SOVIET GENETICS

By

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> Great is the power of steady misrepresentation; but the history of science shows that fortunately this power does not long endure.
>
> CHARLES DARWIN

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FOREWORD

In spite of its title, this little book is not intended to be more than an introduction, for English readers, to contemporary genetic theory in the Soviet Union and to some of the factual and experimental material on which it is based. Attention is given mainly to the scientific aspects of the genetics question, but the social and political background is also discussed in order to present a coherent picture.

The difficulties of the gene concept as the basis for a comprehensive theory of genetics have long been recognised. Michurinist theory represents a positive attempt to overcome these difficulties, and is an important and serious contribution to biological thought. I have tried to explain the new ideas clearly and trenchantly, in the hope that the questions involved may receive more fundamental discussion than has hitherto been the case. Throughout the book the term Mendelism has been used in a general sense to denote the theoretical principles of orthodox genetics (the gene-chromosome theory of heredity, Neo-Darwinism).

The preparation and writing of this book have been the work of rare and limited hours of leisure. No attempt has therefore been made at a complete survey of the Russian literature. The papers listed in the bibliography are only a sample (determined largely by ease of availability) of the material which exists. I have read in full, and in the original, all the hundred or so papers quoted, as well as a good many others (including most of Lysenko's work) to which no specific reference is made. Translations from the Russian are my own, except where official English versions happen to be available.

I wish to record my deep indebtedness to helpers in the Science Section of the Society for Cultural Relations between the Peoples of the British Commonwealth and the U.S.S.R., without whose co-operation the materials for this book could not have been assembled.

A. G. M.

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CONTENTS

I

THE GENETICS CONTROVERSY IN PERSPECTIVE

I

THERE is no doubt that one factor which makes it difficult to appraise the Soviet genetics controversy is a failure to appreciate the way in which it developed. This is partly due to the natural difficulty in absorbing information from an unfamiliar language, but much more to the spasmodic and incomplete manner in which this important matter has been presented outside the Soviet Union, apart altogether from certain highly coloured accounts obviously dictated more by political bias than regard for scientific truth. It is, however, quite impossible to understand the scientific questions at issue without a consideration of the social background in which the attack on orthodox genetics arose, the reasons for this attack, and the history of its development. Readers of some recent commentaries on Soviet genetics might well gain the impression that the new genetical theories had sprung fully armed from Lysenko's head, and that Soviet biologists had adopted them out of wilful perversity, rejecting orthodox theory for frivolous and non-scientific reasons. The superficial nature of such a view can be seen by an examination of the historical facts. The attack on orthodox genetical theory had its origin in certain quite practical problems of Soviet agriculture. From this beginning developed a profound reconsideration of the fundamentals of biology which expressed itself in a controversy lasting over 20 years between the adherents of orthodox Mendelian theory and the followers of the new Michurinist trend of which Lysenko was the leader.

After the October Revolution in 1917, which established the Soviet Government, there took place a very great extension and development of science in Russia. Science existed in Russia prior to the Revolution and was indeed characterised by the work of a series of outstandingly brilliant men, beginning with Lomonosov in the eighteenth century and including such men as Mendeléev, Sechenov, Pavlov, Timiryazev, to name but a few at random. In certain branches of knowledge, such as soil science and soil microbiology, the Russians were pioneers and laid the foundation for subsequent advances. This very high level of science is remarkable in view of the extreme difficulties under which it grew up, owing to the social and political backwardness of Tsarism. Whilst the quality of Russian scientific achievement was unsurpassed, its scale of development was behind that in Britain or Germany, where capitalism with accompanying growth of modern industry had been established earlier.

From the first days of its existence the Soviet Government began a planned development of science on an enormous scale. Lenin concerned himself personally with these plans, for he saw clearly not only the essential function of science for the industrialisation of the country as the basis for its socialist reconstruction, but the even more important role of science after the establishment of socialism, when the final abolition of all restrictions due to the social conflicts of capitalism would permit the fullest use of science for increasing the general welfare of society.

As a result of this planned policy the Soviet Union has for many years devoted a higher proportion of her resources to scientific research than any other country in the world. Particular attention was given within the general programme to the organisation of biological research, especially in relation to agriculture. To meet the needs of socialist agriculture a whole chain of agricultural research institutes, covering all branches of research and including many genetical institutes, was set up, as well as several hundred experimental stations and experimental farms. With the successful completion of collectivisation science began to assume even greater importance as a factor in the rate of agricultural advance, and the demands made by collective farmers on the scientists for advice and help in solving practical problems became more urgent.

The close relation which exists in the Soviet Union between agricultural research and practice is a feature of socialist agriculture which is often imperfectly appreciated in this country. Collective farmers look to their regional research institutes and to scientists in general for active help and are likely to be highly critical if they do not get it or if it is ineffective. At the same time many collectives take part in experimental work which is part of the research programme of an institute. Every collective farm possesses a small laboratory primarily for routine control work but where some research work can be done according to local initiative. Each farm usually employs a trained agronomist and a zoo-technician. Thus the link between science and practice is a very close and living one, and this fact has an important bearing, as we shall see, on those scientific developments which it is the purpose of this book to discuss. It is no exaggeration when Lysenko speaks of Soviet science as "becoming the possession of the broadest sections of the working people—from workers in thousands of collective-farm laboratories to workers in research institutes and academies."

In the field of genetics and plant-breeding there was enormous activity and work on a very considerable scale in many research institutes. Most of this work was from the beginning based on orthodox genetical theory, and was directed and carried out by scientists thoroughly trained in Mendelian genetics. I should like to emphasise this point, because the suggestion has been quite widely made that Lysenko and his followers are not sufficiently acquainted with Mendelian genetics, especially the most recent developments, and that their criticisms are based on misapprehensions and are therefore wide of the mark. But it must be remembered that right up to 1948 almost all university teaching and all courses of higher instruction in biology were based on orthodox genetical theory. In fact all Soviet biologists received a much more thorough grounding in Mendelian genetics than most students get in this country, where less emphasis is placed on genetics in biological teaching.

The idea that Soviet biologists are ignorant of foreign work could only be entertained by those who have never taken the trouble to open a Russian scientific journal. Anyone who makes the effort would find not only references to the most recent work on genetics published in British, American and other foreign scientific journals, but also very frequently complete translations into Russian of articles and reviews which have appeared abroad. It is a great pity that some of our leading scientific journals do not practise the reverse of this informal "lifting" instead of complaining of alleged difficulties of communication with the Russians. Many books by leading Mendelian geneticists have been issued in Russian editions, as, for example, Waddington's *Organisers and Genes*, of which a translation appeared in 1947, and Harland's book on the breeding of cotton, which appeared in 1946 and was reviewed at length in *Agrobiologia*, of which Lysenko is the editor. The position is exactly the reverse of what the critics claim: the Michurinist geneticists are very well acquainted with even the latest developments of Mendelian genetics, whereas the facts and ideas of the Michurinists have largely failed to penetrate the curtain of ignorance and misunderstanding with which the Soviet Union is unfortunately so frequently surrounded.

In passing I must also mention a cruder variant of the criticism just discussed. It is said that Lysenko himself is ignorant, untrained, a practical agriculturalist only, unacquainted with, and therefore incapable of criticising, modern genetics. I will not comment on the scientific snobbishness implicit in this judgment but will merely point out that Lysenko is a trained agronomist, who, though he did not pass through a university, had several years' training in horticulture and plant-breeding after the Revolution, including courses at the Kiev Agricultural Institute. He may thus be presumed to be as well grounded in Mendelism as many of his critics. The charge of ignorance appears to be founded on a statement by Professor S. C. Harland, who, when he met him in Odessa, apparently submitted Lysenko to an informal *viva voce* examination and failed him completely! One suspects, however, that they may have been at cross-purposes. Fortunately, there are less subjective ways of assessing Lysenko's scientific achievement, as will be seen.

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Already before the Revolution a number of aspects of Mendelism were criticised by Michurin with considerable acuity as a result of his own observations. But Michurin's work remained somewhat isolated even after 1917 and there is no evidence that it directly influenced Lysenko's views. Only later was the affinity clearly recognised and the name Michurinism used to designate the new trend in biology.

It is of the greatest significance to note that the first widespread questioning of the prevailing Mendelian ideas arose in connection with a supremely practical problem, the problem of the supply of high-grade seed for sowing to the collective farms. This is an example of how the socialist re-organisation of agriculture begins to raise new problems and make new demands on science, as Lenin had foreseen. The success of collectivisation rendered urgent the problem of seed production in order to ensure adequate supplies of high-quality (élite) seed for all collective farms, as an important means of producing high and stable yields. On the basis of his preliminary experiments, Lysenko proposed in 1935 at a meeting of the Cereals Division of the Lenin Academy of Agricultural Sciences that intra-varietal crossing should be used to improve the quality and vigour of self-pollinating plants such as wheat and barley. These plants are normally fertilised by their own pollen and Lysenko's method consisted essentially in castrating the flowers (i.e. removing the stamens before the pollen ripens), and then fertilising them with pollen from other plants of the same variety. At first the cross-pollination was done by hand but it was very quickly found that castration followed by free wind pollination was much more effective. In addition to renovation of seed by intra-varietal crossing, Lysenko also laid great stress on cultivation of the seed plants in the best possible conditions of nurture.

These new ideas came into sharp conflict with the fundamental principles of orthodox genetics, and both the ideas and the experiments were opposed. I shall discuss the scientific and theoretical questions later. The point to be noticed is that the attack on Mendelian theory did not arise in any accidental or arbitrary way, but directly and naturally from the vigorous interplay of theory and practice engendered by the socialist structure of agriculture.

The question was not simply a clash of scientific theories but also an immediate practical question of great social import: whether certain lines of apparently fruitful research were to be ignored because they were unorthodox. This aspect was put with forceful clarity by Lysenko himself in 1936 at an early stage in the controversy when speaking at the fourth session of the Lenin Academy of Agricultural Sciences.

> The controversy does not represent merely a clash of opinions of individual scientists. It closely concerns major questions of research activity. This alone, in my view, explains why this controversy in an ostensibly narrow branch of science—breeding and genetics—has aroused such widespread interest among the Soviet public generally, and also among experimenting collective farmers. It is not individual minor issues that are involved; the point at issue is the main line to be taken in agrobiological science.

A little later in the same address Lysenko indicates clearly the way in which the practical and theoretical issues are inseparably connected:

> What tasks, then, compel me, along with Dr. Prezent and a number of other scientists, to raise the question of revising the initial positions of genetics? What tasks have led us to the present controversy? There are two problems involved. One is the problem of improving the seeding material of self-pollinating plants by means of intra-varietal crossing; the other is the problem of altering the nature of plants in a needed direction by means of training them accordingly. It is the effort to find a solution to these two problems that has made me join the controversy on the question of heredity and variability.

On another occasion Lysenko again says,

> Our dispute with the geneticists which would appear to have an abstract and theoretical character is in fact concerned with the extremely important practical question of socialist agriculture (Lysenko, 1936a).

The anti-Mendelian trend first found vigorous and coherent expression in connection with the crucial experiments on intra-varietal crossing and a number of questions closely related thereto. Dolgushin (1939) aptly remarks in this connection:

> The idea of intra-varietal crossing is the main battleground in the general attack on Morganist genetics. Numerous investigations and particular questions, raised and solved one after the other in an astonishingly short space of time—inbreeding, selective fertilisation, methods of breeding and seed production, directed change of the nature of plants by training—all these inter-related aspects of profound theory are united in a simple technical process, that of intra-varietal crossing.

But the crystallisation of a new theoretical trend in biology was also assisted by the results of work in another important field which had been going on for some years.

This work, which also sprang directly from practical questions of collective agriculture, was begun by Lysenko at the Kirovabad Experimental Station in Azerbaidzhan whilst studying the period of maturing of peas. From 1925 to 1928 he carried out a series of brilliant experiments, in both laboratory and field conditions, on the development of a large number of agricultural plants—wheat, rye, barley, rape, vetch, etc. This work established Lysenko as a first-class scientist and an experimentalist of skill and originality, and resulted in his appointment to the Institute of Genetics at Odessa to take charge of a specially created laboratory to study problems of vernalisation. On the practical side, his observations and experiments led in 1929 to the first use of vernalisation of winter wheat in actual productive conditions. This technique was quickly taken up by collective farms as its effectiveness in certain definite circumstances became apparent. Already in 1933 more than half a million acres were sown with vernalised seed and by 1941 more than fifty times this area. On the theoretical side, this work led Lysenko to elaborate his phasic theory of plant development. From this theory arose new and extremely important methods for plant-breeding, which, along with the rest of this work, will be discussed in detail later. His study of the relation between environmental conditions and the control of plant development led to the first experiments on the hereditary transformation of spring- and winter- types of cereal. Lysenko and his co-workers by their results called in question the fundamental basis of current genetical theory and they were inevitably led to formulate an alternative theory which should prove a more reliable guide for future advance.

It is of great interest to note that a revolt against orthodox genetics was also developing at about the same time in animal breeding, a field quite remote from Lysenko's own activity, but where likewise theory has to establish itself on the testing ground of practice. In this connection an acute British observer, Dr. A. Walton, has written:

> . . . It was already apparent in the realm of animal breeding when I visited the U.S.S.R. in 1934. At Ascania Nova (a large experimental station for acclimatisation and hybridisation of animals) M. M. Zavadovsky, an eminent geneticist, had crossed the native Ukrainian cattle with the yak from Siberia. The resulting hybrids showed many peculiarities arising from the diverse anatomical structure of these two species, and were of great interest to the geneticist, but of little interest to the farmers. On the other hand, one of the younger men, whose name I have unfortunately forgotten, had taken as his aim the production of a new breed of cattle which should be suitable for the arid lands of south-eastern Russia. After a careful study of the adaptability of the two species to their respective environments, he crossed the Ukrainian cattle with the Arabian zebu, and obtained hybrids which showed fewer genetic peculiarities but were of much greater interest to the farmer. The first experiment illustrates the "orthodox" geneticists' approach to research: interest in peculiarities of little economic significance, and studied without relation to the environment or practical needs; in other words, "pure" research. The second illustrates the Marxist approach: the study of the animal in relation to its environment and with a definite economic objective.
>
> I need not here discuss the theoretical aspects of the two points of view, but the conflict is certainly not a new one. It is the basis of the separation of the work of Burbank from that of the American plant geneticists, and of the work of Hammond from the English animal geneticists. It is safe to predict that in the U.S.S.R. the various aspects will be hotly debated and that the ultimate criterion will be the practical results (*Science in Soviet Russia*, Watts & Co., 1942).

The history of the origin of the genetical controversy in the Soviet Union demonstrates very clearly that the challenge to orthodox genetics did not arise for arbitrary or "political" reasons but directly out of the scientific problems of agricultural research. Certainly it was not a trivial conflict of personalities between the upstart Lysenko and the established academician, N. I. Vavilov. By his theoretical acuity and important contributions to science Lysenko was the natural leader of the new trend. But it is obvious that he represented a considerable and growing body of opinion among Soviet biologists. Of course, in a general sense there had always been an anti-Mendelian trend among Russian scientists, just as there has always been an anti-Mendelian body of opinion among British scientists, a fact which the supporters of orthodox genetics often forget. But the Michurinist trend was and is much more than this. It represents not merely a criticism of the old theory but a fundamentally new theory based on new experimental facts which have been accumulated as a result of the stimulus to science and scientific research made by the astonishing tempo of collective agriculture and the social urgency of its problems.

From 1935 onwards the controversy between the Michurinists and the Morgan-Mendelists in the theoretical field was conducted by means of widespread discussions at conferences and meetings, in the scientific and popular press, and in countless private discussions among scientists themselves. There was a full-scale discussion at the 1936 session of the Academy of Agricultural Science, and another one in 1939 at a conference on plant breeding and seed production convened by the Ministry of Agriculture. In scientific journals there were articles and counter-articles, discussions and replies, especially in *Yarovizatsia*, edited by Lysenko himself, where it is interesting to note that the Mendelians had ample opportunities of carrying the war into the enemy's camp. But discussion extended far beyond the ranks of scientists and the issue was debated at length in the columns of *Pravda* and other newspapers and among the general public.

This wide popular interest in a scientific question seems to have puzzled and slightly horrified some commentators. Yet the explanation is very simple. In a fully socialist form of society, such as exists in the Soviet Union, there are no social barriers to the application of science to production. No one wonders whether science will do him out of a job, for unemployment has long since disappeared. The collective farmer is not troubled by the doubt whether, if he grows more, he can sell his product. On the contrary, there exist pressing reasons why science should be applied to production as rapidly and effectively as possible, and why nothing should be allowed to hinder this application. The decision between two rival scientific theories thus becomes a really burning question of immediate bread-and-butter importance, and this is why the Soviet people concerned themselves actively with what in this country would be considered a purely scientific matter.

While these discussions helped to clarify the questions at issue, and did much to stimulate the Michurinist biologists to generalise the results of their experiments in a theoretical form, the real struggle between the two trends was being decided in the agricultural research stations and on the fields of the collective farms. Already by 1935 Lysenko's work had led to the introduction of two extremely important techniques, vernalisation and the summer planting of potatoes in the Southern Steppes, which revolutionised the cultivation of potatoes in these regions. It is characteristic of Lysenko and his co-workers that they drew hundreds of collective farms into the experimental testing of the new processes, so that the shrewd and hard-headed collective farmers gained first-hand experience of their effectiveness. In the same way the collective farms were drawn into the production and testing of seed from intra-varietal crossing. This work began in 1935 and by 1937 was tested on a sufficiently large scale as to leave no doubt of its value in conjunction with the other measures which the Michurinists advocated. The favourable results won the support of the Ministry of Agriculture, which began in consequence to give increasing encouragement to Michurinist lines of research. In 1938 Lysenko's principles of seed-production were officially adopted as the guide for work in the State Breeding and Seed-production Stations, which were greatly increased in number in order to meet the increasing demand of the farms for high-grade seed and better varieties.

These great advances in agriculture were not simply examples of Lysenko's practical insight, although no one would deny that he possesses this quality in a high degree, but were inseparably connected with the whole theoretical approach to the relation between organism and environment, as his own writings make quite clear. These advances are thus a measure of the correctness of Michurinist theory, which increasing numbers of Soviet biologists came to adopt as a result of practical experience—of its application in agricultural research. By 1939 Michurinist theory had already become the dominant trend among scientists in most of the research institutes in close contact with practical agriculture. The election of Lysenko in that year as President of the Lenin Academy of Agricultural Sciences marked the practical triumph of the new trend among Soviet agronomists.

II

THE VICTORY OF MICHURINISM

I

In the ten years from 1938 to 1948 the two trends in genetics continued to exist side by side, although the relation between them was not a static one, and but for the need to devote all efforts to defeating the German fascists and to repairing the terrible damage which they inflicted, it is probable that the conflict in genetics would have been resolved earlier. Until 1948, however, orthodox genetics continued to be taught to all students in universities and agricultural colleges, and guided the work of some of the older research institutes. Most teachers in the higher institutes of learning were its adherents, as well as the directors of a number of research stations. Thus in a sense Mendelism continued to be the "official" theory.

On the other hand, the number of supporters of Michurinism was increasing very rapidly among the younger scientific workers and especially among those in the more recently established State Selection Stations, where the bulk of the plant breeding and seed production for agriculture is carried on. I shall have occasion to deal in more detail with the work of the Selection Stations in a later chapter. It was here, where research is most closely linked to collective farm practice, that the success of the new methods in seed production and plant breeding, methods based on the new theory, was demonstrated on a large scale. The Michurinists thus accumulated very abundant data testifying to the practical efficacy of their theory. In addition many new lines of experiment were developed which threw doubt on the basic postulates of Mendelism. The publication of this mass of experimental data greatly strengthened the theoretical position of the Michurinists. At the same time their successes in the practical field were reflected in increased support by the Ministry of Agriculture for the new trend.

In the summer of 1948 there took place a meeting of the Lenin Academy of Agricultural Sciences of the U.S.S.R. at which there was a further discussion of the rival genetical theories. This meeting was attended by about 700 scientific workers from every part of the Soviet Union. In addition to forty-seven members of the Academy, the participants included scientific workers from agricultural institutes and experimental stations, and from the biological institutes of the Academy of Sciences of the U.S.S.R. and the biological departments of Moscow State University, as well as agronomists, zoo-technicians, and specialists in farm-mechanisation and economics. The majority were thus active scientific research workers in biology, especially in those branches most closely connected to plant breeding, development and genetics, in relation to agriculture. The gathering was undoubtedly representative of opinion among active Soviet biologists. The significance of this meeting was emphasised by the fact that three high officials concerned with agricultural development spoke in the discussion, namely, the Vice-Minister of State Farms, the Deputy Chief of the Central Grain and Oil-bearing Crops Administration of the Ministry of Agriculture, and the Chief of the Agricultural Planning Administration of the State Planning Commission.

