

FIGURE 3. *a*. Effective response of unselected clover with the normally effective bacterial strain A. *b*. Ineffective response with bacterial strain A of clover homozygous for a simple recessive factor. *c*. Ineffective response of unselected clover with a normally ineffective strain of bacteria (strain H.K.C.).

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HOST FACTORS INFLUENCING INFECTION AND NODULE DEVELOPMENT
 IN LEGUMINOUS PLANTS

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[Plate 12]

Dr Thornton has shown that much of the diversity in the symbiosis between the leguminous plant and root-nodule bacteria can be attributed to inherent bacterial strain differences which show themselves, however, only in the symbiosis and are not causally related to any known *in vitro* property of the bacteria. On the plant side also very little of significance has been discovered connecting the physiology or metabolism of the host with symbiotic behaviour.

As a result mainly of studies of environmental effects, it has been established that in general any factor which increases the proportion of available carbohydrate in the host's tissues at the expense of the nitrogen content tends to be associated with an increase in nitrogen fixation (Fred & Wilson 1934; Wilson 1940, and others). On the other hand, factors decreasing the C/N ratio tend to reduce nodule size, and in extreme cases may so change the behaviour of the bacteria within the nodule as to result in tissue disintegration (Brenchley & Thornton 1925; Thornton 1930). This relation is not sufficiently well characterized to throw much light on the nodulation process, nor can it do so until the qualitative differences in the carbon and nitrogen fractions have been established.

The crucial reactions in symbiosis occur within the living infected plant cell where they are protected from the impact of external agents and are directly influenced only by intrinsic bacterial factors and by the internal environment of the host.

The study of these two sets of factors lies primarily in the fields of genetics and cell physiology. The inherent bacterial strain differences have been dealt with in the previous paper, and it is the object of this paper to discuss the effect of

hereditary plant factors in symbiosis and to show how some of these factors influence the normal functioning of the host.

The genetic studies have been carried out with red clover selected for a wide range of characters of symbiotic interest and analyzed genetically with the results summarized in table 1.

Plants which are completely resistant to infection are very rare and only one such original plant has been found, from which a resistant line has been raised. Resistance is inherited as a simple recessive factor associated with a maternally transmitted component (Nutman 1949*b*). The resistance to infection is complete, all strains of bacteria so far tested failing to enter the root hair. No significant connexions have been found between resistance and other characters: resistant plants tend to be weakly and chlorotic, but so are many susceptible plants. Grafting experiments have shown that neither resistance nor susceptibility can be attributed to a substance able to cross a graft union.

TABLE 1. HEREDITARY HOST FACTORS IN SYMBIOSIS IN RED CLOVER

symbiotic character	mode of inheritance	bacterial strain relationships
resistance	simple recessive and maternal component	independent of strain
infection time	complex	independent of strain
nodule number	(1)* simple recessive	strain specific
	(2)† simple recessive (?)	strain specific
	(3) complex	independent of strain
ineffectiveness	(1)* simple recessive	strain specific
	(2)† simple recessive (?)	strain specific
	(3) simple recessive (?)	independent of strain
	(4) modifying factors	strain specific
	(5) complex	independent of strain

The time at which nodules first appear on the root is also very variable. Earliness or lateness is inherited in a complex fashion, and shows with all strains of bacteria.

The number of infections sustained by the root may also be determined by inherent host factors, and these appear to be of two kinds. In the first, of which two examples have been encountered, abundant infection of the root is associated with a simple recessive host factor reacting specifically with the bacterial strain; that is to say, either of these recessives form large numbers of nodules with the particular strain of bacteria generally used in these experiments but produced few nodules with other effective strains. In the second kind complex hereditary influences are concerned with the susceptibility of the root, and these have been shown to act independently of the bacterial strain. These are considered in more detail below.

The amount of nitrogen fixed by the association of plant and bacteria is also determined by the genetic constitution of the host, and here the situation is somewhat obscure and the analysis has not proceeded far. A simple recessive host factor has been studied which induces a typically ineffective host response with the formation of very large numbers of small ephemeral nodules; this is the gene already referred to as affecting nodule number, and its specificity embraces the

effectiveness of the response as well as the number of nodules formed. With the bacterial strain *A* used in the original selection of the ineffective plant material the response is ineffective, and with other normally effective strains it is effective. There is some evidence for a second gene with similar phenotypic effects and for a third recessive which is ineffective but which induces the formation of relatively few nodules, and unlike genes (1) and (2) the expression of this factor is independent of strain. As the evidence for these last two recessives is not extensive, they are queried in the table. Fourthly, modifying factors have been identified which are able to restore effectiveness with the first-mentioned recessive and which are thus strain-specific. And lastly there are inherent host factors which degrade the response without inducing complete ineffectiveness; these seem to act independently of bacterial strain.

