprived of sleep for about 36 to 40 hours.

Operant-conditioning techniques (*4*) were employed in the following manner. A microswitch was taped to each of the subject's hands, and two electrodes for administering shock were attached to the lower right leg. Whenever 3 seconds elapsed without a response on the left-hand microswitch, a pulse was delivered to the leg. By responding at a rate greater than once every 3 seconds the subject could avoid all shocks. A schedule of "time-out" periods, each of which followed a fixed number of responses (fixed ratio), was programmed on the right-hand key. During a time-out period, lasting either 5 or 8 minutes, all electrical equipment was turned off and the subject was allowed to sleep. The time during which avoidance and ratio-key responding were programmed constituted the scheduled activity period. Ten seconds before the end of a time-out period, a loud buzzer was sounded next to the subject's ear. The buzzer sounded continuously for 10 seconds and terminated with the appearance of the signal light mounted in front of the subject's head, initiating the next scheduled activity period. The first shock was delivered 3 seconds after the onset of the signal light unless the avoidance key was operated. This cycle of events was repeated continuously throughout the session.

Continuous electroencephalographic records were made from several scalp placements. The bulk of the data reported here was taken from bipolar placements of electrodes on the occipital center line. Parietal and frontal monopolar recordings were also obtained and were used in substantiating the various stages of sleep.

The scoring of the sleep stages followed a classification suggested by Dement and Kleitman (*5*) with some modifications. Stage 1A was taken as that portion of the record still exhibiting alpha bursts; stage 1B covered that part of the record between the last alpha burst and the appearance of the first 14-cy/sec spindle and consisted mainly of 3- to 6-cy/sec activity; stage 2 was characterized by spindle activity with low-voltage background, including some 3- to 6-cy/sec activity together with biparietal humps and K-complexes;

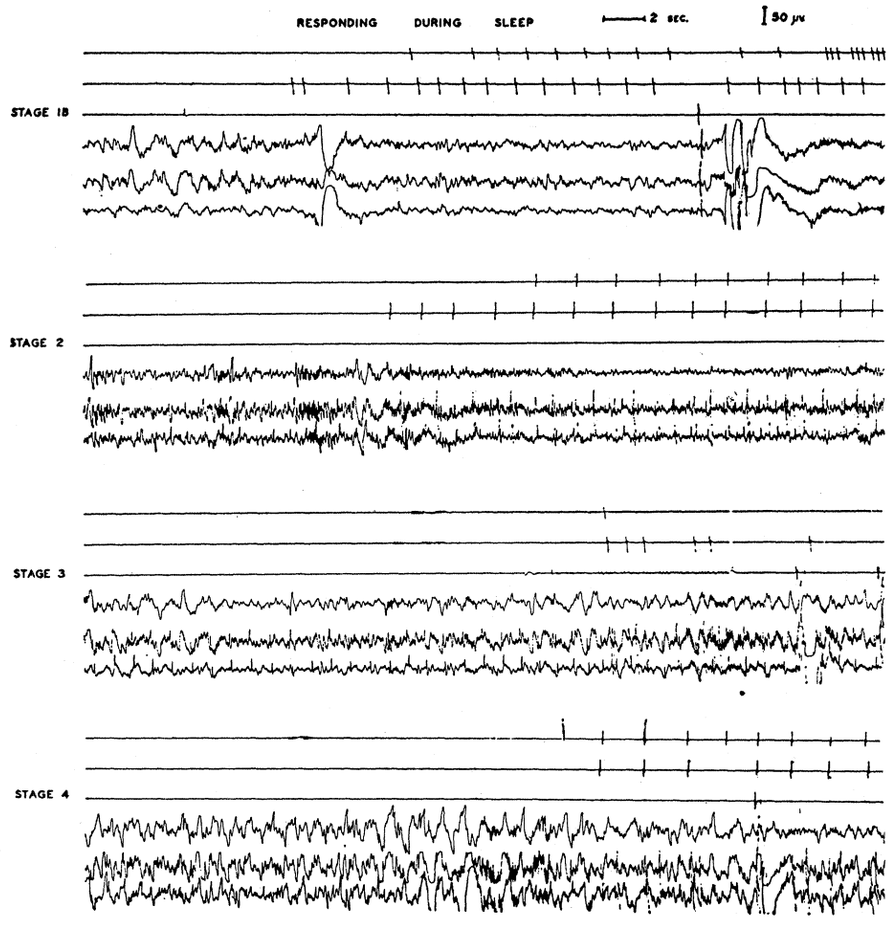

Fig. 1. Responding during electroencephalograph sleep. Stages are defined in the text. The six pens for each stage show from top to bottom: (i) fixed-ratio reinforcement responses, (ii) shock-avoidance responses, (iii) shock administration, (iv) occipital bipolar placement, (v) and (vi) occipital monopolar placements to the left-ear reference for monitoring. The examples of stages are taken from separate subjects.