It is unnecessary to dwell in detail on the proceedings of the Academy session since a complete verbatim report is available in English (*The Situation in Biological Science*: Foreign Languages Publishing House, Moscow, 1949). References to this material will be made as appropriate. The opening address was given by Lysenko who made a fundamental criticism of Mendelism, summing up and giving precision to earlier statements. He then went on to formulate the basis of the Michurinist position and relate it to the important tasks facing Soviet agronomy. There ensued a lively discussion lasting several days in which more than fifty speakers took part, including several supporters of Mendelian genetics. It became clear long before the end of the discussion that opinion was overwhelmingly in support of the Michurinist trend. The strongest support came, significantly, from scientists directly engaged in problems of plant breeding (including the directors of numerous research institutes), and from officials of the Ministry of Agriculture. In his closing remarks Lysenko stated that his opening address had been approved by the Central Committee of the Communist Party of the Soviet Union, which thus declared its support for Michurinism. Finally the meeting adopted a short resolution registering their rejection of Morgan-Mendelism, and recognising the correctness of Michurinist theory as a guide to scientific research. The resolution expressed

> the opinion that scientific research in the field of biology must be radically reorganised and that the biological sections of the syllabuses of educational institutions must be revised. The purpose of this reorganisation must be to help to arm scientific research workers and students with the Michurin theory. This is a necessary condition for success in the work of specialists in production and in scientific research connected with urgent problems in the field of biology.

It is important to note that the Session of the Academy of Agricultural Sciences did not take any executive decisions (apart from electing a number of new Academicians sympathetic to Michurinism and thus strengthening the new trend within the Academy). For the rest, it simply made a final summing up and decision on a long-standing controversy, and recommended that the appropriate measures be taken to ensure that scientific research in biology should proceed in future on the basis of what was considered to be the correct theory. The executive decisions to implement this recommendation were taken a few days later by the Academy of Sciences of the U.S.S.R. (to be distinguished from the Lenin Academy of Agricultural Sciences), the organisation responsible for the general direction of science in the Soviet Union. These decisions will be considered later; what is most important here is to discuss more fully the primary decision taken by the Agricultural Academy session to reject Mendelism and adopt the Michurinist theory, since this decision has been surrounded by a veritable fog of misconceptions and misunderstandings.

In the first place it must be noted that the holding of wide discussions on important questions of public policy is a very characteristic feature of Soviet life. Democratic discussion and democratic control are the basis of every social activity, from elections to the Supreme Soviet to the organisation of a collective farm, from the direction of scientific research to the running of a trade union branch. It is fashionable at the present time to deny the existence of democracy in the Soviet Union, but fortunately this question has been investigated—and settled—by more competent authorities than hack journalists and ill-informed politicians. When the world's most experienced social investigators, Sydney and Beatrice Webb, studied the Soviet Union they were impressed by its democratic structure, by the way in which public matters were widely discussed in advance of action, by the universal "government by committee" at every level. Their careful and sober observations are recorded in their book, *Soviet Communism: A New Civilisation*, and their judgment is summed up in these words:

> . . . There is everywhere elaborate provision not only for collegiate decision, but also, whether by popular election or by appointment for a given term, or by the universal right to recall, for collective control of each individual executant (p. 429).
>
> Our own conclusion is that, if by autocracy or dictatorship is meant government without prior discussion or debate, either by public opinion or in private session, the government of the U.S.S.R. is, in that sense, actually less of an autocracy or a dictatorship than many a parliamentary cabinet (p. 449).

This judgment of the Webbs has never been impugned by any serious student of Soviet affairs. Its correctness has since been strikingly demonstrated by the terrible events of the Nazi attack and by the history of reconstruction in the post-war years. No state, and certainly no multi-national state like the U.S.S.R., not firmly based on popular democracy could have survived the savagery of the Nazi attack and the temporary loss of so much of its richest and most populous territory. And no state which did not rely on the widest democratic initiative of its people could have recovered so rapidly from the terrible devastation which the Nazis created. The reality of Soviet democracy cannot be abolished by the chatter of those who, without comment, classify as democracies the United States of America or the Union of South Africa, states which in practice disfranchise, respectively, one-tenth and four-fifths of their citizens on account of certain differences in the degree of pigmentation of the skin.

The history of the genetics controversy is itself an example of the way in which Soviet democracy works. We have already seen how this scientific question arose and began to assume social importance, and how it was repeatedly discussed and argued about in all its aspects. These debates played an important part in raising general awareness of the problem, in clarifying the points at issue, and in stimulating the proponents of the rival trends to carry out the scientific work which could alone provide the ultimate decision between them. The earlier discussions remained inconclusive because the question was not ripe for decision, but by 1948 the position had changed, the scientific evidence had been assembled, opinion among the majority of scientists had swung away from Mendelism, and it had become a matter of practical urgency to decide which theory should guide biological research in the future.

2

In 1948 the Soviet Union had recovered from the setback caused by the war; the basis of its social system was complete socialism. The Government and the Communist Party were therefore preparing for the advance to the next stage of society, that is, communism. It must be noted that these terms are used in the Soviet Union, and among Marxists generally, in a quite precise way to designate definite forms of society. Under socialism all the means of production (land, factories, machines, natural resources) are in common ownership, and the social product is distributed to individuals in accordance with the work they perform, in other words, as wages, salaries, share of collective farm income, determined by the work put in. This is the state of affairs in the Soviet Union to-day. But once common ownership of the means of production is completely established the basis exists for an enormous increase in the productive power of society, many times beyond what has hitherto been possible. This leads to the next stage of society, communism, in which all the material and cultural goods of society are produced in such abundance that the social product can be distributed to individuals in accordance solely with their needs, and no longer in accordance with the work they do. The Soviet Union now stands at the beginning of the period of transition from socialism to communism, and the energies of her people are being directed to making this transition as rapid as possible. In every branch of production, increases are planned as a result of more widespread and consistent application of the most advanced scientific principles.

One of the major conditions for the transition to communism is a considerable increase in agricultural production. The basis for this is already present in the large-scale organisation of the collective and state farms, which not only permits but also encourages the application of science to every aspect of agriculture. The problem of the application of science to agriculture thus assumes special urgency in the present period of economic development of the U.S.S.R. In this context it is not difficult to understand why the 1948 meeting of the Academy of Agricultural Sciences was called (undoubtedly on the initiative of the Communist Party, a point to be discussed below). The aim was to decide (if possible) which of two biological theories was scientifically correct and therefore more fruitful as a guide to further research, and to prevent waste of scientific effort either by following incorrect theory or by unnecessarily prolonging controversy. In order to settle the question the democratic procedure was adopted of calling together those most competent to decide, the scientists actually engaged on agricultural and biological research.

At the Academy session there was a summing up of the experience of twenty years, and the overwhelming consensus of opinion was that experience had proved the truth of the Michurinist case and the barrenness of Mendelism. The evidence for this conclusion will be examined in detail in later chapters. At this stage I merely wish to emphasise two points about the session which are important for a correct understanding of what was decided. Firstly, the decision to reject Mendelian theory was taken on serious scientific grounds. The Soviet scientists considered that in their opinion the factual evidence was adequate to decide between the two trends in biology and to establish Michurinism as the guiding theory for biological research. I shall return to a discussion of this point. Secondly, the participants were well aware of the very great social implications of their decision. In every contribution to the discussion at the session the note of seriousness and responsibility can be heard, of passionate concern for the future of Soviet agriculture. The speakers fully understood that if a wrong decision were taken the whole future not merely of agricultural research but of the progress of agriculture might be jeopardised. With these wider considerations in mind they pronounced for the Michurinist trend as representing the path of advance in science, and rejected Mendelism as unscientific and actually harmful to the progress of agriculture.

When examined in its historical setting the Academy decision can be clearly seen as the logical culmination of a long scientific controversy, arising out of urgent problems of practice, and fraught with profound social consequences. The majority of Soviet biologists took the opinion that the scientific evidence and the practical experience accumulated in the course of twenty years were sufficient to enable the controversy to be settled. They considered that Mendelism had proved itself unscientific and therefore incapable of solving the problems of Soviet agriculture, and that it was becoming an actual hindrance to scientific progress, just as in the past fallacious and outdated theories have acted as a brake on knowledge until swept away by newer revolutionary ideas. They believed that the weight of scientific evidence was on the side of Michurinism, and that Soviet science and research must base itself on these ideas if it is to advance.

The judgment that was made was thus a scientific one. It is necessary to emphasise this simple fact, since precisely around this point there has been much misunderstanding. Because of the stress laid on the social and political aspects by the Russians themselves, many people have erroneously supposed that the question was decided on other than scientific grounds. This fallacious view arises partly from ignorance of the history of the controversy and partly from failure to appreciate the socio-political questions involved and their vital importance to the Soviet Union at the present stage. Unfortunately, one must add that political prejudice and crude misrepresentation have also helped to confuse the honest enquirer. I shall try to clarify some of the points around which most confusion has arisen.

It has been asserted that the majority of the participants at the Academy session were not specialists in genetics and were therefore incompetent to pronounce on the complexities of genetic theory. I do not see that this argument can be sustained at all. Genetics is the most fundamental branch of biology, and geneticists claim to lay down the basic theory on which the whole of biology must build. Genetic theory must therefore meet the critical demands of all biologists and not merely of one section. Whilst specialists have the responsibility for investigating and critically evaluating the facts in their own field (in this case genetics), the interpretation of the facts in terms of broad fundamental theory is quite properly the task, in the first place, of biologists as a whole. Nor can ordinary intelligent people be denied the right of expressing their opinion.

The idea that fundamental philosophical and scientific questions are the monopoly of the specialist or the expert implies that the mass of the people are deprived of the opportunity of genuine cultural advance. In socialist society, where the emphasis is on the fullest development of human personality, such an idea is inconceivable. In the Soviet discussion on genetics the most active part was naturally taken by the geneticists themselves armed with their expert knowledge, and the critical decision on theory was taken by active workers in the field of biology, that is, by those who by training, qualification and experience were most fitted to take it. The decision was also discussed and approved by wide circles of the Soviet public who, as we have already explained, were deeply concerned with the practical consequences for agriculture.

But what of the attacks on Mendelism in which it was condemned as a reactionary theory, of the calls to Soviet scientists to conduct an energetic struggle against reactionary scientific theories? Does this not imply a judgment based on political considerations, an attack on "Western" science as such? There is no doubt that these expressions have caused genuine concern among many scientists in this country. In order to understand them it is necessary to say a few words about the attitude to science which is held in the Soviet Union. But it is worth noting first that in all their discussions the Russians emphasise again and again that they do not reject or ignore any of the facts accumulated by orthodox genetics. In their published scientific papers they constantly refer to the most recent work of "Western" scientists. It is the theoretical interpretation which they reject, not the facts, where these are critically established. Furthermore they have a profound respect for the best traditions of materialist biological research, especially for the work of Darwin, who is more honoured and studied in Russia at the present time than in the country of his birth. They regard Michurinism as the continuation of the positive features of Darwinism.

3

The Soviet attitude to science is that of Marxism: science is not considered in isolation, but as a social activity which arises and develops in definite social relations to serve definite practical human ends. The science with which we are familiar is characteristically the product of the capitalist form of society—a fact recognised by most historians of science—and it bears within it the marks of its origin and function. The great development of modern science was a response to the technological and industrial needs of the rising capitalist class, the bourgeoisie, to use a historical term. This bourgeois character of science continues in the "West" to the present day, for science is now more than ever financed and controlled by the capitalists as a class, and operates broadly in their interests and not necessarily in the interests of all classes in society. That the division of interests in capitalist society, the clash between opposing classes, between private profit and public welfare, has a distorting and adverse effect on the progress of science is so widely recognised even by the apologists of capitalism as to be almost a truism. But Marxists believe that these features of capitalism can also reflect themselves in a more subtle way in the ideas, the theories of science.

The central conflict within capitalism is a very real one—it is the conflict between the majority who work and the minority who live on the labour of the majority. The very nakedness of this relation between exploiters and exploited leads to the development by the exploiting class of various social, political, religious and philosophical theories which, consciously or unconsciously, are designed to cloak and conceal the social reality of exploitation. All such theories have one feature in common—they are *idealist* in one form or another, that is, they do not conform to objective reality, but distort it and introduce arbitrary concepts from other regions of experience. In this way idealist theories also arise in science, theories which are basically unscientific and which in the long run hinder the advance of science because of the arbitrary element within them, representing in this highly abstract form the concrete social contradictions of bourgeois society. As capitalism declines and its internal conflicts become sharper the efflorescence of idealist theories becomes more marked, as is the case in "Western" science at the present time. Mendelism, for reasons we shall discuss fully later, is believed to be an idealist theory of this type.

In socialist society the position and role of science are changed very radically. The ending of exploitation and class divisions removes the various restricting influences on science, which assumes ever greater importance as the servant of the whole community instead of a particular class. As the tempo of economic development increases, the need for science becomes more urgent, its application more immediate. This is the burning question in the Soviet Union at the present time, when, as we have seen, the transition from socialism to communism is the order of the day. But the maximum development of science demands the continued critical revision of basic theory, especially of theories carried over from an earlier form of society which may contain idealistic and therefore unscientific elements. False theories act as a brake on social progress. The practical experience of scientific research in relation to the problems of socialist agriculture was the root cause of the doubts of the correctness of Mendelism and of its final rejection. At the same time Soviet scientists were necessarily led to a critical re-examination of the philosophical basis of Mendelism which revealed its idealist weakness.

Now the Soviet people, as has been pointed out, do not look at science as something neutral but as a vital social activity which must be concerned with the key problems of socialist development. They therefore regard the struggle against Mendelism not only as a scientific, but as a social, a political one. If the theory is wrong, and metaphysical, as they believe, then its use will tend to hinder and slow up the advance of agriculture and therefore of the great change from socialism to communism on which their aspirations are now set. That is why Mendelism is regarded as a socially *reactionary* theory, representing a relic influence of capitalism holding up the progress of the new society. Hence the exhortations to Soviet scientists to adopt a partisan and not a neutral position, that is, to see that their science is fully used in the service of the people by freeing it from incorrect and inadequate ideas, by striving for the adoption and critical development of the most advanced materialist theory. It is a call to scientists to accept in the fullest sense the obligations laid on them by the needs of society and to perfect their science for the revolutionary role in building the future which it is destined to play. This is the true meaning of the references to the reactionary nature of Morgan-Mendelism and of the need for a partisan struggle against it. It is in no sense a repudiation of the traditional experimental methods of science but rather a plea for the enrichment and more critical use of these methods.

The view of the relations between science and scientific ideas and the social frame within which they develop, which I have so briefly sketched, may be unfamiliar to many. Space does not permit a more detailed explanation, nor am I here concerned to defend these conceptions. I only wish to point out what is the social setting and philosophical basis of the Soviet view-point. Once this is appreciated the so-called "political" attacks on Mendelism become comprehensible, even to those who would by no means agree with the premises on which they are founded. Undoubtedly this question has puzzled many people who find it hard to understand why genetical theory should sometimes be discussed in what are apparently political terms. The point is that in socialist society, where there are no social obstacles between science and its application, fundamental questions of scientific theory inevitably assume also the aspect of practical policy.

The subject of dialectical materialism seems to have caused some misgiving in certain quarters. British scientists tend to be uninterested in questions of philosophical theory and are frequently unconscious of the naïve philosophical basis of their own thinking. They are correspondingly suspicious of the Russians who make no secret of their deliberate use of dialectical materialism as a guide in their investigations. The suggestion is made that the theory of Michurinism was adopted not on the basis of factual evidence but because it agrees with certain *a priori* conceptions derived from dialectical materialism. It is sufficient here to point out that one of the basic principles of dialectical materialism is that theory can be tested only by practice, that it must prove itself not merely by conformity with facts but by the extent to which it gives practical control over nature. This was indeed the test applied to both Mendelism and Michurinism, and the suggestion of *a priori* judgment is founded on a ludicrous travesty of dialectics. The relation between genetics and dialectical materialism forms the subject of fuller discussion later.

4

We must now deal with the role of the Communist Party of the Soviet Union in the genetics controversy, for this has given rise to more surprise and misunderstanding than any other aspect of the controversy. Pictures have been drawn of the Executive Committee of the British Labour Party pronouncing its views on the gene theory, certainly a sufficiently amusing conceit, but one which bears no relation to the position of the Communist Party in the very different society of the Soviet Union. The Communist Party is not only the sole political party but has come to occupy a position of freely accepted and universally acknowledged leadership within the Soviet Union. It is responsible for the primary initiative in every aspect of policy and acts as the constant sustaining and driving force within the fabric of Soviet society. To-day there can be no doubt of the immense prestige and unchallenged leadership which the Party enjoys among the people as the result of over three decades experience of its guidance. Under this leadership Russia has been transformed from the backward Tsarist "prison of nations" to the advanced socialist multi-national state of the present, with modern industry and collective agriculture. Illiteracy has been replaced by universal free education, unemployment has been abolished, the land-hungry, poverty-stricken peasants have become prosperous collective farmers, and the former colonial areas have been raised to complete equality of status and industrialisation with the former metropolitan areas of Great Russia. The prestige of the Communist Party has been further enhanced by the successful defeat of the German fascist attack and by the speed of rebuilding and of economic advance after the war (real incomes have more than doubled in the Soviet Union since the war ended).

The Communist Party does not exercise its leadership either by issuing decrees (which it is not empowered to do) or by itself deciding changes in policy (which is the province of appropriate executive organs). When the Party considers that some important change in policy or direction is required it usually initiates public discussion around the question, in some cases by issuing specific proposals, on other occasions in a less formal manner. After a longer or shorter period of discussion general clarity and agreement is usually reached, and executive decisions are taken by the competent authority, where these are required. This is the general pattern which is very flexible in operation. The method of Party leadership has been described by the Webbs in the following terms:

> It must, however, be noted that the control of the Party over the administration is not manifest in any commands enforceable by law on the ordinary citizen. The Party is outside the constitution. Neither the Party nor its supreme body can, of itself, add to or alter the laws binding on the ordinary citizens or residents of the U.S.S.R. The Party can, by itself, do no more than "issue directives"—that is, give instructions—*to its own members*, as to the general lines on which they should exercise the powers with which the law, or their lawful appointment to particular offices, has endowed them. The Party members, thus directed, can act only by persuasion—persuasion of their colleagues in the various presidiums, committees, commissions and soviets in and through which, as we have seen, the authority over the citizens at large is actually exercised. The 50 or 60 per cent.

> of the Party members who continue to work at the bench or in the mine can do no more than use their powers of persuasion on the ten or twenty times more numerous non-Party workers among whom they pass their lives. By long years of training and organisation this Party membership exercises a corporate intellectual influence on the mass of the population which is of incalculable potency. But the term dictatorship is surely a misnomer for this untiring corporate inspiration, evocation and formulation of a General Will among so huge a population. For it is, as we have seen, the people themselves, and not only the Party members, who are incessantly called upon to participate personally in the decisions, not merely by expressing opinions about them in the innumerable popular meetings; not merely by voting for or against their exponents at the recurring elections; but actually by individually sharing in their operation (p. 430).

The reader will find the Webbs' treatment of the role of the Russian Communist Party extremely helpful and illuminating.

It is clear that the Communist Party, although it embraces only a minority of the population, is not considered by ordinary citizens as something separate from them, but as their own party which they respect and trust, with which they co-operate, and to which they naturally look for guidance. It is worth noting in this connection that members of the Communist Party may at any time have to face criticism at public meetings in which non-Party people form the majority, and where serious complaints about their character or conduct can and do lead to expulsion from the Party.

5

This short account of the position and functioning of the Communist Party may help to explain the vital and accepted part which it plays in Soviet life. It is not easy for British people to appreciate this, especially at a time when communism is being violently attacked in press and radio, and accused of a whole series of contradictory intentions. Two facts must be remembered, however. First, communism is a serious social and political doctrine which has been in existence for over a hundred years, during which time it has continually increased in influence.

Secondly, communism is now the accepted ruling policy of one-third of the inhabitants of the world, and has the enthusiastic adherence of many millions in the non-communist countries. Thinking people, even though they may be opposed to communism, will prefer to form a sober understanding of its strength and its appeal, rather than take refuge in self-delusion.

The history of the genetics controversy illustrates the concern of the Communist Party of the Soviet Union for all matters of public interest. It is evident that the Party leadership realised at a very early stage the practical importance of the work of the Lysenko school. They were acute enough to see that the scientific controversy was pregnant with decision for the future of agriculture, and they therefore encouraged discussions, debates, and polemics on the subject, in accordance with normal Soviet practice, as a means of working towards clarity. Hard-hitting public polemic with a fair field for all and no quarter is an old English custom (unfortunately now fallen into disuse) which the Russians rate very highly. We have already seen how the debate was continued for many years. Since it was clear that expert opinion was deeply divided, the Party leadership was in favour of allowing both trends the opportunity of showing what they could do, thus providing the practical evidence which must be the final criterion, whilst at the same time discussion of fundamental theory was encouraged.