Figure 3, plate 12, shows (3*a*) the usual effective response produced by the normally effective bacterial strain *A* above mentioned on unselected clover, compared with the completely ineffective response produced (3*b*) by this same strain on a plant homozygous for the first recessive gene, and (3*c*) by a normally ineffective bacterial strain on unselected clover. Both ineffective symbioses are phenotypically indistinguishable, the plants being starved and bearing numerous small nodules mainly on the lateral roots.

The recessive line of plants (3*b*) has been under observation in the laboratory for 6 years, in the course of which the bacterial strain to which it responds ineffectively has given rise to stable mutant bacteria which now respond quite effectively with the same line of plants. The phenotypic expression of this recessive can thus be circumvented by bacterial mutation as well as by the action, as noted above, of modifying plant factors.

The degeneration of the ineffective nodule, whether it is due to bacterial or to host factors, involves both the bacterial cells in the central tissue of the nodule as well as the host plant cells containing them and the neighbouring uninfected growing point of the nodule. The reason for this breakdown is not known. This is a focal problem; if the cause of the degeneration of the ineffective nodule was known some light would be thrown on the functioning of the effective nodule in which the bacterial and plant cells both remain active and fix nitrogen over an extended period.

These genetic studies have shown that degeneration in the ineffective nodule involves very specific interactions between bacterial and host factors, so that it is not surprising that the separate study of the plant and bacteria has not suggested an explanation of the effective symbiosis or of its breakdown.

It is, however, possible to represent the interrelations of bacteria and plant above described by a hypothetical scheme such as is shown in figure 4 (Nutman 1951).

In the infected tissue of the nodule, bacterial and plant metabolic processes will be going on side by side, and at certain points they may be interdependent in the sense that at some stage in metabolism a substance of plant origin will be associated with a substance of bacterial origin in the synthesis of a hybrid compound, possibly the primary product of nitrogen fixation. This is represented diagram-

matically in the top figure by the reactions $P_1 \rightarrow P_2$ and $B_1 \rightarrow B_2$ to N. Now, let us suppose that a substance P'_1 is a product of the recessive gene under consideration, which instead of being transformed to P_2 forms some kind of association with B_1 , which prevents the normal completion of the reactions. This association would be due to some special affinity between P'_1 and B_1 , and would therefore be specific to strain of bacteria. The configuration in B_1 which is responsible for this premature association with P'_1 is, *ex hypothesi*, a minor modification of the gene or gene product concerned and would not therefore be essential to the B chain of reactions. A further change in B_1 to B'_1 would, however, break the affinity between P'_1 and B_1 so that the reactions could be completed. This may correspond to a mutation in the bacteria leading to a normally effective response with the recessive line.

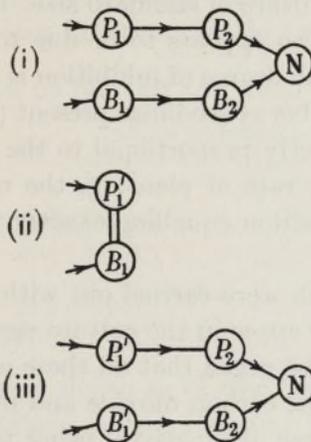


FIGURE 4. A scheme for the genetic interactions of bacteria and plant in the nodule.

Non-specific mutation in the bacteria of the kind described by Dr Thornton may be attributed to a more fundamental change in B_1 or B_2 . It is also possible to envisage other plant or strain factors which may determine the course of these reactions by slightly modifying the intracellular environment; these would be likely to be non-specific.

With a scheme of this kind in which two chains of processes are supposed to interfere with each other we can account for the simultaneous appearance of the bacterial and plant symptoms in ineffectiveness.

Any model deduced from genetic considerations must obviously be reconciled with the biochemical facts, and this very tentative scheme serves to emphasize at a genetic level the very high degree of co-ordination in the functioning of the bacteria and plant in the symbiosis.

The next step in the analysis is to ascertain whether the genes that influence the appearance, development and functioning of nodules produce independent effects on the plant. If so, an understanding of these effects might throw light on the mode of action of the same genes in the symbiosis. Many of these genes influence the number of infections resulting in nodules.

With regard to the genetic factors determining the time at which the primary infection of the root takes place, some interesting observations on the physiology

of infection in lucerne have been made, prior to these genetic studies, which seem to have some connexion with them.

Normally, the infection of the root takes place at about the time of the opening of the first leaf, and it was shown by Thornton (1929) and Ludwig & Allison (1935) that this time could be advanced by planting the test seedling among older seedlings which had already formed nodules, the stimulation being due to the exudation from the older roots of a nodule-initiating substance. It was later shown by West (1939) that root secretions stimulated the growth of nodule bacteria *in vitro*, though it was not known whether these effects were in any way connected.

It may also be shown with either lucerne or clover that the actual *numbers* of nodules formed is *greater* on plants growing singly than on plants growing in pairs or in larger groups within a culture of standard size. This inhibition of nodulation on plants growing together also appears to be due to the diffusion of some substance from the roots, since the degree of inhibition is related to the volume of the medium as well as to the number of seedlings present (Nutman 1945). The number of infections per plant is directly proportional to the volume of the medium and inversely proportional to the rate of planting, the reduction brought about by halving the volume of the medium equalling exactly that following a doubling of the planting rate.

In these experiments, which were carried out with plant culture in test-tubes, there is a severe restriction of space in the culture vessel as well as a limitation in nutrient supply, and it may be urged that all these effects are caused by competition between plants for light, carbon dioxide and nutrients. Experiments were carried out to investigate these alternatives, using plants making very different demands on the available nutrients and space.

TABLE 2. INTERACTIONS BETWEEN DIFFERENT KINDS OF RED CLOVER PLANT

companion plant	test plant	mean no. of nodules on test plant
none	} susceptible plant	33.7
susceptible plant		22.7
resistant plant		23.5
none	} effective plant	39.2
effective plant		26.7
ineffective plant	} ineffective plant	20.0
none		83.5
effective plant		47.5
ineffective plant		50.5

Table 2 shows the results of experiments on the interaction between resistant and susceptible plants and between effectively and ineffectively responding plants. The results show that clover plants which are hereditarily unable to form nodules have as great an inhibitory effect on nodule formation on a neighbouring susceptible plant as a second susceptible plant. Also plants which respond ineffectively and grow very little and make negligible demands on the space and nutrients of the medium reduce the numbers of infection to the same degree as do plants bearing effective nodules.

The results shown in table 3 also suggest that the interactions between clover and lucerne may be ascribed to the secretion of physiologically active substances from the roots rather than to competition. The numbers entered on the table are the mean numbers of nodules (with a minimum of 15 replicates) formed on lucerne and clover grown singly or in the presence of inoculated or uninoculated clover or lucerne plants, (C) or (L) or (C+L) indicating inoculation by clover bacteria or lucerne bacteria, or both. Within each cross-inoculation group the results are consistent and in accord with previous experiments, but the interaction between plants of different cross-inoculation groups clearly depends on the inoculation procedure. Nodulation on clover is equally depressed by inoculated and uninoculated lucerne, but nodulation on lucerne is only depressed by inoculated clover, uninoculated clover having no effect. These results again point to the production of substances by the root having differing specific activities.

TABLE 3. INTERACTION OF CLOVER AND LUCERNE PLANTED TOGETHER

companion plant	no. of nodules on test plant	
	clover	lucerne
none	35.7 ± 3.3 (C)	14.6 ± 1.4 (L)
clover	20.4 ± 8.1 (C)	14.0 ± 5.1 (L) 5.5 ± 1.2 (L+C)
lucerne	22.4 ± 3.2 (C) 21.0 ± 1.6 (C+L)	7.9 ± 0.7 (L)

Successive plantings of agar slopes have also been made with the object of avoiding mutual shading of plants sharing the same tube; the results of a factorial experiment are shown on table 4. The number of nodules on plants of either a sparsely nodulating or an abundantly nodulating line is reduced by preplanting the agar slope. This reduction is more pronounced if the cut-off root is left in the agar but is not affected by the number of nodules formed on the previous crop.

TABLE 4. REPLANTING AGAR EXPERIMENT

treatment	mean no. of nodules per plant on	
	(1) sparsely nodulating line	(2) abundantly nodulating line
control	11.1	41.8
1 previous planting	6.1	37.0
3 previous plantings	5.8	25.3
replanted after removal of roots	7.8	32.7
roots left in agar	4.2	24.9
previous planting with line (1)	5.9	28.4
previous planting with line (2)	5.8	29.7

Experiments have been undertaken with the object of extracting the root secretion directly from the medium but have not as yet been successful, and experiments are now in progress to adsorb it first on to a suitable surface-active material.