That the initiative for the 1948 genetics discussion came from the Central Committee of the Communist Party is undoubted: and is clearly stated in a leading article in *Pravda* (June 29, 1950). We have already discussed the reasons for raising the question again at this juncture. The Central Committee was pre-occupied with the mobilisation of popular energy for the task of transforming socialist into communist society. As a preparation for this new phase of social activity discussions were initiated in a number of fields including philosophy, the arts, architecture, science. The general purpose of all these discussions was the same. It was to raise the awareness of the people of the immediate social tasks and to secure their reasoned and enthusiastic co-operation in fulfilling them. And it was also to gain, as far as possible, theoretical clarity in every field on the basic line of approach, so that no efforts should be wasted fruitlessly and that all energies could be directed most effectively to raising the economic and cultural level of the people.

It must be understood that the Russians believe emphatically that all activities have to be consciously guided by clearly defined scientific theory, the correctness of which is tested by its efficacy in the course of carrying out the activity. They do not believe in what is popularly known as "muddling through" and, more politely, as "the empirical approach."

The very great practical significance of the issue in biology has already been dealt with, and the reasons why the Central Committee of the Communist Party initiated the biological discussion are sufficiently clear.

The decision in favour of Michurinism was not dictated beforehand by the Central Committee, as is quite obvious from the verbatim report of the discussion. The attitude of the Central Committee was not announced until Lysenko's closing speech, by which time the opinion of the great majority of scientists was perfectly obvious. In fact, what the Central Committee did was to accept and endorse the considered opinion of Soviet biologists on a major question of scientific policy. Throughout the controversy the role of the Communist Party had been a stimulatory or catalytic one, directing attention to a scientific problem of social urgency, creating the general conditions in which it could be solved, but not interfering with the scientific work necessary for its solution. Not until scientific opinion was substantially agreed did the Party finally endorse the Michurinist trend, and this endorsement was intended to signify that administrative decisions should now be taken, and was interpreted in this way. Of course I do not wish to imply that scientific opinion was completely unanimous. The report of the Academy session shows that it was not so. But this is a position that has to be faced by any government or policy-determining body which is not committed to a course of eternal drift.

A few days after the conclusion of the session of the Academy of Agricultural Sciences there took place a specially summoned meeting of the Academy of Sciences. This meeting took a number of decisions on the future organisation of biological research and teaching. These will not be recapitulated in detail:

a complete version appeared in the *Anglo-Soviet Journal* (1948, Vol. IX, No. 4).

Briefly summarised, the main results were as follows. Three laboratories, engaged on work on animal and plant cytology, were closed down, and the director of one of them (Academician Shmalhausen) was relieved of his duties. One of the laboratories closed down was that of Professor Dubinin. The plans for scientific research in the establishments under the Biological Department of the Academy were to be revised so as to develop work along Michurinist lines. Publication of more work on the theoretical aspects of Michurinist biology was planned. The plan of training of post-graduate students at the Institutes of the Department of Biological Science was to be revised. The composition of the scientific councils of the Biological Institutes and of the editorial board of the scientific journals of the Biological Department was revised by removing supporters of Mendelism and replacing them by Michurinists. Lysenko was included in the Bureau of the Department of Biological Science of the Academy. It is interesting to note that Lysenko had not previously been a member of the Bureau, although he was elected to the Academy in 1939.

The general effect of these changes will be to strengthen the Michurinist trend in Soviet biology and make it more and more the guiding theory in research and teaching. The changes were carried out entirely by the Academy of Sciences, the organisation of scientists which has official responsibility for the general planning and supervision of scientific work in the U.S.S.R. Thus both the scientific decision between Mendelism and Michurinism, and the organisational consequences of this decision, have been the responsibility of the Russian scientists themselves. The Communist Party and the Government (mainly in the form of the Ministry of Agriculture) actively and persistently encouraged the scientists to come to a decision, undoubtedly they provided facilities for the rising Lysenko school to develop its experiments, but they did not at any stage interfere in the scientific conduct of the battle.

It may, however, be said that nevertheless the decision to reject Mendelism has "official" force and that by suppressing a particular theory it represents an attack on the freedom of science. I do not think we need dwell on this point very long. Every government which provides money for scientific research claims and exercises the right to general control over the research programmes which it supports. If the Soviet Government is convinced that Lysenko is right and the Mendelians wrong then it is obviously within its rights—and is indeed only fulfilling its duty to its citizens—in insisting that research work within officially sanctioned programmes shall proceed along the general lines which most of its scientists believe to be fruitful. Certainly this is the view of the vast majority of Russian scientists who are sincerely and passionately concerned with using science in the interests of human progress. At the same time it may be noted that Russian scientists enjoy much wider freedom than scientists in most capitalist countries to pursue researches along unconventional lines and into problems apparently remote from any practical application. An interesting example is the support given to Gurevich for work on mitogenetic rays, although this work has never found general acceptance either in the Soviet Union or elsewhere.

Defenders of abstract freedom in science are apt to forget that some four-fifths of Britain's scientists are employed either by the Government or by private industry, their programme of work is laid down (frequently within very narrow limits), and many of them have experienced the arbitrary shutting down of promising lines of work, or the sudden shifting from one job to another for inexplicable or inadequate reasons. If some Russian Mendelians have had to change their field of scientific activity at least they know that the reason is based on major policy which has been widely and publicly ventilated. There is no evidence that Mendelians have been either victimised or intimidated. Those who spoke in the Academy discussion were obviously in no trepidation. There is certainly no question that any of them will be prevented from continuing their scientific activity, although they may have to change their field of work (a necessity which has also fallen to the lot of many British scientists, for different, though for no less compelling, reasons). Professor Dubinin, for example, who was most severely criticised by Lysenko, is known to be still teaching and lecturing and doing research work in zoology, although he has stopped his investigations into the cytology of *Drosophila*. A paper by Professor Zhebrak, who spoke for the Mendelians in the discussion, was accepted and appeared in the Reports of the Academy of Sciences about a year after the biological discussion; whilst Academician Zavadovsky is also still publishing (1950). There is no reason to suppose that other Mendelians will fare any worse.

Before concluding this chapter it is necessary to add a few words about the contentions raised by Professor Julian Huxley in his book, *Soviet Genetics and World Science*. Huxley's main thesis, which he repeatedly stresses, is that in the U.S.S.R.: "There is now a party line in genetics, which means that the basic scientific principle of the appeal to fact has been overriden by ideological considerations." All other issues are, in his opinion, "either irrelevant or merely subsidiary to the major issue, which is the official condemnation of scientific results on other than scientific grounds, and therefore the repudiation by the U.S.S.R. of the concept of scientific method and scientific activity held by the great majority of men of science elsewhere." This latter statement itself is extremely confused, since there has been no repudiation, official or unofficial, of scientific results, i.e. critically ascertained facts. It is only certain interpretations of these facts which have been repudiated. However, Huxley's general meaning is clear in spite of its loose formulation. He considers that Michurinism was adopted because it represented the pet theory of the highest leaders of the Communist Party and the Government, and not for scientific reasons.

Now the interest of the Soviet Government in rapidly raising agricultural yields is obvious to all. Indeed, hostile critics of the U.S.S.R. like to stress the alleged deficiences of Soviet farming. Why, therefore, should the Government, which has the responsibility of feeding the people, and the most obvious reasons for doing so as well as it can, deliberately force on the scientists a false unscientific theory which can only lead to disaster? Why should a Government, which by universal admission has fostered science and its application on an unprecedented scale, frivolously insist that scientific method is not to be applied to one of the branches of research where its application is most urgent? To these questions Huxley is unable to give a coherent answer in the whole of his book, and in spite of dragging in a host of "irrelevant or merely subsidiary issues" at inordinate length. There is no answer, because Huxley's picture bears no relation to reality. The Communist Party did not adopt Michurinism because it coincided with some pre-conceived ideas of their own, but because after serious consideration of the scientific evidence they concluded that Michurinism is a more scientific theory than Mendelism, and that its application to research and agriculture would be more fruitful. It is quite open to Professor Huxley or anyone else to believe that the Soviet Government and scientists were wrong, that they made up their minds on insufficient or even incorrect evidence. But it is a profound mistake, which leads to a misunderstanding of the whole issue, to imagine they did not consider the question primarily as a scientific one.

The origin and development of the controversy as they have been outlined completely disprove the contention that Mendelism was rejected for non-scientific "ideological" reasons, and I shall not recapitulate what has already been said. I should like, however, to make two quotations from very different sources which seem to me to put the matter in perspective. The first is from a correspondent in the *Economist*, who gives the following shrewd appreciation of the practical background of the genetics controversy:

> The layman cannot judge the strictly scientific pros and cons of this controversy, which has baffled even some of the prominent western geneticists. Much clearer is the practical interest involved in it. The Party leaders apparently believe that at least a vital part of their agricultural policy depends on the answer which the geneticists give to the problems of heredity. . . .
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> The problem with which the Ministry of Agriculture has been confronted emerges from a statement in the *Bolshevik* that in 1948 not less than about 18 million acres of collective farmland have been planted with seeds prepared in accordance with the Lysenko method. An area as large as the land under grain cultivation in this country has now in effect been put at the disposal of the Lysenko school as a sort of a gigantic experimental station. In fact, the 18 million acres are, of

> course, scattered over many parts of the country. Whatever the scientific rights and wrongs, the scale of this association between biology and agriculture is remarkable. The Ministry of Agriculture claims that it has been encouraged to go ahead with this vast experiment by Lysenko's previous successes. In 1946–47, it is said, hydrid seeds prepared according to his method . . . began to produce crops in a way which convinced the Ministry that it was justified in expanding the experiment to its present dimensions. The crop of Lysenko's frost and drought-proof seeds is claimed to be several hundredweights higher per hectare than that of all other standard seeds. In justification of its present course, the Ministry explains that, ever since the 1924 drought, it has given the Morganist geneticists the chance to go on with their work; it has financed their experiments which involved many costly expeditions; and so on. The Morgan school, however, has not delivered the goods; whereas Lysenko has. And now the Ministry has had to make up its mind about its attitude towards the competing theories.
>
> One can only sympathise with the practical administrators and their difficulties. They have had to decide to which of the two schools they ought to entrust so many million acres, and they have probably made their decision on a strictly practical basis (*Economist*, January 22, 1949).

The second quotation is from the speech of Professor Turbin at the Lenin Academy session:

> The new Michurin theory of heredity did not arise in our country by chance, it was not the result of the failure of its adherents to understand the chromosome theory of heredity, as we often hear the opponents of Michurin genetics say. This theory arose in the regular order of things as a result of the higher demands presented to agrobiology by our socialist agriculture and of the creation of conditions which facilitated both the presentation and the correct solution of the big new scientific problems connected with the search for means of directing the development and heredity of agricultural plants and animals. It arose as a result of the thorough tests to which previously known facts had been subjected, and of the discovery of new ones which proved that the explanation of heredity given by the chromosome theory is useless.

The evidence is overwhelmingly against Huxley's view that the controversy was settled on non-scientific grounds by ideological pressure from the Communist Party or the Government. It may be wondered how Huxley could have been led to so unrealistic a standpoint. There seem to the writer to be three reasons. In the first place, Professor Huxley's own distinguished contributions to science have all been within the framework of Mendelian (Neo-Darwinian) theory and he has become so convinced of its truth as to be unable seriously to consider the possibility that it may be wrong. Indeed, much of the argument in his book is vitiated by the assumption that world science is equivalent to belief in the gene theory of heredity. He is unable to appreciate the strength of Lysenko's criticisms, just as he is blind to the basic weaknesses which have at the present time thrown orthodox genetic theory into profound crisis. Secondly, Huxley neglects, or is unaware of, the way the new ideas in genetics have arisen from practical problems—a fact which is essential for their comprehension. Michurinism thus appears to him as an arbitrary invention of the devil Lysenko and not as a natural development. Finally, Huxley is ignorant of the large body of scientific evidence which the Michurinists have accumulated and has been wrongly led to believe that it is negligible.

I have had to discuss the general history and background of the genetics controversy at some length in order to remove, if possible, some of the confusion with which it has been so assiduously surrounded. It has been shown how the theoretical question arose, from the practical requirements of socialist agriculture and how it was decided in a democratic manner as a scientific question fraught with important social consequences. In the remaining chapters we shall be concerned with a critical discussion of the scientific evidence on which Michurinism is based.

III

THE THEORY OF THE GENE

I

BEFORE proceeding to a consideration of the positive features of Michurinist biological theory and the experimental evidence on which it is based, it will be well to discuss the basic reasons advanced by the Russians for the rejection of Morgan-Mendelism. These reasons centre round a fundamental criticism of the gene theory of heredity. Michurinism is much more than a mere attack on the gene theory, but since attention has been concentrated on this focal point it is logical to begin our discussion from this negative side.

It is not my task to give an account of orthodox genetics. Readers who are unfamiliar with the subject will find many excellent text-books as well as more popular expositions readily available. For the purpose of the ensuing discussion it is only necessary to state the central assumptions which underlie the detailed structure.

According to Mendelian genetics heredity is determined by special material particles—the genes—contained in the nucleus of the cell, and arranged in linear order within the chromosomes. The genes are conceived as self-reproducing particles probably consisting of nucleoprotein material, and each cell of a living organism contains a complete set, since cell division is accompanied by reproduction and division of the genes. The gene is spoken of as the "atom of heredity" and each gene is assumed to control specifically some process of development; a common view is that many, if not all genes control the synthesis of specific enzymes. Genes may interact with one another, and their activity is also believed to be greatly dependent on the position they occupy relative to other genes in the chromosome, in other words, heredity depends not only on the presence of the genes but also on their arrangement within the chromosome. Other hereditary particles lying outside the nucleus and free in the cytoplasm have been postulated. These are called plasmagenes: they play a minor role compared with the nuclear genes, and indeed Mendelian geneticists are not unanimous in asserting their existence.

The basic position of Mendelism is stated by Huxley:

> Neo-Mendelism is the general science of particulate heredity. It has demonstrated that the hereditary units postulated by Mendel do actually exist. We now call them genes, and define or describe them as self-reproducing units of living matter. Each kind of gene may exist in a number of different forms, called allels (or alleles). The genetic difference between tallness and dwarfness in Mendel's peas was due to difference between two allels of the same kind of gene.
>
> But it has gone much further: it has discovered that in all types of organisms so far investigated . . . there exists a material basis for inheritance, a special organ of heredity. This is constituted by the total assemblage of genes (which in higher animals, must amount to several thousand different kinds). Furthermore the genes are arranged in a definite linear order within the cell-organs called chromosomes; their number is also kept constant (usually two of each kind of gene in each cell). The whole system is thus extremely complex and highly organised—as we would expect if it has to discharge the varied and delicate functions demanded of an organ of heredity. . . . The chromosomes are thus a distributing mechanism in heredity. The organ of heredity has other functions to perform, notably to influence and regulate the processes of development, whereby the egg or spore develops into the adult animal or plant (*Soviet Genetics and World Science*, p. 3).

This may be compared with a similar statement by Darlington:

> Genetics rests on the axiom that the character of an organism depends on the reaction of its genotype and its environment. Where a plant is propagated by graftings or cuttings all over the world and for a great space of time, its environment and its observable characters change continually but its genotype remains the same. When it is brought back to the old conditions its old character reappears. We therefore say that there must be material particles within the

> organism which reproduce themselves without change and determine this constancy within it. That at least was the simplest assumption and one that was made long before any such particles were seen. The corpora genitalia of the ancients became the ids of Weismann and the genes of Johannsen. Now, however, we find that all cells contain certain visible particles lying inside the cell nucleus. These particles alone are indispensable to the reproduction of a cell or of a whole organism. They are characteristic and similar in their behaviour in plants and animals. We therefore assume that the nuclear particles are responsible for heredity. The nucleus is in fact the seat of the genotype very much as the brain is the seat of the mind. We merely know more about the organisation of the nucleus than of the brain.
>
> This brings a contradiction into the notion of genotype and environment. The organ of the genotype is not one but many nuclei distributed throughout the body. These nuclei are surrounded by a material, the cytoplasm, through which they exert their effect on the organism and on one another. They must be capable of interacting in the course of development. The cytoplasm is therefore the agent through which differentiation is established between the parts of the organism. It constitutes an inner environment coming between the organs of the genotype and the outer environment (*The Evolution of Genetic Systems*, 1946, p. 1).

The genes, according to this picture, interact in a complex manner with the external environment during the development of the organism, so that the characters of the adult organism are a product of this interaction. The environment does not however affect the hereditary constitution directly. The source of the variation shown by living organisms is to be found in apparently spontaneous changes which arise in the apparatus of genes. The matter is expressed in the following way by Huxley:

> The genes possess the essential property of life, in that they are self-copying. But self-copying is not always exact: inexact self-copying occasionally occurs and produces mutations. These still possess the properties of self-copying and further mutations. The mutations are random, or we had better say undirected, in the sense that they occur in many directions, and that they are not adaptively related either to the

> environment or to the general evolutionary direction being pursued by the stock, or to the agencies which have produced them. Some of them, indeed, seem to be entirely due to chance, in being due to spontaneous rearrangement of subatomic structure (*Soviet Genetics and World Science*, p. 145).

These mutations are then subjected to natural selection and form the basis of evolutionary change. This, according to Darlington, is the "essential Darwinian principle of evolution by the natural selection of spontaneous and originally unadapted variation." Whether this view can be justifiably called Darwinian may be questioned, but it is certainly the basis of Mendelian theory.

The two propositions on which Mendelian genetics rests are, the determination of heredity by a specialised part of the organism, the genes, and the origin of variation by undirected mutations within the gene apparatus. The gene theory thus assumes the existence within each cell of a living organism, of a definite "organ of heredity," consisting of a specific linear arrangement of self-reproducing material particles, in other words, it assumes the existence of a special hereditary substance. This last phrase is used by Lysenko in his criticism of the gene theory, and will occur in our discussions. It is as well to explain at the outset that it is not intended to credit the Mendelians with belief in a single specific substance as the material basis of heredity. It simply refers to the assumed existence of a special organ of heredity, the system of genes.

Now the proponents of the gene theory have been so impressed by its admitted aptitude for describing the results of breeding experiments that the extreme shakiness of its foundations, and the powerful criticisms which have been directed against it, are generally forgotten. I am not referring to the attacks on Mendelism made by the biometric school in the early years of the century, although they raised some points of substance which have never been answered. Their criticism of the ill-defined, non-quantitative, subjective nature of many Mendelian "characters" is well founded. They also correctly pointed to one aspect of the formalism of Mendelian genetics, namely, its attempt to ascribe effects in the offspring to particular structural characters in the parents without reference to the previous history of the parents. The weakness of the gene theory lies much deeper, however, in the concept of the gene itself.

In this country the philosophical objections to the gene concept were stated very cogently by Woodger (in *Biological Principles*, 1929). He draws attention to a common but fallacious mode of reasoning by which change is "explained" in terms of some persistent feature of that change (usually a material substance):

> Wherever persistence is discoverable it tends to be interpreted as persistence of stuff. . . . We see the same tendency in theories of "heredity." The persistent mode of characterisation of a race of organisms is interpreted as a consequence of the persistence of a kind of stuff in their germ-cells. Explanatory entities in natural science thus always tend to take the form of enduring things which are supposed to persist unchanged and *account for* the changes which are actually observed (p. 207).

Woodger seems to regard such reasoning as a natural human error and does not make explicit its connection with some form of philosophical idealism. Nevertheless his exposure of it is extremely penetrating, and leads him to a fundamental criticism of genetic theory along the same lines. He points out that the aim of the gene theory is to explain the mode of development of organisms. But it is impossible to explain development in terms of something which does not itself develop, and therefore the gene theory cannot form an adequate basis for a general theory of biology.

In this connection Woodger remarks:

> . . . The present position in regard to the chromosomes seems to be that they offer a model for the interpretation of Mendelian ratios, but the genetical theories appear to have no point of contact with the problems of the embryologist. If the geneticists state their theories in a purely conceptual form—the so-called chromosome maps being regarded as expressing certain abstract relations within the organised system upon which the characterisation of the organism depends, they remain in a perfectly firm position. But nothing seems to be gained, at least from the embryological

> standpoint, by expressing such a conceptual scheme by means of an imaginable picture. Such a picture has undoubtedly been of great heuristic value as is so often the case, but it seems to add nothing to biological knowledge at present which is of any avail for the interpretation of development (*Biological Principles*, p. 370).

Woodger does not himself completely reject the gene theory, although this would be the logical conclusion of his analysis. The reason doubtless lies in the fact that he never advanced to the position of dialectical materialism (indeed he seems either to have been unaware of its existence or to have neglected it entirely). Thus his very brilliant analysis of the weaknesses of idealist theories in science and of the mechanistic conceptions which often accompany such idealism remains rather negative. But his closely reasoned discussions of the illogicalities of the gene theory have lost none of their destructive force with the passage of time and the increasing complexity of the theory. They are worthy of close study, especially by those who appear to believe that only Lysenko has had the temerity to attack the notion of genes.