Vantsis & Bond (1950) have already shown that activated charcoal markedly stimulates nitrogen fixation in peas growing in sand culture, at the same time,

however, causing a fall in nodule number. Experiments set up with clover using various adsorbents have confirmed Bond's results on nitrogen fixation but have shown that under the conditions of test-tube culture employed the number of nodules was markedly increased. The effect of adding charcoal, bentonite or fullers' earth at different pH is shown on table 5; in all cases there is a marked increase in nodulation with the adsorbent. Further experiments have shown that the stimulation affects rooting as well as nodule formation, is independent of strain of bacteria and is proportional within limits to the amount of charcoal added. Stimulation occurs if the charcoal is enclosed within a cellulose membrane but does not occur with ashed charcoal.

TABLE 5. NUMBERS OF NODULES ON RED CLOVER IN THE PRESENCE OF 1 % CHARCOAL, BENTONITE AND FULLERS' EARTH

initial pH	5	6	7	8	9
control	1.3	30.8	18.9	22.4	15.9
charcoal	21.9	42.5	50.3	55.4	57.4
bentonite	14.1	31.2	30.1	51.2	47.2
fullers' earth	33.4	33.1	40.7	48.1	41.2

There remains to be considered the internal host factors concerned in limiting infection, in particular those which are polygenetically determined. These heritable differences have been shown to be of considerable extent (Nutman 1946). Moreover, closer examination of the root systems showed that the nodules were more closely packed on abundantly nodulating roots, so that the differing numbers of nodules on the contrasting families were not due simply to random infection on root systems of differing size. Contrasting lines of plant obtained by selection were next examined to ascertain whether their differing susceptibilities could be related to any other feature, and it was found that abundantly nodulating families invariably produced larger numbers of lateral rootlets than sparsely nodulating families, whether or not they were inoculated (Nutman 1948).

This relation suggests that the bacteria are only able to penetrate certain points or foci on the root bearing some relation to the normal centres of meristematic activity in the root. This view of the infection process, which is Beijerinck's (1894) original view that the nodule is an infected lateral root, would explain the fact that there are many more abortive infections of the root hairs than there are nodules formed (McCoy 1932), but it also raises a number of difficulties which do not appear if the plant is looked upon as a passive agent in the infection process.

It is evident, in the first place, that *all* the meristematic foci are not infected, but that a balance is maintained between nodules and rootlets. Infection in clover always takes place through the young growing root hair, and it is possible that the balance between nodule formation and rooting is maintained by the intervention of this mechanism, nodules forming from meristematic foci within those parts of the root bearing growing root hairs and laterals outside them.

A second difficulty presented by the view that nodule formation takes place only at meristematic foci is to account for the greater apparent infectivity of ineffective strains. On the one hand the plant has been shown to limit the number of infections with an effective strain to a proportion of the meristematic foci

which it is hereditarily capable of producing, but, on the other hand, this number of infection points can be doubled simply by substituting an ineffective strain in the rooting medium.

Three possible explanations suggest themselves. First, there may be two kinds of foci within the susceptible zones of the root, one set only being susceptible to infection by effective bacteria and both sets by ineffective bacteria. Secondly, the initiation of the nodule primordium may itself be induced from outside the root, as proposed by Thimann's heteroauxin hypothesis (1936), effective and ineffective strains differing in their auxin production. Thirdly, that there may be a differential inhibition of foci on plants inoculated with effective and ineffective strains of bacteria.

The first two possibilities are contrary to the results of previous reported experiments (Nutman 1949*a*), in which the rates of nodule formation at low temperature was studied on plants inoculated with effective and ineffective strains of bacteria. It was there shown that the infection rates for the two strains were at first exactly the same and only diverged after infection had been proceeding for some 3 weeks. This result indicates that the number of susceptible foci for effective and ineffective strains are initially the same and also that the bacterial strains themselves do not differ in their infective virulence, due to differing rates of auxin production.

The difference in the infective rates by the two kinds of bacteria under these conditions arises at the time when a difference in structure first appears between the two kinds of nodule. Chen & Thornton (1940) have shown that, after about 10 days, under normal conditions which would correspond at the lower temperature here used to 20 days, the first-formed ineffective nodules have completed their growth, and their apical meristems have aborted and contents are already degenerating, whereas the effective nodules are actively growing and will continue to do so for a month or so. This suggests that the bacterial strain differences in infection rate is due to the difference in nodule behaviour. Each effective nodule may be supposed to inhibit further meristematic development in the root, so limiting further infection of the root, and each ineffective nodule because of its ephemeral nature, to have no further influence on meristem formation or on nodulation. This influence of the effective nodule may be due to the activity either of the meristem or of the bacterial tissue, since in ineffective nodules both these tissues are transient.

This morphogenetic view of the infection process is open to experimental examination, and experiments have been undertaken on the effect on infection of excision of nodules and of the root apices (Nutman 1952).