The views of Woodger probably represent the clearest theoretical expression of the anti-Mendelian trend among British biologists. Unfortunately this body of opinion was never able to reach a positive alternative to Mendelism. The distinctive feature of Michurinism is that it not only completes and gives precision to the criticism of Mendelism on a consistently materialist basis but that it is able to provide a satisfactory alternative.

2

We must first briefly examine the conception of dialectical materialism in its application to natural science, since this is the basis of Lysenko's philosophical criticism of the gene. Why does Lysenko demand that biological theories must be consistently materialist? The basic postulate of materialism as a philosophical theory is that there exists a real universe of things and processes which is independent of the human mind which observes it. The term materialism is sometimes used in other senses, but we shall use the term only in its fundamental sense, as it is invariably used by dialectical materialists, including Lysenko. Lenin crystallised the theory of materialism in this way. "Materialism in general recognises objectively real being (matter) as independent of consciousness. . . . Consciousness is only the reflection of being, at best, an approximately true reflection of it." Thus materialism has nothing to do with crude theories that the world consists of "nothing but" matter. On the contrary it recognises the existence of a world of *matter in motion* (each inconceivable without the other), a world of matter in various forms of movement, organisation and complexity, but existing independently of the human mind which is itself a product of highly organised matter. Furthermore materialism asserts that the objectively existing world develops and changes according to its own laws, and that these laws can be discovered and used by man in the course of his practical interaction with the external world. The laws of development of nature, however imperfectly we may understand them, have thus an objective character and are not just arbitrary or "convenient" conceptions imposed by the human mind.

But do not all, or at any rate the vast majority of scientists, accept materialism in the sense that they believe in a real external world which they investigate? This is doubtless true, but the implications of an acceptance of materialism go much deeper. Consistent materialism in natural science demands the most painstaking efforts to reveal the objective laws of nature without including in them, either consciously or unconsciously, conceptions not deriving from the facts themselves. In the investigation of complex natural processes it is unfortunately only too easy and tempting to invoke arbitrary "extra-natural" concepts as explanations where elucidation of the real laws proves difficult. The classical example in biology is the assumption of a "vital force" which has been used to blanket ignorance and discourage investigation. Of course crude vitalism would now be rejected by all biologists, but subtler manifestations still persist in biological theory, as we shall see. When we demand that science stand on the basis of materialism we mean more than a recognition of the reality of the world and its laws. We mean that the explanation of natural phenomena must not be made in terms of concepts which are at variance with our general knowledge of natural processes. Such concepts represent ideas which are arbitrarily imposed on, or imputed to, reality, and in this sense they are characterised as *idealist*, since they imply to some extent a retreat from the basic standpoint of materialism. Most scientists would, in principle, agree that scientific theory must be materialist in the sense that we have outlined.

Whilst scientific investigation must be based on materialism it can only fully reveal the laws of movement of matter if it is also guided by the dialectical method. This method is based on the recognition of the unity and manifold interconnections between all natural phenomena, and the universal occurrence of change and development. The source of change and development is to be found in the existence of contradictions within the unity of each process. As a consequence development does not only take place by gradual quantitative change but also by sudden leaps accompanied by sharp qualitative changes. The dialectical method demands that all natural phenomena are studied not as isolated, static things, but as interconnected processes. The aim must be to define the essential interconnections and to analyse the form of movement of each phenomenon in terms of the concrete contradictions which underlie it.

The use of dialectics is founded on the practical and theoretical experience of mankind which shows that the world does in fact display the *dialectical* character and behaviour that we have indicated. As Engels remarked, "Nature is the test of dialectics, and it must be said for modern science that it has furnished extremely rich and daily increasing materials for this test, and has proved that in the last analysis nature's process is dialectical." Dialectics is thus a scientific method which guides investigation by directing attention to those essential features of phenomena which are requisite for their comprehension. It is not a ready-made recipe for prediction, nor a substitute for experimental investigation, but it is a guide to experiment and to the interpretation of experimental data. According to dialectical materialism the decisive test of the correctness of a theory, that is, of its correspondence to the objectively existing laws of movement of matter, lies in the extent to which the theory can be used to give practical control of nature by transforming it.

After this brief statement of the essentials of dialectical materialism we must proceed to consider the nature of the fundamental criticism of the gene theory made by Lysenko.

3

In the first place Lysenko rejects the conception that heredity is controlled by a special unchanging hereditary substance (the system of genes). He maintains that heredity can only be considered as a property of the organisation of living matter, a property inherent in the organism as a whole. To assume the existence of a special organ of heredity is at variance with everything we know about the nature of living matter. For it presupposes that within the metabolic unity of a living organism there exists a part which controls metabolism without itself taking part in it.

Thus we have the proposition that the genes, which remain unchanged in the midst of the manifold transformations continually occurring in the cell (in itself a sufficiently surprising property), have the further property of controlling and regulating the developmental changes which take place in the rest of the organism. But it is contrary to everything we know of the processes of nature to suppose that change and development can be determined by something which itself undergoes no change and development, and the situation cannot be saved by additional assumptions such as interaction between genes, gene-action at different times, cytoplasmic genes, position effect and so on.

That this is the basic Mendelian position is clearly shown by the following statement of C. H. Waddington:

> . . . The study of heredity by Mendelian methods has revealed the presence within the egg of a collection of unit genes, which control nearly all those characters of the adult which our experimental methods have been able to investigate. This in itself is a strong temptation to the view that organisms can be adequately summarised by enumeration of the genes they contain. . . . At the present day, in fact, it

> is probably orthodox to accept the view that an organism can, basically, be represented by its constituent genes.
>
> (*S.E.B. Symposia, II, Growth*, 1948, 2, 145)

The very serious difficulties which arise from this point of view have indeed been widely recognised by the Mendelians themselves. For example, the development of all higher organisms involves a remarkable differentiation of tissues. But if, according to hypothesis, each cell receives a complete and identical set of genes, how is it possible to account for the differences between various tissues? The same difficulties arise in embryology, in the study of organisms showing sharp metamorphoses during their life history, and in every aspect of development. All higher plants, for example, show an alternation of two generations which are usually quite dissimilar in external form. Yet they only differ in that one generation usually possesses twice the number of chromosomes (and therefore of genes) than the other. Frequently, owing to irregularities in normal reproduction, both generations have exactly the same gene complement, yet they continue to show the same characteristic differences between the generations. It is impossible in fact to derive an epigenetic theory of development from the basic Mendelian assumptions.

It was remarked above that the conception of unchanging hereditary material isolated from metabolism was in itself contrary to what is known of living systems. Supporters of the gene theory may, however, argue that this material does take part in the normal processes of metabolism, that the nucleoproteins of the genes are continually formed and broken down, and that what persists is only a certain specific structure. The maintenance of this structure must, however, depend on the organisation and functioning of the cell as a whole, which is in fact Lysenko's position, that there is no special hereditary substance. In any case the impossibility of accounting for development in terms of an unchanging specific structure still remains.

A gene is usually considered to consist of specific nucleoprotein material, probably with a definite structure and capable of self-reproduction. Now it is obvious, and this point is made quite clear by Sewall-Wright ("Genes as Physiological Agents," *The American Naturalist*, 1945, 79, 289), and by Mather, ("Nucleus and Cytoplasm in Differentiation," *S.E.B. Symposia, II, Growth*, 1948, 2, 196), that the food substances and energy required for gene-reproduction must be furnished by the cytoplasm. The gene cannot therefore be the autonomous determinant of heredity since it is dependent on the cytoplasm, and heredity must thus be determined by the whole organisation of the cell and not by part of it. The autonomy of the gene can only be maintained by assuming that it is dependent on the cytoplasm for food and energy in the same way that, for example, a bacterium is dependent on a nutrient medium for its food and energy. In other words the gene possesses the characteristic of a living organism. The "vital force" expelled from every other field of biology finds its last refuge in the gene. The *reductio* might indeed be taken further, since if the gene is a living organism it must itself be endowed with hereditary determinants in the form of genes, and we are thus led to one of those infinite regressions which is a sure indication that the original premises are fallacious.

Indeed, to speak of the self-reproduction of the gene betrays an extraordinary confusion of thought. For a molecule of nucleoprotein can no more reproduce itself than can a molecule of water. The reproduction of specific substances is a property of living systems and not of nucleoprotein, even though the latter be an extremely important and essential component of living systems.

The gene (identified with a segment of the chromosome) is moreover usually pictured as much more complex than a uniform aggregate of nucleoprotein molecules. It is believed that more than one specific type of protein, in addition to other substances, may be involved in the formation of a framework with characteristic structure and arrangement of the components. The reproduction of the chromosome with this elaborate structure is a sufficiently difficult problem of metabolism without complicating it by confused and metaphysical hypotheses of autonomy and self-reproduction, which disregard the normal laws of biochemistry and cellular physiology.

There is a further consequence of the gene hypothesis which has been pointed out by Waddington. The gene has not only the property of producing a replica of itself. It must also produce some other product (possibily an enzyme) by which it influences the rest of the organism and, while remaining itself unchanged, regulates all those complex processes of change and development which constitute the life history of the organism. One cannot help echoing the comment of Woodger, that the gene is, indeed, a very remarkable entity.

It is clear then that the postulation of a special organ of heredity in the form of particulate hereditary determinants or genes, is incapable of explaining the facts of development, and therefore of fulfilling the main task of any serious genetical theory. The idea of the gene is in conflict with the generally established laws of cellular metabolism, and leads to absurdities when critically examined. It is impossible to conceive of heredity except as a property of the whole organisation of living matter, that is, as a *process of metabolism*, not as a static structural pattern of material. The gene is thus a mental concept, an idealist picture, not consistent with the laws of development of living matter. The gene is a metaphysical entity which cannot have a real existence because it is endowed with properties which no part of a living system can possess. The nucleoprotein aggregates in the chromosome cannot be identified with genes for the same reason. To do so is to ascribe to material parts of a biological system completely foreign, non-biological, characteristics.

To deny the reality of the gene as a special organ of heredity does not imply denial of the reality of chromosomes or of their internal differentiation. There is no doubt that chromosomes possess a highly complex structure, and that they play a very important part in the life processes of the cell. What is denied is that they can possibly have the role in heredity which is assigned to them by the gene theory.

But have not geneticists demonstrated repeatedly that changes in the detailed structure of chromosomes (induced, for example, by the action of X-rays) result in changes in hereditary characteristics of the organism, and that it is sometimes possible to correlate a particular mutation with a visible change in a particular chromosome region? In a few cases it has even been shown that the reversal of a mutation leads to a reversal of the chromosome change with which it was associated.

There are two points to be noted in this connection. In the first place, because changes in some characters of an organism can be correlated with changes in the chromosomes, it cannot be concluded that all changes can be correlated in this way. Secondly, changes in hereditary constitution express themselves in many cases as definite changes in an organism's external form, in some variation in the appearance of a particular organ. It is natural to suppose that such changes in hereditary constitution may also, in some cases, simultaneously express themselves in a definite change in the form of the chromosomes, which are certainly internal organs of the cell although not organs of heredity. The change in chromosome form cannot be regarded as the cause of the change in external form or other character of the organism. Both are the expression and the result of a changed type of metabolism.

It is perhaps necessary to comment on the preposterous assertion sometimes made, that genes have actually been seen. This is based on an examination of chromosomes by the electron microscope (see *Science*, 1949, 109, 8) which gave evidence of structural differences in different bands. Since few would deny the probability that the chromosome shows heterogeneity of structure, these observations, interesting as they are, have no bearing on the question of whether parts of the chromosome can function in the manner ascribed to genes.

This analysis of the basic concept of the gene theory shows, I think, that on scientific and philosophical grounds it cannot possibly be upheld (except in a trivial sense as a statement of observed regularities in mating experiments). Lysenko's rejection of the doctrine of a special hereditary substance on the grounds that it is inconsistent with the materialist character of science is thus well founded. Indeed it is a brilliant example of the power of dialectical materialism to illuminate the theoretical foundation of a whole branch of knowledge.

It is now possible to see why the Soviet scientists reject the conception of the gene as idealist. This is something which has puzzled orthodox geneticists not a little. Heredity is ascribed to genes which are material particles. Why, then, they say, does Lysenko accuse us of being idealists, for surely nothing can be more materialist than this? But it will be seen that to these material particles are ascribed a series of properties which no material particles can possess. They are integral parts of biological systems, yet they do not develop, and on the other hand they are assumed to control development. In addition they have to possess all sorts of other biologically inconsistent properties. Thus the "material" gene is seen on analysis to be an idealist concept.

Some Mendelian geneticists have protested that Lysenko's criticism is misconceived because according to Mendelian views genes are not unchanging. This is surely a confusion of the fundamental Mendelian position, which clearly assumes that the genes are the persistent determinants of heredity during the cycle of individual development of the organism. This position is not altered by the occurrence of undirected mutations which lead to hereditary changes in later generations. Nor is the conception of the gene made any less metaphysical by endowing it with more properties, and adding to its property of remaining unchanged during ontogeny the still further property of undergoing mutational change.

There is another difficulty of the gene theory which arises in connection with evolutionary change. Mendelism does not admit a directed influence of the environment on the germ plasm. The source of variation is the undirected mutational changes in the hereditary material, that is, primarily gene mutations (but including gene rearrangements, reduplications, etc.) which may, of course, be caused by environmental factors. But if evolution proceeds only as a result of the mutation of existing genes it could hardly get very far. Furthermore it would appear that the primitive ancestors of present day forms must on this basis have possessed the same number of genes as their more highly developed descendants. In order to escape from these difficulties the Mendelians find it necessary to provide some mechanism for the creation of new genes. It is unnecessary to discuss in detail the various speculations which have been advanced. The impasse is a result of the incorrect treatment of the role of the environment in orthodox genetics.

This brings me to a discussion of the second main criticism levelled by Lysenko against Mendelism.

4

The Michurinists consider that Mendelism puts forward a view of the role of environment which is just as unreal and idealist as the doctrine of a special hereditary substance with which it is closely connected. Now Mendelian genetics does not, of course, deny the importance of the environment. The manifold adaptive and regulative relations between the organism and its environment at every moment of its life are recognised by every biologist. It is impossible to separate the conception of a living organism from that of its environment.

But the relation between heredity and environment which is assumed by Mendelian genetics is a mechanical one. The environment is considered as a background with which the unchanging hereditary material (unchanging, that is, apart from occasional mutations) interacts to give the characters of the organism. The environment affects the degree and form of expression of the characters but not the genes which ultimately determine them. It should be repeated that we are here referring to the life cycle (ontogeny) of the individual organism. The basic Mendelian assumption is that the genes remain unchanged and unaffected by the environment during development, except for the fortuitous occurrence of mutations. Mutations are assumed to result from changes in the genes which are either spontaneous or caused by external factors (ultraviolet radiation, particular substances, X-rays, etc.). Their characteristic feature is the lack of any ordered relation between the assumed gene change and the environmental factor which causes it.

Such a mechanical view of the relation between organism and environment is, in the first place, very far removed from the active adaptive interrelations observed in physiological and biochemical studies of living systems. In the second place, it implies that, although the organism is in such active organic connection with the environment that it cannot be separated from it, there is nevertheless a part of the organism which is unaffected by the environment. Yet this part which is isolated from the influence of the environment has to be credited with the ability to control (as the ultimate hereditary determinant) precisely those adaptive relations between the environment and the rest of the organism which are the essence of living matter. Thus the Mendelian conception of the action of the environment leads to the same illogicalities as the conception of a special hereditary substance.

It has already been pointed out that this conception is also a source of difficulty in connection with evolutionary change. If the environment is not the primary cause of hereditary variation in organisms then genetics is led into a sterile search for mechanisms of formation of new genes out of pre-existing ones. At the same time it becomes almost impossible to explain adaptation, that surprising yet most characteristic feature of living things.

It is unnecessary at this point to do more than indicate the essential nature of Lysenko's criticism of the Mendelian view of heredity and environment. This question will receive more extended treatment in connection with the experimental evidence in the next chapter.

Michurinism thus rejects the basic postulates of orthodox genetics as the result of a serious and profound criticism of its whole philosophical position from the standpoint of materialism. In so doing the Michurinists claim to be the inheritors of the materialist tradition in biology which was founded by the work of Darwin. When they deny the existence of a special organ of heredity and regard heredity as a metabolic property of the whole organism they are putting forward a more precise and accurate formulation of Darwin's essential position. Darwin himself reached no final conclusions about the source of the variation which is acted on by natural selection, but towards the end of his life he inclined more and more to the view that direct influence of the environment played the determining role in evolution. He also recognised the influence of the environment and of the somatic tissues on the germ-plasm. Thus Darwin's own theory of pangenesis, according to which particles pass from every cell of the somatic tissues into the germ-plasm, whilst idealist in form has a materialist core. It accepts the influence of the soma on the reproductive cells. The Michurinist theory removes the idealistic features of Darwinism but maintains and develops its materialist foundation. The Michurinists are philosophically and scientifically correct in their claim to be the creative interpreters of Darwin.

The critical re-examination of the foundations of the gene theory to which Lysenko has been led as a result of much experimental work over many years thus reveals a fundamental idealistic error at the base of that theory. For it depends on the assumption of material units of heredity, the genes, which are endowed with unphysiological, unbiological, properties and which therefore can have no real objective existence. Vitalism is untenable as a biological theory because it "explains" the working of biological systems by invoking forces or entelechies *outside* biological law. The gene is inadmissible for exactly the same reason: because its assumed characteristics are inconsistent with the general laws of behaviour of living systems.

This is not to deny the success of the gene theory in giving a description in formal terms of the segregations of "characters" in breeding experiments. But this very success largely derives from the idealistic nature of the theory, since the genes are merely hypothetical entities to which are arbitrarily assigned those properties of the complete system which are to be explained. The insuperable difficulties in extending the gene theory from a formal statement of offspring relations to a genuine theory of development have already been discussed. The attempts to construct a developmental theory in Mendelian terms have brought out very sharply the scholasticism which characterises orthodox genetics to-day, a scholasticism which arises from the idealist and fallacious nature of its fundamental postulates. There is an extraordinary proliferation of speculation and hypothesis and an almost frantic invention of fresh types of gene to do duty for a real epigenetic theory of development which is lacking. There are genes which suppress the action of other genes, genes which intensify or modify the action of other genes, polygenes, inert genes, "invisible" genes, and even genes which control the mutation rate of other genes. If required there can presumably be genes which control the mutation rate of genes which control the mutation rate of other genes.

The real reason for the scholasticism of Mendelian genetics is not understood by its supporters, but the existence of a profound crisis in gene theory can no longer be denied. Strangely enough the crisis is becoming most marked in just those fields where the triumph of the gene was believed to be most complete. Thus the most recent studies of the correspondence between chromosome regions and gene effects (in *Drosophila*) not only show important and complex position effects (mutual effects of genes depending on their arrangement) but indicate that genes may overlap, and that the picture of separate individual genes like beads on a string cannot be sustained. The implication of these results for the classical theory is sufficiently startling to have caused Goldschmidt to propose abandoning the concept of the gene. He does not however see that it is the basic assumption of a special hereditary substance which is at fault, and tries to preserve it in an equally metaphysical form as the whole chromosome instead of individual genes. Yet an essay of Goldschmidt's (*Experientia*, 1946, 2, 250) provides a picture of the confusion and incapacity of the gene theory at the present time, which is all the more instructive coming as it does after a lifetime of research along Mendelian lines.

The hypothesis that each gene is responsible for producing one specific enzyme recently acquired considerable popularity as the key which was to unlock the secrets of heredity. A number of cases were found in micro organisms which could be interpreted as gene mutations blocking a single enzymatic step in a chain of biochemical syntheses. The investigation of these blocks has indeed led to considerable advances in the knowledge of biochemical processes. Closer study is beginning to show that in several instances the situation cannot be interpreted in so simple a manner. For example, there is a mutation in yeast known as "little colony," which is characterised by the absence of the enzyme cytochrome oxidase. Genetic analysis showed, however, that the production of the enzyme must be dependent on between 6 and 20 pairs of allelomorphic genes (Ephrussi, Hottinguer, and Tarlitzki; Ann. Inst. Pasteur, 1949, 76, 419). This conclusion was too much for the authors who invoke "cytoplasmic inheritance" as an explanation but suggest rather lamely that this must be ultimately under gene control. In a number of fungus mutants lacking the power to synthesise particular nutrients it has been shown that the synthetic power is present over certain ranges of acidity of the external medium, but is lacking outside this range. These and many other facts which could be quoted throw doubt on the adequacy of the simple gene-enzyme picture.

There can be no doubt that Lysenko's criticism of Mendelism and of its inadequacy as a genetic theory of development is very weighty. We now have to consider whether Michurinism can provide a satisfactory alternative, free from the weaknesses of Mendelism. In the following chapters an account will be given of some of the experimental facts on which Michurinism is based, and in the course of this its fundamental theoretical principles will be developed and discussed.

IV

CHANGING THE NATURE OF PLANTS

I

THE Michurinists claim that the hereditary nature of plants can be altered in a directed manner by controlled changes in the environment. The experimental basis for this claim must now be considered, and it will be well to begin with experiments on the conversion of winter forms of cereals to spring forms, since these were the first experiments carried out in this field.

The characteristic of winter cereals is that if sown in the spring they fail to form ears although they will continue to grow vegetatively until the end of the season. It has been shown by Lysenko that the capacity to form ears depends on the plant's passing through a definite internal qualitative change, known as vernalisation. Once this stage has been accomplished the plant becomes capable of forming flowers in favourable conditions, but if the vernalisation stage has not been passed then flower formation is impossible even though all other conditions are suitable.

Vernalisation requires definite external conditions in order to take place, conditions that are quite precise and specific for each kind of plant. The characteristic feature of winter cereals is their requirement of rather low temperature for vernalisation. If sown in the autumn they find the required low temperature during the winter months and will proceed to ear normally in the following summer. If sown in spring they miss the low temperatures and are unable to pass the vernalisation stage and so remain growing vegetatively without earing. Spring-type cereals differ from the winter-type in that they require somewhat higher temperatures for vernalisation, and are thus able to ear when sown in the spring. The phenomenon of vernalisation was noted as an isolated fact by a number of observers prior to Lysenko, but he first comprehensively investigated it and realised its deeper significance as a general feature of plant development. The property of being spring-type or winter-type is a stable hereditary characteristic.

Before 1930 Lysenko had shown that the vernalisation of winter wheat can be accomplished before it is sown. The process is, in brief, to allow the grains to take up water and swell, and then to keep them for the required time (determined by experiment) at a temperature of 0° to 3° C. The grains are then dried off: they show no signs of germination but when subsequently sown in spring they ear at the normal time, showing that they have passed through the phase of vernalisation. This treatment, it must be noted, has no effect on the hereditary behaviour of the plants. The progeny of the pre-vernalised spring-sown wheat is still winter wheat; if sown (without pre-vernalisation) in the following spring it will not form ears. However, in a series of experiments carried out mainly between 1935 and 1940 Lysenko and his co-workers established that permanent changes in heredity can be induced by appropriate changes in external conditions at the critical period of vernalisation.

In the earliest experiments winter wheat was sown in the greenhouse and kept at a temperature higher than the temperature required for vernalisation in normal conditions. Thus Shimansky (1938) raised winter wheat "Kooperatorka" in this way, using as initial material six typical ears which were sown and harvested separately. After 152 days 30–40 per cent. of the plants eared and gave ripe seed, indicating that these plants had succeeded in completing the vernalisation stage, although very slowly, at the higher temperature. The seeds were sown and raised again in the same conditions. This time the plants eared in 77 days, whilst controls sown at the same date showed no signs of earing at 77 days. A third generation was raised in the same way and gave ears at 46 days. The seed from the three generations which had passed the vernalisation stage at the higher temperature was then sown in the field, together with some of the original seed material as control, on March 20. The controls and experimental material emerged simultaneously, but whereas the experimental plants behaved as spring forms and eared on June 5 and ripened by June 29, the control plants did not ear at all.

Such experiments indicated the means of inducing hereditary change in a directed way. With characteristic insight, Lysenko suggested that the later stage of vernalisation was the critical period. To change the conditions of vernalisation of a plant, it should be allowed to undergo vernalisation in the normal conditions, and then towards the end conditions should be altered *in the desired direction.* If the right moment is selected the plant will, although slowly and, as it were, with difficulty, complete the process of vernalisation. In these critical conditions the change will become hereditarily fixed (provided always that the conditions for the development of the new character are present in subsequent generations). Thus, concretely, to change winter wheat to spring wheat, vernalisation should begin at the normal low temperature but complete the last stages at a higher temperature.

There are three methods which can be used to convert winter to spring forms (based on the method outlined):

1. Vernalise in glass-house conditions forcing the plant to complete the phase at a higher temperature.
2. Seeds are vernalised for varying periods before sowing. They are then sown in the field in spring, keeping each pre-treatment separate. Seeds which were completely vernalised before sowing will give ears at the normal time, whilst those which were still incompletely vernalised will not form ears at all. But there will be one or two treatments which were incompletely vernalised but which managed to complete the process at a higher temperature after sowing. These come into ear very late, and seed is taken from these treatments and sown in spring.
3. Sow seeds in early spring at intervals of two days. Seed is taken from those treatments which come into ear late, and is sown in spring. The principle of this method is the same as method 2 except that vernalisation takes place after sowing in the field instead of before.

By using these methods Lysenko and his co-workers converted several winter wheats (Novo-Krymka 204, Kooperatorka, Stepnyachka, Ukrainka, Hostianum 237) into spring wheats (Khitrinsky, 1949; Avakyan, 1938, 1948). The changed forms were already completely spring types by the third sowing in spring. They eared uniformly, and simultaneously with standard spring varieties. No selection was carried out during training (i.e. on the spring sowings).

An experiment with winter barley will illustrate the methods used and the type of result obtained (Khitrinsky, 1939). Five varieties of winter barley were used as starting material. Seeds were vernalised at daily intervals at 0° to 1° C. so that at the time of sowing material was available which had been vernalised for 14 varying periods from 0 to 60 days. The seeds were then sown in the field in spring on the same date. Each variety showed the same general picture and it will therefore be clearer if the behaviour of one variety (No. P02494) is described which is typical of the others. The unvernalised seeds did not ear, and those vernalised for periods from 1 to 6 days only gave a few individual plants which eared. Seed vernalised for 19 days or more gave plants which all eared normally. Seeds vernalised from 7 to 18 days showed evidence of incomplete vernalisation; the plants eared late and irregularly.

All the fertile seed from each variant was collected and sown in the spring of the following year on the same day *without* any previous vernalisation. Normal seed of the variety was sown as a control. The first leaves appeared simultaneously in all plants. The control plants failed to ear. Plants from one variant (the one which had 17 days' pre-sowing vernalisation in previous year) formed ears simultaneously on June 7. In every other variant either no ears were formed at all or, in a few cases, one or two stray ears.

Exactly the same behaviour is observed in the other four varieties. The controls failed to ear, and one variant only (in one variety, two variants with respectively 5 and 8 days' vernalisation in the previous year) eared fully and normally (June 7–11). In every case the plants which are completely converted to the spring type are those which in the previous year had been sown partially vernalised and had completed the phase at spring temperatures. The results confirm Lysenko's view that new heredity, the spring character, arises in winter plants when the vernalisation stage is completed at a higher temperature. Very similar results have been reported by Filipchenko and Shelomova (1946), who converted a soft winter wheat into a spring wheat in the same way.

The third method mentioned above has been used by Lukyanenko (1948) at Krasnodar. By sowing winter wheat Voroshilov at intervals during March individual plants were obtained which eared late and irregularly during the summer (June–September). The harvest of these plants was collected and 100 lines were sown in the following year on March 30 (the normal sowing date for spring wheat) together with controls of the original Voroshilov and a standard spring wheat. The control Voroshilov did not ear. The standard spring wheat eared on June 15, whilst 80 lines of the "changed" Voroshilov eared between June 15 and June 29, 7 lines gave earing and non-earing plants, and 13 lines did not ear. When 65 lines of the changed wheat were sown in the following year on April 4 (i.e. late) they nevertheless behaved as typical spring forms.

Experiments have also been carried out with cotton, in which the vernalisation requires a high temperature. By giving varying periods of cold treatment at the end of the initial warm period seed was obtained which when sown in the field gave plants considerably earlier than the controls. (Bereznyakovskaya, 1941).

The transformation of winter into spring forms has now been repeatedly carried out at dozens of experimental stations in the Soviet Union. The experiments have been met nevertheless with a vast amount of suspicion, doubt, and criticism. Some of the objections that have been raised seem to be based on mere prejudice or a reluctance to face inconvenient facts. It is not true that the Soviet workers do not employ adequate controls; the published work makes perfectly clear that they do, and that they are well aware of the normal scientific precautions. Another objection frequently advanced is that the original material was not genetically pure. This argument seems to be more of a smoke-screen than anything else and even its sponsors do not really take it very seriously. For the control experiments show that, whatever variations may exist between the various lines of the orginal population of self-pollinating wheats, they all unquestionably possess the winter character; and they could not be heterozygous for this character since the spring character is dominant. In fact the experiments show that in the varieties used the length of the vernalisation period (in given conditions) does not usually vary by more than a day, indicating the substantial uniformity of the population.

It has been said by Professor C. H. Waddington that the hereditary changes have been followed through too few generations. However he is apparently not aware that some of the changed winter wheats have now been followed through as many as eight and nine generations, and that they continue to behave as typical stable spring types. According to Huxley (*Nature*, 1949, 163, Nos. 4,155 and 4,156) the suggestion has been made by Professor Ashby that the hereditary change from winter- to spring-type is only apparent. The changed types are assumed to ripen so late that the grains are vernalised in the ear by the low autumn temperatures, thus giving the false appearance of a permanent hereditary change. This ingenious explanation is rendered nugatory by a study of the actual dates of earing and ripening given by the Russian workers which show that the transformed types do not differ from standard spring varieties by more than a few days in time of ripening of the grain. It is true that Lukyanenko records that his changed Voroshilov wheat takes 2–3 weeks longer to ripen than do standard spring varieties, but as it ears simultaneously with the spring varieties, this only brings the period of ripening to the middle of July.

The most serious argument that has been brought against the results is that selection was not ruled out. On this basis the observed transformations would be due to selection of already existent genetic differences instead of through the inheritance of the direct effect of treatment. This is the orthodox Mendelian picture of hereditary change proceeding by the selection of "autogenetic" variation (i.e. variation which arises spontaneously in the genotype and not as a result of the direct influence of the environment). Now the selection hypothesis is the type of "blanket" hypothesis which, suitably modified, can almost always be used to explain away direct environmental effects;

and it is correspondingly difficult to carry out experiments which rigorously exclude it (since on any evolutionary theory selection must be operative as one factor). However, a survey of the experiments on the transformation of winter- to spring-cereals makes it very improbable for a number of reasons that the results can be explained by selection of pre-existing genetic differences.

In the first place the control sowings and vernalisation studies show a negligible proportion of types with the required genetic differences, whereas the effective treatments (even in the earlier experiments when the precise factors were not so clearly understood) change the bulk of the population in a definite direction. In the later experiments the effective treatments change the whole of the population. Moreover the effective treatments are quite specific—a particular winter wheat requires seventeen days vernalisation with subsequent spring sowing in order to convert it in the following year into a spring form: sixteen or eighteen days vernalisation is ineffective. In other experiments, sowing winter wheat at the end of March gives only plants which do not ear. By sowing early in March a proportion of the plants ear late in the same year, and the progeny of the majority of these behave as complete spring forms in the following year. It is rather far-fetched to claim that these results can be accounted for by simple selection, and the explanation given by Lysenko seems much more reasonable.

Furthermore, the spring wheats derived from the winter forms in most cases lose their winter-hardiness completely as a consequence of the change in their requirements for vernalisation, which is further evidence against the simple selection hypothesis. This argument is strengthened, rather than weakened, by the fact that some changed forms (see Lukyanenko) do retain their winter hardiness, for hardiness depends both on the requirements of the vernalisation stage and on other physiological factors.

A brief digression into another field is relevant at this point. In the study of the adaptation of bacterial populations under the influence of external factors the question of the role of selection is likewise very important. Is there directed adaptation to external factors, or is there simply selection of chance mutations?

In this connection Professor Hinshelwood, who has studied problems of bacterial adaptation, has written:

> With suitable auxiliary assumptions some form of the selection hypothesis can be made to account for nearly all the facts; but it is because these auxiliary assumptions themselves appear to increase in arbitrariness and complexity as one proceeds, that one concludes by declining the main thesis as improbable (*Chemical Kinetics of the Bacterial Cell*, Oxford, 1946).

In place of the selection hypothesis he puts forward a simpler theory based on the direct action of the environment on cell metabolism (a theory that is much more akin to Lysenko's position than to current Mendelian genetics). In recent work (*Proc. Roy. Soc.* (B), 1950, 136, 562; 137, 88) he has shown conclusively that bacterial adaptation takes place as a result of directed adaptive change in the whole population, not by the selective growth of spontaneously adapted mutants. (This does not mean that the latter process cannot also occur.)

It is also pertinent to note some remarkable directed changes in the hereditary character of bacteria which have recently been carried out. By using increasing concentrations of penicillin in the external medium, Gale (*J. Gen. Microbiol.*, 1949, 3, 127) caused the discontinuous change of a spherical bacterium, *Staphylococcus aureus*, into a rod-shaped form with completely different nutritional and staining properties. The transformation of one type of *Pneumococcus* into another by means of nucleic acid material extracted from the cells is now well known. Quite recently an Italian worker has obtained changes in the enzyme equipment of certain bacteria, including the acquisition of enzymes not previously possessed, by cultivating them for a number of generations in the presence of nucleic acid extracts of other bacteria of the same and different species (Dianzani, *Experientia*, 1950, 6, 332). Similar work has been reported by Gracheva (1946) in the Soviet Union, using a strain of *Bacterium coli* which was transformed into a new species (near to *B. Breslau*) by training in a medium containing rabbit serum together with the dead bodies of *B. Breslau*. The new organisms were distinct in biological, serological and pathogenic properties.

These transformations are quite as startling as any which Lysenko claims to have induced in higher plants. Their significance is that they appear as discontinuous hereditary changes which arise in the course of metabolism in consequence of some continuously acting environmental factor. It will be seen that the course of events in bacteria closely resembles that found in higher plants, and is consistent with the Michurinist standpoint.

Returning to experiments with higher plants it must be noted that Soviet workers have also carried out many experiments on the reverse change from spring types to winter types (Shimansky, 1940; Solovei, 1939; Lukyanenko, 1948; Khitrinsky, 1950; Koltsova, 1950). Spring types normally perish during the winter if sown in the autumn. The reason for this is that, in contrast to winter types, they do not require very low temperatures for vernalisation. Consequently they are able to pass the vernalisation stage after sowing in the autumn, and in the post-vernalisation phase they are much more susceptible to frost injury. The method employed in all these experiments is to sow spring grain late in the autumn, not at the normal autumn sowing time (September–October, depending on crop and region), for this leads to practically complete loss of the young plants during the winter, but late in November or early in December. The vernalisation stage thus begins in the autumn but is not completed before really cold weather starts and the plant is therefore forced to complete vernalisation at a lower temperature than normal.

In these conditions a considerable proportion of the plants (usually 30–40 per cent.) successfully survive the winter and form grain. The seed is usually sown again in autumn at a late date. After two or three overwinterings in this way, seed is obtained which when sown at the normal early autumn sowing date gives a high proportion of winter-hardy plants. When tested by sowing in spring a high proportion of the seed is found to possess the winter character, that is, it will not form ears, showing that it has acquired the requirement of low temperature for vernalisation. These experiments are of necessity not so clear cut as the ones first described. It is obvious that there may have been some selection, but this can hardly account for the pronounced changes that take place. The controls show no sign of the hardiness or the winter character which is so completely developed by 2–3 years' training. Furthermore the method of training (late sowing) is specific in a way which is again consistent with Lysenko's explanation. In work with barley, for example, truly winter-hardy forms were only obtained from October–November sowings of spring barley, never from earlier ones. It is important to note that even after only one year's winter treatment a significant proportion of winter forms is found among the seed of the treated plants.

There seems therefore no good reason to doubt that these directed transformations of the hereditary nature of higher plants have in fact been accomplished. The results fall into line with similar directed changes that have been observed in micro organisms. The development by insects of resistance to insecticides would also appear from the evidence available to be a direct adaptation of this kind. There is also some evidence that hereditary changes may be caused in plants by alteration of critical conditions at the photo stage, as shown for example by the interesting experiments of Razumov (1939) working with pure lines of wheat and millet.

These experiments are generally recognised to be of great significance, for if they are correct, as would appear to be the case, they destroy the main theoretical basis of Mendelian genetics. On the other hand, they provide striking evidence of the correctness of Michurinist theory.

2

It is now time to attempt an outline of the Michurinist view of heredity. This view is closely connected with the phasic theory of development which was elaborated by Lysenko and which is the basis of the experimental work on vernalisation to which reference has already been made. A close study of the relation between an organism and its environment reveals that a distinction may be made between development, that is, the form-building differentiating processes, and growth, that is, simple increase in weight and size considered in abstraction from development. Development appears as an obligatory series of qualitatively distinct phases through which the organism must pass between the zygote and the formation of reproductive organs. Each phase is characterised by requiring a specific complex of environmental conditions. The required complex of conditions includes not only the external but also the internal environment, in other words the passing of each phase is also one of the conditions for the passing of the next phase. This implies the irreversibility of the phasic processes. Thus the specific internal requirements at each phase provide for the ordered development of the living organism, whilst the specific external requirements link its development adaptively with the external environment.

The two phases which have been most investigated are the vernalisation and photo phases in plants. The specific requirement for the vernalisation phase is for a particular temperature condition for a certain length of time, together with a sufficient supply of water and the presence of certain food substances produced by the plant. Until this qualitative stage is passed the plant cannot proceed to form flower initials. The complete development of the flowers depends, however, on passing a further qualitative stage characterised by definite requirements with respect to light (day length). The passing of the photo-phase also requires the internal condition that the vernalisation phase must already have been passed. It is clear that these two phases are closely linked in their specific external requirements with the normal conditions in which the plant grows, that is, they are adaptive relations which ensure proper correlation in development between the plant and its environment. At the same time they are also internal conditions of development.

This example illustrates very briefly the essential features of the phasic theory of development. Although primarily based on a study of annual plants, it clearly forms the basis for a general theory of development of all living organisms, both plants and animals. Vernalisation and the photo-phase are but two of a whole series of obligatory qualitative changes which make up the complex course of development. One of the central tasks of genetics is the definition and investigation of the most important of these qualitative transitions in plants and animals.

We are now in a position to understand the definition of heredity given by Lysenko, a definition which is rather different from the usual one. Heredity is the property of an organism to require definite conditions for its life and development, and to respond in a definite way to various conditions. Heredity is not a property of some special part of the organism, some organ of heredity, but is a property of the whole organism, of the mode of organisation of the living system.

This brilliant and penetrating definition of heredity links it to the process of development, for the essence of development consists in an ordered series of qualitative changes each of which is the internal condition (requirement) for the next one and each of which requires specific external environmental conditions for its realisation. Thus heredity is not looked at in a static formal guise as the summation of characters or as a collection of genes which supposedly determine these characters. On the contrary heredity is a process, a concrete aspect of metabolism, which expresses the active, changing, dialectical relations between an organism and its environment at every stage of its life. When the relations between organism and environment are described as dialectical, it is not a mere phrase but is intended to convey a definite meaning. It means that, firstly, the organism *actively* selects from the environment the specific conditions which it requires, and that, secondly, the environment penetrates the organism through the specific requirements of each qualitative phase, and in this way plays an active part in the formation and control of these requirements, that is, of heredity. Thus Michurinism does not separate heredity from the environment and its effects.

Each organism develops out of the conditions of its environment in its own way according to its own specific requirements. For this reason, quite different types of organism can flourish in the same environment. Provided an organism finds the conditions suitable, it develops in the same way as in preceding generations. If the environment remains more or less constant then succeeding generations will resemble one another rather closely. "Reproduction of beings similar to itself is the general characteristic of every living body." The usual definition of heredity as the capacity of an organism to reproduce its like appears therefore as a partial aspect of heredity which follows from the more profound definition given by Lysenko.

Two points need to be emphasised. The conception of heredity as the property of a living body to require definite conditions for its life and development, and to respond to various conditions in a definite way, has nothing vague or mysterious about it. It directs attention to those concrete problems of metabolism which are the real content of heredity, and demands an experimental investigation of the precise nature of each organism's specific requirements and their relation to environmental conditions, as the way to understand and control heredity. Further, it provides the basis for a genuine, epigenetic theory of development, which the Mendelian gene theory is incapable of doing. A complete theory of development is impossible with the limited knowledge we possess at present, but the Michurinist conception of heredity shows the type of investigation needed, and provides a materialist theoretical framework within which a complete theory may one day be developed.

3

It will be clear from what has been already said that Michurinism recognises the inheritance of acquired characters. This term is used in the sense in which it is understood by all biologists, as a somewhat loose expression or piece of verbal shorthand, to mean the inheritance of the capacity to develop previously acquired characters in the appropriate conditions. More accurately it implies the inheritance of characters acquired as the result of the direct adaptive influence of the environment. It is this type of inheritance of acquired characters which is rejected by orthodox genetic theory. On the other hand, Mendelism recognises the inheritance of mutational changes and characters, whether spontaneous or induced by external agencies such as X radiation or cellular poisons. Mutational changes are thus "autogenetic," since even if they are ultimately due to environmental influence, this influence is conceived as indirect and non-specific.