Table 6 (top half) shows the result of an experiment in which the number of excisions of root tips or nodules was varied, the treatment effects being expressed in terms of the mean of the logarithm of the number of nodules found at the end of the experiment. The effect of excision is highly significant, and a significantly larger stimulation follows the excision of the larger number of nodules or root tips, but the stimulation following the excision of three or six nodules does *not* differ from that following the excision of the same number of root tips, so that in respect of their inhibiting activity nodules and root tips do not differ.

Included in the lower half of this table is the result of another experiment on the excision of the nodule meristem, leaving the rest of the nodule still attached to the plant. This has as stimulating an effect as the excision of the whole nodule and confirms the supposition that the source of the inhibitory activity is confined to the growing point of the nodule.

The removal of the cut-off nodules from the culture tube or the addition of cut-off nodules has been shown to have no influence on the rate of infection. The inhibitor is evidently no longer produced by the nodule when it is removed from the plant.

As we have seen, the amount of stimulation following excision is related to the number of excisions made, it has also been shown to vary inversely with the inherent susceptibility of the plant operated upon. With abundantly nodulating plants this stimulation is small, and with sparsely nodulating plants it is large. This suggests that the inherent differences between plants are themselves related to their sensitivity to their own inhibitor.

TABLE 6. EXCISION OF NODULES AND ROOT TIPS FROM RED CLOVER INOCULATED WITH AN EFFECTIVE STRAIN OF NODULE BACTERIA

treatment	mean log no. of nodules	mean differences
control (C)	1.470	
3 nodules excised (3N)	1.633	excised - C $0.190 \pm 0.059^{**}$
6 nodules excised (6N)	1.707	6 - 3 $0.113 \pm 0.049^*$
3 root tips excised (3R)	1.566	N - R 0.040 ± 0.049
6 root tips excised (6R)	1.712	
control (C)	1.430	
6 whole nodules excised (6N)	1.689	6N - C $0.259 \pm 0.090^{**}$
6 nodule meristems excised (6NM)	1.683	6N - 6NM 0.006 ± 0.116

Levels of significance: * $P = 0.05$, ** $P < 0.01$.

TABLE 7. EXCISION OF NODULES AND ROOT TIPS FROM RED CLOVER INOCULATED WITH AN INEFFECTIVE STRAIN OF NODULE BACTERIA

treatment	mean log no. of nodules	mean differences
control (C)	1.851	
3 nodules excised (3N)	1.834	excised - C 0.071 ± 0.055
6 nodules excised (6N)	1.943	
3 root tips excised (3R)	1.955	R - C 0.097 ± 0.059
6 root tips excised (6R)	1.941	

If we now turn to consider the results of excision experiments with ineffective strains of bacteria, given on table 7, we find that no stimulation follows nodule excision. This result was anticipated and confirms the hypothesis that the inhibitory activity is absent in the ineffective nodule whose growing point is transient. There is a small amount of stimulation after lateral root excision. This reduced effect might also be expected because of the poor growth of the lateral roots on the plants with ineffective nodules.

We can therefore attribute plant differences in susceptibility, whether they are ultimately controlled by simple or polygenetic factors as well as bacterial strain

differences in infective virulence, to a single morphogenetic factor which is itself concerned with a fundamental aspect of root growth, namely, apical dominance.

Work is projected on the identification of this factor, which may be related to the inhibitory substance which has been shown, on quite other grounds, to be excreted by the root, if it is not indeed the same substance.

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ALGAE IN ASSOCIATION WITH HETEROTROPHIC OR HOLOZOIC ORGANISMS

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The association of an alga capable of photosynthesis with another organism dependent on a supply of organic food, be it another alga, a fungus, or an invertebrate animal, is a very widespread phenomenon. The algae concerned are usually unicellular or simple filamentous forms, and, apart from the Zooxanthellae inhabiting marine invertebrates, are for the most part members of the Chlorophyceae or Myxophyceae. My theme is a very wide one, and it will therefore be necessary to confine my remarks to certain selected examples.

The combination of alga and fungus to constitute a lichen has been the subject of repeated investigation and has been variously interpreted. Whilst in the past penetration of the algal cells, or gonidia as they are commonly called, by fungal haustoria had only been rarely reported and was regarded by many as something quite unusual, if not abnormal, the more recent work of Fry (1928), and especially that of Geitler (1933, 1934, 1937, 1938) and of his pupil Tschermak (1941, 1943), has shown that it is comparatively common. In some lichens the haustoria penetrate deeply into the algal cells, seemingly occupying an invagination of the protoplast, but not necessarily leading to its destruction. In heteromerous lichens it is