According to the Michurinist view the inheritance of characters acquired as a result of the directing influence of the environment is possible and is the main source of evolutionary change. This does not imply that each and every altered character is necessarily fixed in the progeny. There is abundant evidence that this is not so and this negative evidence has led to scepticism about the inheritance of acquired characters at all. The Michurinists maintain that acquired characters resulting from changes in metabolism are only fixed in heredity in certain specific conditions which will be discussed in more detail in a moment. But first it may be well to consider the general evidence bearing on this point.

Some of the positive evidence for the inheritance of acquired characters in certain conditions has already been summarised, not all of which comes from Soviet sources. Space does not permit a review of the older experimental work (see e.g. Detlefson, *Physiological Reviews*, 1925, 5, 244). There can be no doubt, however, that some of this work is extremely suggestive, and that the negative attitude to it which is common among biologists is often more a result of a predilection for Mendelian theory than of a critical appraisal of the results. The classical experiments of Kammerer are certainly very striking, and it is unfortunate that they should have been surrounded by so much irrelevant prejudice. It is no argument to say that they have not been confirmed merely because no one else has undertaken the necessary laborious investigation.

In more recent times there have been the striking experiments of Guyer and Smith on inherited eye-defects in rabbits, which are now generally accepted. Some interesting examples of inherited change of instinct in insects as a result of change in the nature of their food have recently been given by Gilyarov (1949). An influence of type of food on the varietal character of bees has been claimed by Gubin and Khalifman (1950). An inherited effect of exercise has been observed in rats (Bloor, *Journ. Biol. Chem.*, 1940, 132, 77). As long ago as 1909 Klebs (*Sitzungsberichte der Heidelberger Akad. der Wissenschaften*, 1909 (5), 1) obtained an inherited change in the floral form of *Sempervivum* as a result of experimental treatment. This work is particularly interesting because the method of treatment was such as to cause a sharp change in the nutrient supply to the reproductive organs. This is consistent with Lysenko's view that changes in heredity result from critical changes in metabolism.

The fact that Michurinists believe in the inheritance of acquired characters—and with a good deal of evidence to support them—does not mean their acceptance of Lamarckism. They recognise that the great contribution of Lamarck was his understanding of the active, formative role of external conditions in causing evolutionary change. In this Lamarck was fundamentally and historically correct, and nearer to the right track than the so-called Neo-Darwinists. But Lamarckism contains idealistic weaknesses deriving from the period when it arose. Because adaptation is considered as a process separate and apart from development, Lamarckism is unable to clarify the *specific conditions* in which adaptive variations arise and become heritable, and hence arbitrary conceptions of purpose or volition are introduced, or naïve ideas of the inheritance of acquired characters in general. According to Michurinist ideas adaptation and development are inseparably connected: the organism changes as it develops.

The way in which heredity and variation is approached by Michurinist genetics has already been broadly indicated, but the question must now be considered in a little more detail. According to this view, heredity is an aspect of metabolism, indeed, it is the fundamental and definitive aspect of metabolism—the existence of specific requirements for, and responses to, the conditions of life. Expressed in another way, heredity is the active selection and assimilation of external conditions in development. The external conditions thus enter into the process of development and become the internal conditions for further development. Every character of an organism is the result of the assimilation of the particular conditions needed for its formation. Thus the environment constantly enters as a factor in the preservation of the pattern of heredity.

The chain of metabolism which constitutes the process of development ends with the occurrence of reproduction, that is, with the formation of germ cells or gametes. The germ cells normally undergo sexual fusion, and the resulting zygote is the starting point of the next cycle of development. The germ cells have two characteristic and essential properties. They have concentrated within themselves the previous developmental history of the organism and its immediate progenitors (the heredity); and they are rejuvenated and must begin the whole process of phasic development anew. The effect of the environment thus enters the germ cells as a part of the little understood process by which the specific developmental requirements of the organism become, as it were, accumulated in these cells.

The nature of this accumulation or concentration of developmental metabolism is one of the most profound and difficult problems in biology. Michurinist genetics does not pretend to be able to "explain" it but endeavours to investigate it and its controlling factors as a metabolic process, to the elucidation of which many branches of biology, including biochemistry, physiology and cytology, will have to contribute. This approach is at least a more fruitful one than the formal and idealistic Mendelian conception of a special hereditary substance passed on from generation to generation.

An organism normally develops within the fairly close limits of the average conditions to which it has become adapted in the past. At the same time, as has been pointed out, the organism possesses the characteristic of actively selecting or seeking out the specific conditions for its development. One aspect of this selective activity is, paradoxically, the power to wait or delay until the required conditions become available. In normal development, therefore, the specific metabolic phases of an organism are not disturbed, and the environment only penetrates the organism as an influence which preserves, and strengthens, the existing hereditary constitution. This is the reason for the normal stability of heredity and the universally recognised fact of the absence of inheritance of normal (phenotypic) variations.

Hereditary variation arises only when the norms of metabolism are disrupted. This can take place if the organism is exposed to sufficiently sharp changes in the appropriate environmental conditions at critical metabolic phases. Consider the example of winter wheat which has been already described. The critical requirement of a winter wheat for the vernalisation stage is a certain degree of low temperature for a certain number of days, in presence of adequate water to allow swelling of the grain. The wheat shows selective power in that it can "assimilate" the low temperature either in one period or in several periods separated by higher or lower temperatures depending on weather conditions (Razumov, 1950). The time required to complete vernalisation may thus vary, but the number of days at the required temperature (the period of actual vernalisation) will be practically the same. The wheat also shows selective power in being able to accomplish the vernalisation stage over a certain definite, although narrow, range of temperature. In the usual environmental conditions the qualitatively important phase of vernalisation proceeds in the normal metabolic manner, evoked by its historically adaptive relation to the environment.

If the temperature is completely outside the required range vernalisation will not take place and the plant will not complete the reproductive cycle. If, however, conditions are such that slow or partial vernalisation takes place and is completed at a temperature higher than its critical requirement, then the normal course of metabolism at the critical phase is disturbed. Such a disturbance is transmitted to the germ cells and causes what Lysenko calls de-stabilised or "shaken" heredity. This means that the disruption of the metabolic norm during development causes an increase in the adaptive capacity of the progeny *in the direction of the inducing environmental factor*. In other words, the progeny will have a greater capacity to adapt themselves to a higher temperature for completion of the vernalisation phase. If sown in the spring so that they "assimilate" the higher temperature, the new adaptive capacity will be fixed as a new hereditary requirement for higher temperature for vernalisation, and the winter wheat becomes a spring form. It is an essential part of the Michurinist conception that the new adaptive capacity resulting from shaken heredity can only become fixed by the action of the appropriate external conditions, acting if necessary over several generations. This action of the appropriate external conditions is often referred to in the Russian literature as "training."

Thus it will be seen that the conception of "shaken" heredity is a clear and definite one, based on experimental investigations. Those who are amused by the term "shaken" should try the exercise of translating into English some of the technical terms employed in classical genetics.

The primary influence of the environment on hereditary constitution is therefore an effect on the physiological processes of the organism, on the numerous qualitative metabolic phases which make up the course of ontogeny. Reference has been made to the vernalisation phase simply because it has been studied in some detail. But the life cycle of any organism depends on a whole series of obligatory phases; the study of some of these is now being taken up by Soviet plant physiologists (Maximov and Genkel, 1949). Organisms may thus be expected to undergo regular adaptive changes in response to changes in the environment, as a result of the "assimilation" of the changed conditions. The evidence that this is the process of change in micro-organisms has already been mentioned, and there are clear indications that heritable changes in plants occur in the same way. For example Lesage (*C. R. Acad. Sci., Paris*, 1937, 205, 872) found differences in earliness acquired by *Lepidium sativum* (cress) by cultivation in different habitats. These differences were preserved for at least eight generations on returning the changed plants to the original habitat. Using plants derived from a single seed he was able to induce inherited differences in physiology (growth rate) by cultivation at different temperatures and sowing dates.

Extremely interesting experiments have been carried out by Baranov (1939, 1950) in the introduction of plants to the high Pamirs. Seed of 44 varieties of barley was reproduced at Leningrad and also near Tashkent in Central Asian desert conditions, and seed from both sources was then sown in the Pamirs at a height of 3,860 metres. In practically every case the seed from Leningrad gave a somewhat shorter period from germination to earing than did the desert seed. But the period from earing to ripening was so much longer in the Leningrad than in the desert seed that only 12 varieties ripened at all, whereas every variety from the desert reproduction ripened and gave fertile seed. Certain differences in leaf form between the Leningrad and the desert plants were reproduced in the uniform conditions of the Pamirs. When the 12 varieties which ripened from the Leningrad seed were cultivated further in the Pamirs the varieties behaved variously. Some failed completely, but others became adapted and developed well.

Further work has shown that in all plants cultivated in these alpine conditions characteristic adaptive changes take place in their physiological processes, and these are accompanied by certain changes in external form and in anatomy. These experiments emphasise the importance of directed changeability of organisms in a new environment. They support the Michurinist conception of the formation of heredity by the "assimilation of external conditions."

The cause of heritable variation is on this view primarily due to a fundamental type of metabolic change, induced by the action of external conditions, and leading to shaken heredity, that is, to an alteration in the adaptive possibilities of the organism. Such a change in physiological behaviour, if sufficiently marked, is likely to be expressed also in morphological changes. It has in fact been found that morphological changes occur as a result of shaken heredity, when the disruption of normal metabolism is rather deep-seated.

A number of examples are known where pure varieties have given morphological variants when transferred to new localities with markedly different climatic conditions. Thus according to Savich-Strogonova a variety of soy produced by long-continued individual selection in South Manchuria gave great multiplicity of form when transplanted to another region, whilst a variety of wheat when grown in Far Eastern conditions similarly broke up into a series of new forms. The same phenomenon has been observed with barley when grown in the extreme north (Palchikova, 1939).

Even more striking results have been recorded in some of the experiments on the transformation of cereals which have already been described. Thus in Khitrinsky's experiment, winter barley was transformed by the appropriate vernalisation treatment into spring barley in a single year. The winter barley had uniformly many-rowed ears, but the changed barley showed considerable morphological variety, including ears with two rows of grains and others with two and more rows within one ear. Morphological changes are reported by Koltsova (1950) in a spring wheat transformed into winter wheat by autumn sowing.

Lukyanenko transformed the standard spring wheat *hordeiforme*

027, a stable form with conservative heredity, into winter wheat by three generations of late sowing which caused the end of the vernalisation phase to coincide with lower temperatures. During the change from spring to winter forms he observed accompanying morphological changes in such genetically stable characters as colour and form of ears, awns, etc. New botanical varieties appeared, with some ears with spikelets partly red and partly white, and intermediate forms between hard and soft wheats. On the other hand, some of the lines appeared identical with the original material and yet were fully transformed to winter types. The transformation of hard into soft wheat may be compared with the results of Karapetyan (below).

Another example of the same phenomenon is the conversion of *Carum Carvi* from a biennial to an annual form (Glushchenko N.N., 1949). This was accomplished by very late sowing to cause shaken heredity in the plants, followed by spring sowing. The annual form which was produced did not differ in yield from the original biennial form but showed certain morphological changes.

Filipchenko and Shelomova (1946) converted a soft wheat of winter type (*ferrugineum*) into spring types in one year by the appropriate partial vernalisation treatment. These changed plants were remarkable for their morphological variation, which was quite outside the limits of the normal specific variation of *Triticum vulgare*. Variants morphologically similar to *dicoccum*, *spelto*, *durum*, were observed, as well as the original types and some uncultivated forms. The variants were not apparently examined cytologically. The authors point out that the nature of shaken heredity caused by the assimilation of changed conditions of life is similar to that resulting from distant hybridisation. The results show that the usual Mendelian explanation of hybridisation as the recombination of genes cannot be correct, since precisely similar effects are given by a pure variety in consequence of the action of changed conditions. The significance of hybridisation is that it causes shaken heredity and an increase in the adaptive capacity of the organism.

Of the greatest interest in this connection is the work of Karapetyan (1948) who claims to have converted hard wheat

(*Triticum durum*) into soft wheat (*Triticum vulgare*) by late autumn sowing for three successive years, according to the technique that has already been mentioned in an earlier chapter. Two varieties of hard spring wheat (*hordeiforme* 010 and *melanopus* 069) were subjected to three autumn sowings. The number which survived the winter increased with each year, whilst in the third year the hard wheats produced a large number of forms of soft wheat. Thus of 857 plants, 707 were hard wheats, and 150 were soft wheats of different varieties (*ferrugineum*, *caesium*, *milturum*, *cinereum*, *lutescens* and *pseudolutescens*). The appearance of these forms is ascribed to shaken heredity caused by cultivation in unusual conditions.

This work was mentioned by Lysenko at the 1948 Session of the Lenin Academy of Agricultural Sciences, and has been greeted with doubt and derision by geneticists outside the Soviet Union. Their disbelief arises from the sudden and profound nature of the change, which implies the conversion of one species with 28 chromosomes into another with 42 chromosomes; and various explanations have been suggested, all of which assume errors of observation or of experimental technique. Time will show who is right, but meanwhile it may be pointed out that the facts are really doubted because they appear contrary to accepted theory. The experimental technique has however been considered satisfactory by Soviet biologists, who are quite as well aware of the dangers of impure stocks or accidental cross-pollination as are biologists in the rest of the world.

The results are indeed quite in line with the data from other experiments which have just been quoted. They are also consistent with the theory of hereditary change which has been outlined. Changes in the environmental conditions are assimilated by the organism and lead to progressive physiological change, since the directing influence of the environment is maintained in successive generations. At a certain stage the physiological nature of the organism becomes so deeply altered that it gives rise to sharp changes in external and internal form, even including changes in the number and form of the chromosomes.

The importance of these results in connection with the nature of the evolutionary process is clear. They indicate how new morphological and specific forms may arise as a result of hereditary changes caused by the environment. It is easy to see on the basis of Michurinist principles how a slow change in the environment may be gradually impressed on the physiological character of the organism, steadily changing it in a definite direction, until the advancing quantitative change becomes a qualitative one, marked by the sudden appearance of new morphological characters.

4

In the foregoing account I have tried to explain very briefly what are the guiding principles of Michurinist genetics in relation to the central question of heredity and environment, and to show that these principles are not in any way arbitrary but arise from a consideration of the experimental facts. The fundamental difference in principle between Mendelian and Michurinist genetics lies in the treatment of the role of the environment. The Mendelian view of the interaction between the genotype and the environment is a mechanical one. The genotype is a special hereditary material which is not directly affected by the environment. It is sometimes said to be "buffered" from environmental effects. The environment simply governs the expression of the genotype, and also by natural selection preserves those undirected changes in the genotype which are advantageous to the organism.

The central theme of Michurinist genetics is the inseparable unity of the organism and its environment. There is no special hereditary material: heredity is a property of the whole organism and therefore it cannot be in any way "buffered" or protected from the environment. On the contrary, heredity is continually created, preserved and changed by the environment; and the distinction between genotype and phenotype is unreal and metaphysical. This view raises difficulties in the minds of many biologists because it might seem to imply that all minor "phenotypic" variations should be inherited, whereas experience shows that this is not true, and that heredity appears to be very stable. Two plants of one species growing within a few feet of each other but in different soil conditions may differ by as much as a thousand times in adult dry weight. But if seed from the two is grown side by side in uniform conditions the resulting plants will scarcely differ in size.

This stability is referred to by Lysenko (1946) as the "conservatism" of heredity and may be understood in the following way. Changes in heredity arise from changes in the norms of metabolism caused by the environment, but can only be preserved if they find in subsequent generations the same conditions which called them forth. The organism lives within a range of average conditions, and therefore oscillations within this range cannot be expressed in any permanent changes in heredity since, in effect, they cancel each other out in successive generations. More significant, however, for the conservatism of heredity is the selective activity of the organism, to which reference was made a little earlier. This activity, itself the result of a long history of natural selection, operates to ensure the normal functioning of metabolism in a variable environment, and is the foundation of the stability of heredity.

There is also another factor concerned, which may perhaps be regarded as a further aspect of the organism's selective activity. Lysenko has pointed out that within the assemblage of cells that constitute an organism equilibration does not occur. On the contrary, certain cells, in particular the reproductive cells which play so essential a part in the life of the species, receive preferential treatment compared with less essential parts of the living body. As far as possible the germ cells are ensured all conditions for their normal regular development. Plants may be enormously reduced in size owing to unfavourable conditions, they may produce only one or two seeds instead of the usual large number, but their internal adaptive adjustment is such, that the few seeds which are produced are formed with normal food supply and as a result of normal metabolic processes. Changes in the metabolism of the organism are thus not necessarily or readily transmitted to the reproductive cells.

An interesting experiment carried out by Bazavluk (1946) at Lysenko's suggestion illustrates this point. It is well known that within a given variety of sugar-beet there may be considerable variation in the sugar content of individual roots. If seed is selected from high-sugar and low-sugar roots and sown separately, the resulting two sets of plants will not differ in their mean sugar content and the individual roots of each set will vary in sugar content over the same range as the original clone. The flowering shoots in sugar-beet are usually produced from buds in the apical-central zone of the root where the sugar-content is lowest; for the amount of sugar also varies considerably in different regions of the same root.

Small pieces, each containing a bud, were cut from the apical-central and peripheral zones of a number of roots, that is, from the regions of lowest and highest sugar-content respectively. The buds were rooted in moist soil and developed normally into mature plants. The sugar-content of these plants showed consistent but not fully significant differences between the two groups, those from the apical-central region having a lower mean sugar-content than those from the peripheral region. The plants in each group were self-fertilised and the seed generation from each was raised in 450 sq. metre plots. The seed progeny of buds from the peripheral zone showed a higher percentage of sugar in the roots than the progeny from the apical-central zone, and the difference was fully significant (19·14±0·06 per cent. in plants ex peripheral zone, compared with 18·52±0·098 per cent. in plants ex apical-central zone). When the same seed material was sown again the following year similar results were obtained, the sugar in the peripheral-zone plants being 1 per cent. higher than in the others. These experiments demonstrate that genetic changes may occur in the germ cells as a result of disturbance of the normally uniform and highly regulated processes involved in their formation.

Michurinist theory is thus capable of giving a satisfactory explanation of that conservatism or stability of heredity which is one of its pronounced features. The contrast between this explanation and that offered by orthodox genetic theory is very striking. Mendelism seeks the permanence and stability of heredity in the formal conception of an unchanging material structure, isolated from direct influence of the environment—a conception quite alien to the nature of living systems. To the Michurinists, however, the stability of heredity is not passive, nor is it based on mechanical notions of enduring structure; it is the dynamic stability of the continuous adaptive and selective activity of biological systems in relation with the environment. This is a biological conception which is consistent with the behaviour of living matter. The Mendelian and the Michurinist views of permanence in heredity accurately reflect the difference between a mechanical and a dialectical attitude to natural phenomena.

The Michurinist explanation of the origin of hereditary variation through disruption of the norms of metabolism also solves in principle another problem—the question of adaptation—for which Mendelian theory is incapable of accounting. Gene mutations, which, on the latter theory, are the basis of variation, are changes of molecular structure or grouping which happen if sufficient energy is available, in whatever form, to bring them about. They are essentially undirected changes which bear no ordered relation to the cause which induces them; and their effects are unrelated to the physiological processes at work in the organism or to the nature of the environmental factors. Moreover a mutational change in a particular direction cannot be repeated in an ordered manner in response to definite environmental change. It is impossible on this basis to account for continued regular adaptive change through successive generations, except by arbitrary and metaphysical assumptions.

According to Michurinist theory the nature of hereditary variation is connected in a regular and ordered manner with environmental change through the internal physiological processes of the organism. This metabolic connection establishes the adaptive relation between the quality of the changes in external conditions and the quality of the hereditary changes. In this way there arises that orderly continuation of variation through many generations, to which Darwin drew attention, and which gives rise to the adaptive characters and functions of organisms.

This conception of evolutionary change leads to a more profound view of selection, both natural and artificial. Selection is not, as in Mendelian theory, merely a mechanical sieve which operates on the undirected variations provided by gene mutations, preserving some and eliminating others. In the process of evolution, selection is creative, leading directly to the formation of new adaptive processes and characters. Natural selection is the form in which the environment exercises its creative function in changing and enriching the hereditary constitution of living organisms.

5

It is now necessary to deal briefly with a group of facts relative to inbreeding depression and its obverse, hybrid vigour, or heterosis. In this connection Lysenko makes the following observation:

> The depression and degeneration of the progeny in many inbred cross-pollinated plants is explained by the geneticists by the appearance of homozygous lethal and semilethal genes, that is persistent particles in the chromosomes. But how is it possible from the standpoint of the particulate theory to explain the numerous cases when in the same genotype inbreeding in some circumstances is so harmful that seeds are not even formed, whilst in other circumstances in the same genotype seed formation is normal and gives rise to normal plants? (Lysenko, 1936b.)

It was known to Darwin that the ill effects of inbreeding both in animals and plants could be partly or wholly removed by raising them in different environmental conditions. Thus closely related animals can give healthy offspring if, for example, they are raised on different farms. Similar effects were found by Darwin in his experiments on cross-fertilisation in plants. These results were interpreted by him as an effect of the environment on the germ cells, leading to slight differences in their heredity.

The experiments of the Soviet workers have strikingly confirmed Darwin's conclusions. Pogosyan (1946) carried out the following experiment with rye, which is a strict cross-pollinator. Complete plants were dug up and divided at the tillering phase into a family of separate shoots. Each family was isolated and grown in greenhouse conditions in pots and seven different manurial treatments were given to the plants within each family. As a result of this treatment varying amounts of fertile seed were formed in the different families, as may be seen from the following table.

Family	No. of pots	No. of sterile ears	No. of fertile ears	No. of seeds
1	10	30	17	29
2	11	10	45	170
3	9	19	16	41
4	14	13	46	165

Control families of shoots raised in uniform soil conditions gave no fertile seed at all. Thus the growth of different parts of the same plant in different conditions partly removes inbreeding depression. It does not do so entirely, possibly owing to difficulties in getting the various treatments to flower simultaneously, and also to insufficiently pronounced differences in treatment.

The control families as already mentioned gave only sterile ears. These were removed in June and new cuttings were taken from the base which were then raised in pots with fresh soil and differing manurial treatments. These formed fertile ears at the end of the vegetative period. This second set of cuttings gave 37 sterile ears, 51 fertile, and a total of 380 seeds. This seed as well as that from the families cited in the table, gave when sown a normal generation of plants quite free from the sharp segregation and signs of degeneration characteristic of plants from normal inbreeding.

A similar experiment (quoted by Lysenko, 1936c) was carried out with sugar-beet. Single roots were divided into 10 to 15 parts and these were raised in pots to the stage of flowering. Each group was normally sterile when crossed within itself, but gave fertile seed when the individual plants were grown in different environmental conditions. Again, Tsitsin showed that the flowering shoots of a single plant of the grass *Agropyron junceum* are completely incapable of forming seed when fertilised among themselves. If however the individual shoots are separated from one another and grown for one or two years in the field they become interfertile.

It has been shown by Arakelyan (1949, 1950) that inbreeding depression in rabbits may be removed by raising the animals, before crossing, in different places, where food, climatic, and geographic factors vary. Similarly inbreeding depression in *Drosophila* can be partially removed by raising the parents at different temperatures or by adding certain inorganic salts to the diet of one or other parental strain (Borisenko, 1939).

These results are incompatible with the Mendelian conception of the uniform hereditary basis of the members of a clone, and its independence of the environment. They are readily explicable in terms of the Michurinist view that heredity is formed by the assimilation of environmental conditions. Close inbreeding leads to depression and degeneration because of the extreme narrowing of the adaptive possibilities of the organism which it causes, in consequence of the practically identical heredity of the parents. If however the parents are grown in different environments their heredity, i.e. their specific requirements, will differ to a greater or lesser extent so that their union will preserve or strengthen the adaptive capacity of the new organism. This emphasises the importance of the developmental history of the genotype, in contrast to the formal Mendelian analysis of the genotype as an assemblage of unchanging components.

The phenomenon of hybrid vigour can clearly be explained in a similar way. It arises from the favourable effect on the adaptive capacity of an organism of combining within it the possibilities of two differing but complementary heredities. The degree of expression of hybrid vigour depends on the specific interrelations of the hereditary constitution and developmental histories of the parental forms, as well as on the existing environmental factors within which the hybrid develops. Hybrid vigour is a special form of the increased viability of organisms which results from the union of two slightly differing metabolisms in the normal sexual process within a single species or variety. This is the biological significance of sexual union. "The contradiction which arises between the two united but relatively unlike sexual cells enhances the internal life energy, the property to change and metamorphose," says Lysenko. This increased activity of change, of adaption, can only rise because of the property of heredity to include in itself changes in the environment. It is significant that orthodox genetics, with its mechanical separation of heredity and environment, has been unable to develop even a formally satisfactory explanation of hybrid vigour in terms of the gene theory.

A closely related question is that of the significance of intra-varietal crossing in self-pollinating plants. It has been pointed out in the opening chapter that this question, because of its practical importance, was responsible for starting the critical attack on the theoretical foundations of Mendelism. The Michurinists as a result of experience and observations of practical agriculture accumulated evidence of loss of vigour in self-fertilising plants (e.g. wheat, barley) during cultivation, which they attributed to the deleterious effects of prolonged self-fertilisation (inbreeding). Some experiments with cotton, normally self-fertile, illustrate this point (Krasovsky, 1941). Flowers were isolated to compel self-fertilisation and exclude accidental crossing for several generations. The seed from several generations of obligate self-fertilisation was compared with control seed from open flowers in which a certain amount of accidental crossing may have taken place. The plants from obligate self-fertilisation were markedly less vigorous and productive, and bore fewer fruits and seeds, than the controls.

Lysenko proposed the renovation of seed of wheat (in the first instance) by intra-varietal crossing. This was based on the assumption that other plants of the same self-fertilising variety would nevertheless show slight differences in heredity properties because of their exposure to slightly different environmental conditions, and that crossing them should lead to an increase in vigour. This assumption was brilliantly justified in practice. Within very few years extensive comparative trials on many collective farms demonstrated the effectiveness of the technique in raising yields (Dolgushin, 1939). It was shown to lead to increases in the metabolic vigour of the plants and in their resistance to adverse conditions (see, for example, Bassarskaya *et al*, 1940; Kovpak, 1939). The effect of intra-varietal crossing lasts for 6 to 8 generations but is ultimately lost (Dolgushin, 1941). Some results with barley are given by Mukhin (1949), who compared eight generations of seed after intra-varietal crossing with normal seed. The increase in yield of grain of the renovated seed over control seed was +27·4 per cent. in

F_3, +16·9 per cent. in F_4, +6·1 per cent. in F_6, +9·6 per cent. in F_7, and +4·6 per cent. in F_8.

There is now an enormous mass of evidence for the effectiveness of intra-varietal crossing, not only in self-pollinating cereals but in other crops, e.g. cotton (Tsinda, 1941), tomatoes (Brezhnev, 1949). Part of this effectiveness is due to the associated phenomenon of selective fertilisation, the discussion of which is deferred to a later chapter. But its basis lies in the process of formation of heredity in the assimilation of external conditions, as revealed by Michurinist genetics. The truth of this explanation is shown by the well-established fact that the effectiveness of intra-varietal crossing can be enhanced by growing the plants to be crossed in differing environmental conditions.

Thus Kuchumov (1949) grew winter wheat in normal conditions of culture completely surrounded by large plots of the same species given 10 different manurial treatments. The maternal flowers of the wheat were castrated and wind-pollinated from the surrounding plants in different conditions of culture. Control maternal forms were treated in the same way except that they were pollinated from a surrounding mass of the same species grown in identical conditions. Not only did the experimental plants (pollinated from the same species in differing environmental conditions) give a higher yield of seed than the controls, but when the seed was sown in uniform conditions the yield was +8·5 per cent. higher in the experimental than in the control seed. In the same experiment Kuchumov showed that the effectiveness of the cross-fertilisation of rye was similarly increased if the group of plants were grown in various differing conditions instead of in identical conditions. The yield from the seed of the former group of plants was +6 per cent. higher than that from the latter, when sown and raised in uniform conditions.

Similar results have been obtained with sunflowers, which are also cross-pollinators (Morozov, 1940). Plants of a particular variety of sunflower were raised from seed for several years in five different districts and the seed from these localities was sown together in an isolated plot at Saratov with free cross-pollination. Next year the seed from this "ecological population" was compared in variety trials with élite seed of the same variety which had been raised continuously at Saratov. The yield from the plants grown from seed of the "ecological population" was 30 per cent. higher than from the élite seed.

In maize also it has been found that to avoid depression of yield of hybrids the parents (taking due account of their previous history) must be raised in different cultural or ecogeographical conditions (Salamov, 1950).

All this experimental work indicates the important role of the environment in the formation of the hereditary nature of the germ cells. It is consistent with the general Michurinist theory of heredity which I have tried to outline, and, together with the evidence quoted earlier, it constitutes a powerful indictment of the theoretical inadequacy of Mendelian genetics.

V

VEGETATIVE HYBRIDS

I

SOME experimental work on the production of plant hybrids by grafting must now be discussed, since it has acquired considerable importance in the criticism of orthodox genetics. If hereditary determinants are carried in the cell nucleus, as the gene theory assumes, then hybridisation can only occur by the union of nuclei from two different organisms by sexual fusion, or by the continued association in the same cell of two nuclei from different organisms, as happens in certain fungi.

When a scion of one plant is grafted on to the stock of another, both components will, if the graft is successful, continue to grow and develop. There is an exchange of food substances and other metabolites between the graft components, but there is no nuclear fusion and no exchange of nuclei or chromosomes. The hereditary character of each component should, on the accepted view, remain unchanged by the grafting. Provided the graft components are genetically pure (homozygous) seed from stock or scion should give offspring true to type and free from hybrid characters, as long as it is self-fertilised and protected from accidental crossing.

Whilst hereditary independence of stock and scion is undoubtedly the rule, Soviet scientists claim to have shown a hereditary effect of one graft component on another in a certain number of instances. Such an effect, if confirmed, would represent a true vegetative hybridisation without nuclear fusion or association, and would strongly support Lysenko's conception of heredity.

It is well known that grafting occasionally leads to the production of chimæras, that is plants in which tissues belonging to both graft components have become united in an intimate way. The chimæra thus shows characteristics of both components as a result of the association of their tissues within one plant body. Graft hybrids of this type, originally investigated by Winkler, have been much studied by Soviet workers, who have repeated many of Winkler's experiments. Although they recognise the existence of tissues of double origin within such graft hybrids, the Soviet workers nevertheless regard them as a special kind of vegetative hybrid (see Glushchenko, I. E., *et al*, 1948). I shall not enter into a discussion of this rather specialised question. In the work to be described in this chapter only those examples of vegetative hybridisation are considered in which the question of chimæras does not arise.

This matter has a long history in Russia because Michurin, over a period of many years, frequently used grafting to influence the character of fruit trees in the developmental stages, and regarded as vegetative hybrids many new forms which have become important in practical horticulture. This evidence is impressive in the aggregate; but his experiments were mainly directed to practical ends and were not designed to provide critical evidence for vegetative hybridisation.

Between 1938 and 1946 a number of experiments were carried out by Khazina (1949) in which varieties of tomato were grafted on other tomato varieties as well as on species of other genera of *Solanaceae.* In a number of cases the seed progeny from the grafted plants showed inherited changes in succeeding generations. Thus the seeds from Tomato Humbert grafted on *Solanum nigrum* showed greatly increased earliness: morphological changes were observed in several instances in consequence of grafting. The seed progeny displayed considerable diversity of form and sometimes economically useful characters, such as larger fruits and high yield.

The most extensive series of experiments which have been carried out are those of I. E. Glushchenko (1946, 1948; full summary, 1950). The work was done on a considerable scale and detailed reference will be made to some typical results. Tomatoes were used as experimental material and forms were selected with sharply contrasting characters: red and yellow fruits, plurilocular or bilocular ovaries and erect or normal types of growth.

In the earliest experiments split grafting was used and the graft components were taken at different ages. The component, whether stock or scion, in which it was desired to produce changes was taken at the younger stage. In later experiments a slightly different method was adopted. Seeds which had been previously soaked for 24 hours in water to start germination were grafted on to 30-day-old stocks. In some cases also inflorescences were grafted at the period when flower-bud formation was just beginning. These later methods led to an increase in the number of positive results. The leaves were removed from the component in which it was hoped to induce changes.

The flowers of all experimental plants were carefully isolated in order to avoid accidental cross-pollination. Large numbers of control plants were raised each year to test their genetic purity and stability. In addition, controls from the plants actually used in grafting were raised, as far as this was possible, by rooting the portion removed from plants used as stocks, and by preserving plants from which portions were removed to serve as scions.

Changes were very rarely observed either in stock or scion in the year of grafting, but in a certain proportion of grafts heritable changes were observed in the seed generation in the following year. Over a period of several years inherited changes were observed in the progeny of some 10–15 per cent. of the total number of grafts made.

In one experiment the red-fruited variety of tomato Fikaratsi was grafted as scion on to a stock of Golden Queen (yellow-fruited). Both varieties belong to *Lycopersicon esculentum.* From the Golden Queen stock 4 fruits were obtained which were typically yellow in colour and contained a small number of seeds.

The seed of these fruits was sown and 31 plants were raised, of which 7 produced fruit. One plant had yellow fruits, 4 had red fruits, 1 had raspberry-coloured, and 1 had yellowish-red fruits. Thus under the influence of the red-fruited scion of Fikaratsi the yellow-fruited (recessive) stock of Golden Queen shows the dominant red fruit-colour in its offspring (F_1).

A second generation of plants was raised from the seeds of F_1 fruits, sown separately according to fruit colour. The results are shown in the following table:

Colour of Fruit in F_1	Number of Plants raised in F_2	Number with ripe fruits	Number of plants in F_2 with each fruit-colour			
			Yellow	Yellowish-red	Red	Raspberry
Yellow	58	54	42	6	1	5
Red	24	24	8	–	15	1
Raspberry	59	57	10	4	2	41

Further seed generations (F_3 and F_4) were raised from fruits of all four colours. Plants from each type of fruit continued to show segregation for all four colours. This is shown by the results for F_4 which are quoted in following table:

Colour of Fruit in F_3	Number of Plants with Ripe Fruits (F_4)	Number of plants in F_4 with each fruit-colour			
		Yellow	Yellowish-red	Red	Raspberry
Yellow	90	17	16	8	4
Yellowish-red	840	123	674	36	7
Red	58	3	15	36	4
Raspberry	76	2	14	24	36

The vegetative hybrids show continued segregation in a similar manner to normal sexual hybrids, but they differ in the type of segregation and especially in the fact that forms with the recessive character give rise to dominants.

In this experiment hundreds of control plants were grown simultaneously and showed no changes in fruit-colour with the exception of a slight reddening of 5 fruits of Golden Queen. The seed from these fruits was tested separately, but the offspring proved to be completely normal. Normal sexual crosses were also made between Golden Queen and Fikaratsi. Red fruit-colour was completely dominant to yellow in F_1, and in F_2 there was sharp segregation of red and yellow in a 3 : 1 ratio; yellowish-red and raspberry colours were absent.

Golden Queen was used as the stock in the experiment just described. In a further experiment it was used as the scion and was grafted on a red-fruited stock Sparks. In the year of grafting two fruits were obtained on a scion of Golden Queen, which had wavy red stripes all over the surface skin. The seed generations (F_1 and F_2) from these fruits gave plants with pure yellow, and plants with yellow-red fruits. Some of the plants also showed ribbed, flattened fruits characteristic of Sparks and sharply contrasting with the smooth round fruits of Golden Queen. The sexual crosses between Golden Queen and Sparks were also made for comparison. They showed sharp segregation of fruit colour, with red dominant, and complete absence of yellow-red fruits.

Another of the many experiments which might be quoted is of interest because here grafting caused permanent changes in several characters but not in fruit-colour. The variety Mexican 353 (*L. cerasiforme*) was used as stock and was grafted with Yellow Peach (*L. esculentum*). Mexican has very small red fruits (mean weight 3 g.) which are always 2-locular, whilst Yellow Peach has large yellow fruits which are usually 3-locular (less frequently, 2- 4- and 5-locular).

Mexican was used as stock and 15 fruits were obtained which were typical in external appearance, except that two were slightly larger than usual and five of them had 3 or 4 loculi. The two larger fruits, both of which had the usual 2 loculi, were used to raise further seed generations. As controls 160 plants of Mexican were grown for 3 generations, as was also the actual control (the rooted tip of the stock). No changes were observed.

The F_1 of the two fruits from the graft showed sharp variations in fruit size within a plant, ranging from normal to ten times the normal weight (3 to 30 or 40 g.), and a large proportion of the fruits had more than 2 loculi. In later generations the size of fruit increased further and the number of loculi were usually 4 or 5. The yield of the Mexican vegetative hybrid in 1946 was 52·9 tons per hectare compared with 9·7 tons per hectare from Mexican controls.

These results must be due to the plasticity of the material evoked by grafting. They cannot be due to accidental sexual hybridisation since the flowers were isolated. Furthermore the recessive character yellow fruit did not once appear in the progeny as it would have done had accidental crossing taken place in the year of grafting.

Not only do vegetative hybrids show certain characters of both graft components, but in a number of instances they show the formation of new characters. This phenomenon is most frequent where grafts are made between less closely related plants, as between different species or even genera. For example, the tomato Humbert (*L. esculentum*) was grafted on *L. pimpinellifolium*. The former has 2-locular, occasionally 3-locular, fruits of mean weight 20 g. or more. The latter has very small fruits (1 g.) which are invariably 2-locular. No changes were evident in the year of grafting but in the first seed generation (from Humbert) plants showed marked hybrid vigour and an increase in the size of the fruits. The mean weight of over 1,000 ripe fruits was 36 g.

There was also an increase in the number of fruits with 3, 4, 5, and 6 loculi. These new characteristics were inherited in F_2. The mean weight of 300 fruits from 50 plants was 40 g. compared with 24 g. which was the mean weight of the same number of fruits from 50 control plants grown in identical conditions. The plurilocular character of the fruits also persists.

Similar changes in the character of Humbert caused by grafting on to *Solanum melongena* have been shown to be inherited through 13 generations.

In some cases an examination of the biochemical characteristics of vegetative hybrids has been made, in order to compare them with those of the components of the graft. For example, plants of the F_2 and F_4 seed generations from Golden Queen grafted with Fikaratsi have been compared with control plants of Golden Queen and Fikaratsi with respect to the content of sucrose, reducing sugars, ascorbic acid, and the activity of several enzyme systems. In general, the results show that the effect of scion on the seed progeny of the stock is expressed not only in morphological changes but also in significant changes in biochemical properties.

All the vegetative hybrids obtained in these experiments have been studied cytologically. Those from inter-varietal and inter-specific grafts do not show any deviations from the parental plant either in the number or in the form of the chromosomes. Changes in the normal number or behaviour of the chromosomes is only found in inter-generic grafts. In these cases the metabolic disturbance caused by grafting is doubtless more profound and expresses itself in variation in the chromosome apparatus in addition to changes in external characters. The tomato Humbert, for example, has 24 chromosomes, but the vegetative hybrid which was produced by grafting it on *Solanum nigrum* has 26 chromosomes.

These experiments were carried out at the Institute of Genetics of the Academy of Sciences and certainly represent the most complete study of vegetative hybridisation that has yet been made. The results are very impressive evidence for the reality of the phenomenon of vegetative hybridisation. They cannot be dismissed on the grounds of faulty technique, since the most careful precautions seem to have been taken, and the experiments and controls were also on a very considerable scale. A study of the results makes it clear that they cannot be explained by accidental cross-pollination or by virus infection, as has sometimes been attempted.

2

A considerable mass of supporting evidence is available from many other laboratories in the Soviet Union, but only a few contributions will be mentioned. Essentially similar results to those of Glushchenko were obtained by Khachatryan (1948) at the Armenian Institute of Genetics in experiments with graft and sexual hybrids between four varieties of tomato. Changes in fruit form in the seed generation (F_1) of the tomato Humbert grafted on to *Capsicum annuum* were observed by Kovalevskaya (1939).

Polyakova (1946) raised three seed generations from two varieties of tomato, grafted on *Solanum dulcamara*, and on the potato Epicure respectively. The offspring of the tomato grafted on *Solanum dulcamara* showed rather marked changes in the number and size of fruits and other features, but the form and number (24) of the chromosomes remained unaltered. The offspring of the potato graft showed small differences in F_1, but in F_2 and F_3 certain changes in morphology occurred (in branching, fruit form, appearance of potato-type leaves). In these plants very marked changes in the chromosome complex had taken place. The number of chromosomes in the somatic cells of five plants examined was found to be 48, 48, 50, 51 and 51 respectively, and there were also changes in the forms of the chromosomes. These results are of considerable interest since the most marked changes in external characters after grafting are found in the plants in which the number of chromosomes remained unchanged.

In a study of vegetative hybridism in potato Filippov (1938) records numerous examples of morphological and other changes in both stock and scion as a result of grafting. An interesting feature of this work is that tubers taken from grafted plants continue to show the hybrid characters (leaf-form, colour, earliness, etc.). The changes are thus not due simply to nutritive factors, but continue to be transmitted in the course of vegetative reproduction after the components of the graft are separated.

Not all the experiments on graft hybridisation have been done with species of *Solanaceæ*. Mention has already been made of the work of Michurin with fruit trees. Some interesting experiments showing the transmission by the seed of characters acquired by grafting have been performed by Enikeev (1946). In a cross between two species of cherry, *Cerasus Besseyi* and *C. tomentosus*, the F_1 hybrid plants were treated in three ways. One group was grown in the ordinary way on their own roots. A second group was grafted at an early stage on to *C. Besseyi*, and a third group was grafted at an early stage on to *C. tomentosus*. Seedlings of the F_2 generation from these plants were then raised on their own roots in uniform conditions.

The F_2 seedlings were classified into 3 groups, according to whether they resembled one or other parent or were intermediate in certain defined characters. The results are shown in the table on p. 100, which clearly indicates that an effect of grafting in the previous generation is transmitted through the seed.

Vegetative hybridisation has been used in the breeding of new strains of soy bean by Leshchenko and Tyugina (1950). Soy was grafted on *Phaseolus* and control self grafts of Soy to Soy were made. Highly significant changes in the vegetative period

Treatment of F_1	Number of seedlings in F_2			
	Like *C. Besseyi*	Like *C. tomentosum*	Intermediate	Total
Grown on own roots	8	10	13	31
Grafted on *C. Besseyi*	14	5	3	22
Grafted on *C. tomentosum*	6	18	11	35

were apparent in a number of the offspring from the Soy-to-*Phaseolus* grafts. Thus the vegetative period of *Phaseolus* is 79 days and of Soy 112 days, whilst the period of the F_1 seed generation of 6 plants of the vegetative hybrid was 77 to 79 days. These new forms are now being used for selection work, in order to extend the cultivation of soy to the North.

A novel method of grafting has been developed by Osipov (1949) working with grasses. This consists in the transplantation of developing embryos of cereals from one species to another. In this way inherited changes have been induced in a number of species of oats, barley and *Bromus*. In some cases these differences appear in the year of grafting and are transmitted by the seeds. Sometimes, however, there are no changes in the year of grafting but these appear in the first, or even the second, seed generation following.

It is sometimes stated that attempts to obtain vegetative hybrids made by non-Soviet experimenters have always given negative results. This is not true in every case, however. The French botanist L. Daniel, for instance, in researches extending over many years, obtained numerous examples of hereditary changes produced by grafting. Reference may also be made to some more recent work by Georgieva (1947), done in Sofia.

These experiments were conducted with tomatoes. All the experimental plants were isolated and controls were taken from the actual plants grafted. Visible changes were rare in the year of grafting but a small proportion of changes were observed in the first seed generation, and these were inherited in F_2. The component to be changed must be young, and be kept defoliated whilst the other component should be older, not defoliated, and if possible forming flower buds.

Some typical results may be briefly quoted. From the graft of var. Red Plum (fruit red) on Golden Trophy (fruit yellow) seed was taken from the first component. The characteristics of the F_1 plants are shown in the table below (comparison of 20 plants from one fruit each of control and graft):

	Control Red Plum	F_1 Red Plum Grafted on Golden Trophy
Total No. of fruits	279	262
Mean weight 1 fruit (g.)	14·58±0·626	33·41±0·68
Mean fruit length (cm.)	4·22±0·053	5·14±0·094
Mean fruit breadth (cm.)	2·71±0·049	3·52±0·020
No. with typical Red Plum fruit form	279	52
No. with non-typical fruit form	0	210
No. of red fruit	279	28
No. of yellow-red fruit	0	234

In another experiment var. Yellow Plum (yellow) was grafted with var. Plovdiv (red). Of 633 control fruits in F_1 all were yellow. Of 838 fruits from the graft 696 were yellow, 34 were yellow-red, 46 were yellow with red pith, and 62 were red. Details are given of several other experiments showing similar results.

This work confirms the Soviet work with tomatoes which was described earlier. It is not without interest that Georgieva seems inclined to a Mendelian explanation of her results in terms of physiological effects on the genes.

There is thus a considerable body of experimental evidence for the existence of vegetative hybrids which cannot be disregarded simply because some workers have had negative results. In this connection certain facts, repeatedly emphasised by the Soviet investigators, deserve consideration. Hereditary changes are only found to occur in a comparatively small proportion of grafted plants, not more than about 10 per cent. even in the most favourable conditions. Therefore experiments on a fairly large scale may be needed in order to obtain unequivocal results. Moreover morphological changes in the year of grafting are in most cases absent or insignificant and it is therefore essential to study the seed offspring in the following year. The absence of visible changes in the year of grafting does not mean the absence of qualitative changes in the generative cells.

It is also important that the component to be influenced should be in as early a developmental stage as possible, whilst the other component is more advanced in development, preferably nearing the critical stage of flower formation. The influence of one component can be enhanced by removing the leaves from the other one and so making it more dependent for its metabolites on its partner in the graft. It appears from the work of Glushchenko that a graft can also be influenced at a later stage (flower formation), provided that only the young inflorescence is grafted, which thus develops at a critical phase, free from the influence of its own leaf system, and almost completely dependent on that of the other graft component.

A significant fact about most of the examples of vegetative hybrids which have been mentioned (including those produced by Georgieva) is the absence of cytological changes. Since only metabolites and plastic substances are exchanged between stock and scion, and not nuclei or chromosomes, the occurrence of vegetative hybridisation is powerful evidence against the gene theory of heredity, and has been recognised as such by supporters of the gene theory. It is of course true that, with the aid of accessory assumptions, an explanation in orthodox terms can be given. This possibility is inherent in the idealist weaknesses of the gene theory, for additional properties can always be postulated of a hypothetical entity which is already endowed with such surprising versatility. Nevertheless the phenomenon of vegetative hybridisation (if admitted) is generally agreed to throw serious doubt on the basis of Mendelian genetics.

According to Michurinist theory vegetative hybrids demonstrate the correctness of the thesis that heredity is not the property of some special material distinct from the general body of the organism. It is a property of all parts of the living organism, and this is shown by the transmission of hereditary characters from stock to scion, and the reverse, as a result of the exchange of plastic substances between them.

The fundamental relationship between vegetative and sexual hybridisation is stressed by the Michurinists. This similarity in principle is shown by the fact that in both types of hybridisation any character or property can be transmitted from one component to the other and can become fixed in inheritance, and segregation also takes place in the offspring in both types. In both vegetative and sexual hybridisation segregation is interpreted as the result of shaken heredity resulting from profound metabolic changes, induced in the one case by grafting and the assimilation of unaccustomed plastic materials, in the other case by sexual union. A fuller discussion of segregation is given in a later chapter.

There are, however, a number of specific differences between the two types of hybridisation. In vegetative hybridisation segregation usually begins in the first generation, and shows a different pattern from that in sexual crosses. A different form of the phenomenon of dominance is characteristic, in which plants with recessive characters give a considerable proportion of offspring with the corresponding dominant character. This is shown both in the selfed plants and also in crosses between vegetative hybrids (see Glushchenko, I. E., 1950).

The comparative rarity of graft hybrids may be understood in this way. Grafts between mature plants cannot normally cause hereditary changes since such plants have already passed through the various irreversible phases which constitute the path of development, and hereditary changes can only arise through metabolism during the course of development. Thus plants which are regularly reproduced vegetatively by grafting of mature tissues, such as fruit trees, in general remain unchanged by the process.

Even grafts of young organisms in the majority of cases do not show hereditary changes. This is due to the fundamental property of selectivity possessed by all organisms, which was discussed earlier. In consequence of this property, grafted organisms are able to select the particular metabolites that they require, and to reject and refuse to assimilate others, so that frequently they are able to continue to grow quite "autonomously" in the grafted state. Sometimes, however, the organisms are forced to assimilate unusual or foreign plastic materials in consequence of grafting, and in these conditions hereditary changes may be induced.

The experimental facts of vegetative hybridisation thus seem to be firmly based, and to be in accord with the fundamental principles of Michurinist genetics.

VI

THE NATURE OF FERTILISATION

I

THE nature and significance of sexual fertilisation is one of the fundamental problems of biology. The discussion of Lysenko's views on the nature of the sexual process can best be introduced by an account of some experimental work which presents a revolutionary challenge to traditional ideas. This work provides evidence that in certain conditions it is possible for plants to inherit characters from two paternal forms.

A series of careful experiments was carried out at Leningrad between 1945 and 1948 by Turbin and Bogdanova (1949) using several varieties of tomato. Maternal forms were chosen which possessed two or more recessive characters, and these were crossed with two paternal forms which had one, but not both, of the corresponding dominant characters.

Two varieties were used as maternal forms. The variety Golden Michurina has two recessive characters: yellow fruit colour and erect ("tree") habit. The variety Golden Peach has the same two recessive characters and also an additional one—downy fruit.

Male parental forms were chosen which possessed either bushy habit (dominant to erect) or red fruit colour (dominant to yellow). Seven combinations of crosses were made, six with Golden Michurina and one with Golden Peach. In each cross one male parent was Planovy (red fruit, erect habit) in combination with one of six varieties with yellow fruits and bushy habit.

The maternal flowers were castrated and isolated with parchment bags, and the isolators were not removed from the experimental flowers until the fruits were harvested. Pollination was carried out by two methods. In the first method a mixture of the two parental pollens was made and placed on the stigma of the maternal plant. Alternatively the maternal flowers were pollinated with the two parental forms separately, with an interval of half an hour to one hour between the pollinations. Control crossings were also made with each parental pollen singly.

In this way 57 hybrid fruits were obtained from the double pollinations and 24 fruits from control single pollinations. All the progeny from the control pollinations behaved perfectly normally, that is, only the particular dominant character carried by the paternal form appeared in the offspring, the second character remained recessive since both parents were recessive for it. Thus crosses between the maternal form, with yellow fruit and erect habit, and the paternal form, with red fruit and erect habit (Planovy), gave offspring that were all erect with either yellow or red fruit, but none combining red fruit and bushy habit. Similarly the maternal form crossed with any one of the yellow fruited bushy paternal forms gave offspring with yellow fruit and either erect or bushy habit, but none combining red fruit and bushy habit.

Among the offspring of the double pollinations, however, a certain number of plants appeared which showed both red fruits and bushy habit, and which therefore combined the dominant characters from two paternal forms. When Golden Michurina was crossed with Planovy and Golden Cherry, of 142 plants in F_1, one plant showed the characters of both male parents. In the cross of Golden Michurina with Planovy and Golden Pear, 36 plants out of 159 showed the characters of two male parents. In two other combinations two plants out of 166 and four plants out of 43 showed the characters of two male parents.

In the other three combinations no forms showing double paternal inheritance appeared among several hundred plants. In one of these combinations, however, three such plants appeared out of 235 in the second generation (F_2). The behaviour of the offspring of the double pollinations was followed through three generations. The number of plants showing double paternal inheritance in F_1 was just under 4 per cent. of the total number investigated (43 plants out of 1,160).

The hybrid plants which inherited the characters of two male parents were submitted to cytological examination. They were all found to possess 24 chromosomes in the somatic cells, and were thus normal diploids. The results cannot therefore be explained by irregularities of chromosome behaviour.

Some similar results have been obtained with cotton plants by Ter-Avanesyan (1949). The maternal form was *Gossypium hirsutum* var. Bolgarka No. 78 which possessed four recessive characters: absence of red colour in leaves or stems, low habit (short internodes), no anthocyan spots at the base of the petals, absence of yellow filaments. Two paternal forms were used. The first was another variety of *G. hirsutum* Red-leaf No. 1,677, with the dominant character of red anthocyan colouring of leaves, stems, and margin of corolla; the other three characters are recessive as in Bolgarka. The other paternal form was *Gossypium barbadense* (No. 35–1) which possesses the dominant characters of long internodes, spots at the base of the petals, bright yellow filaments; the absence of red colour in the leaves is recessive as in Bolgarka.

All three parental forms had been raised for three years from selfed seed to ensure their purity. The maternal flowers were castrated and isolated just before they opened. The male flowers from which pollen was to be taken were also isolated. In the first two years of experimentation various methods of pollination were tried but only perfectly normal hybrids of of either Bolgarka × Red-leaf or Bolgarka × *barbadense* were obtained.

In the third year the following method of pollination was adopted. The maternal flowers were divided into 8 groups of 15 flowers each. All were pollinated first with 10 pollen grains of Red-leaf; each group was then pollinated with a large quantity of *barbadense* pollen at intervals of, respectively, $\frac{1}{2}$, 1, $1\frac{1}{2}$, 2, $2\frac{1}{2}$, 3, $3\frac{1}{2}$ and 4 hours after the first pollination.

From the seed of all groups, except that with the 3-hour interval between pollinations, only normal hybrids were obtained, of which 126 were Bolgarka × *barbadense*, and 18 were Bolgarka × Red-leaf. The seeds of the 3-hour pollination gave 28 plants and 8 of these showed very marked heterosis, with intermediate red colouring of the leaves.

In these 8 plants the characters of two paternal forms were quite clearly expressed. They had long internodes and yellow filaments, dominant characters inherited from *barbadense*, combined with red anthocyan colouring in all parts, the dominant character inherited from Red-leaf. The remaining dominant character of *barbadense*, spots on the petals, was suppressed, presumably owing to "absorption" by Bolgarka and Red-leaf, for this character appears in normal Bolgarka × *barbadense* crosses in F_1. This character reappeared, however, in the mixture of forms in F_2 obtained by self-fertilisation of the double hybrids.

The ovaries in the F_1 plants showing double inheritance were elongated, 3-carpellary, with minutely pitted surface, characters usual in Bolgarka × *barbadense* hybrids, and distinct from the 4-carpellary valvate ovaries with smooth surface which are found in Bolgarka × Red-leaf hybrids.

These results were subsequently confirmed by the same author using another variety of American cotton as the maternal form. This was pollinated with 10 grains of Red-leaf pollen and 3 hours later by a pollen mass from another variety of American cotton having brown cotton hairs. A number of forms were obtained combining reddish leaf colour with brown cotton fibres.

Soviet workers have also obtained evidence of double paternal inheritance in wheat (Kocharyan, 1948), maize (Salamov, 1947), peas and other plants.

These results are irreconcilable both with the gene theory and with the Mendelian conception of fertilisation. According to this conception the essence of fertilisation is the union of the chromosomal material of the maternal and paternal cell by the fusion of their nuclei. In this way the zygote comes to contain two sets of hereditary determinants or genes, one set from each parent. The fusion of the sexual cells is conceived as the mechanical mixing of independent sets of maternal and paternal genes through the association of two sets of chromosomes in a single zygote nucleus. However, the occurrence of double paternal inheritance, as well as the facts of vegetative hybridisation described earlier, clearly make this view untenable, and necessitate a fundamental reconsideration of the nature of sexual fertilisation.

That some revision of ideas about fertilisation is required is already strongly suggested by certain other facts which have been known for a long time. Although it has been definitely established that only one pollen grain is needed for effective pollination, there is no doubt (as Darwin himself showed) that an adequate supply of pollen ensures more vigorous and sturdier offspring. Some account of the large amount of Russian work on this subject will be given in a later chapter. In animals also a single sperm only is concerned in sexual fusion with the female nucleus, although it is not unusual for several sperms actually to penetrate into the egg-cell. It is widely recognised, however, that the amount of semen has a marked effect on the quality of the offspring.

In the light of these and many other facts Lysenko puts forward a critical reinterpretation of the process of sexual fertilisation. The essential nature of fertilisation, according to Lysenko, is to be seen in the fact that it is a process of metabolism, which possesses certain peculiar and specific features.

The characteristic of normal metabolism is the continuous assimilation (using the word in its extended sense) of substances and conditions of the external environment by the organism, and the building up of living matter, or protoplasm. The living matter thus created has itself a dynamic, not a static, existence. Its existence depends on the continuous and simultaneous synthesis and breakdown of protein and other material substances of the protoplasm. As soon as the energy supply or the organisation necessary for this ceaseless transformation of material is no longer present, living matter becomes dead matter. Life, the enduring organisation of living matter, thus depends on metabolism, that is, on the continuous transformation of its material structure, which is permanent only because it is perpetually broken down and renewed.

The type of metabolism in grafted plants differs from the normal in that there exists the possibility that one or both the components may assimilate, not only the usual food substances, but also plastic materials from the other component. In certain cases this may lead to sufficiently sharp changes in metabolism to cause changes in heredity, and give rise to vegetative hybrids.

The specific feature of fertilisation is that it is a form of metabolism in which two equivalent sexual cells assimilate one another. It is obvious on reflection that this is in fact a correct and accurate description of what happens at fertilisation. Both male and female cells are in a state of extremely active metabolism, each is a dynamic organised system of all the numerous enzymes concerned in the continuous transformation of protein and other cellular materials which is the essence of metabolism. A supply of energy-giving nutrient materials is present, either in the sexual cells themselves or provided by the tissues of the parent organism.

In these conditions, when the sexual cells fuse there must take place complex metabolic interactions, for the enzyme systems of one cell must take part in the metabolic transformation of the proteins and plastic substances of the other cell. The result of this intense metabolic activity, of the synthesis and breakdown of the protoplasm of the two cells by their combined enzyme systems, is the formation of a new cell, the zygote, by a profound mutual reconstruction of the participating sexual cells. This transformation and reconstruction necessarily includes the nuclear and chromosome material which is subject to metabolism like every other part of the cell.

Lysenko's characterisation of fertilisation as the mutual assimilation of equivalent sexual cells is thus a straightforward description of biological facts. It is completely in accord with contemporary views of the nature of metabolism derived from biochemical and physiological studies. Indeed, his interpretation of the phenomenon seems almost self-evident once it is understood. It is nevertheless a brilliant example of Lysenko's ability, using the dialectical method, to penetrate to the reality of biological processes, and it leads to a deeper understanding of the laws of living systems. In laying bare the essential metabolic nature of fertilisation Lysenko shows the falsity of the Mendelian view of fertilisation as the mechanical union of the chromosomes of two parents. This view is quite unbiological and remote from reality. It implies a formal union of cellular material which is at variance with the fundamental facts of physiology.

It will be useful at this point to include a quotation from Turbin and Bogdanova (1949) which will clarify and supplement the exposition of the Michurinist view of fertilisation which I have tried to give:

> The conception which has hitherto reigned in biology, which regards fertilisation as union of the chromosome material of the parents, is fundamentally incorrect. The idea of fertilisation as the mechanical summation or joining together of the chromosomes is crudely mechanistic and unphysiological. The essence of fertilisation, as Lysenko first showed, consists in the process of metabolism between the sexual cells united in the zygote, in the process of mutual assimilation by the parts of one sexual cell of the substances of the other. The distinctive character of the process of fertilisation from all other biological processes which are also fundamentally processes of metabolism consists only in this, that here not one, but two systems, assimilate one another. In the metabolism of any living body the living protoplasm builds particles of protoplasm similar to itself. Assimilated substances enter only as structural material for the assimilating living body. In fertilisation both the sexual cells are equivalent. Both these cells mutually assimilate each other, or more accurately particles of the living body of one cell assimilate and transform in their own way the substances of the other cell. In the final result neither cell remains unchanged, preserving its original individuality. Instead of two cells there appears a third, a new one, the zygote, which gives rise to a new organism uniting in itself hereditary characteristics of the parent forms.
>
> It must not be thought, however, that one gamete necessarily assimilates the substance of the other gamete. The living body of the embryonal cell is complex and not uniform in its constitution, the various parts are qualitatively different in their physiological potentiality and in the intensity of their assimilatory activity. The processes of assimilation, therefore, which take place at fertilisation are carried out by separate parts, or by parts of the same cell, with different intensities or in different directions, as a result of which the parts of the living body of the zygote are qualitatively different in their nature. Some of them may be similar in their heredity to the paternal and others to the maternal cell. In addition other parts may possess intermediate heredity or heredity not similar to either of the parents. This heterogeneity of the living material of the hybrid zygote is the basis

for the development from it of the adult hybrid organism showing diversity in its characters and in the character of different parts of the its body. The mutual activity of the sexual cells in fertilisation is of great biological significance since on it depends the capacity for development of the progeny.

The occurrence of double paternal inheritance, which is incompatible with Mendelian theory, may be understood in principle, although not yet in detail, on the basis of the Michurinist conception of fertilisation. If fertilisation is the mutual assimilation in metabolism of (normally) two cells, then it is possible that more than two cells may be concerned in some degree or other in this metabolic process. In this connection Turbin and Bogdanova make the following comment, when discussing their own results:

> A very important and difficult question which arises in this connection is the nature of the simultaneous influence of several fertilising gametes on the mother cell. Do several male cells unite with the single female or is there no union at all but only the kind of influence which a hybrid embryo can exert on the tissues surrounding the ovum? It cannot be excluded that when fertilisation takes place the mass of developing pollen tubes from both male parents may bring about a profound change in the normal course of the physiological processes in the tissues of the flower, and that this in its turn has a directing influence on the embryo-sac and the zygote developing within it. In order to answer these questions further cytological investigations are required. There is, however, some basis for the supposition that the participation of several male cells in the fertilisation of a single ovum does not necessarily depend on the union of these cells with the ovum. The fertilising influence of the male cells on a single ovum may take place by way of metabolism without union with the ovum, that is for example by means of the same physiological mechanism which causes metaxenia.

Metaxenia refers to the indirect effect of pollination on the surrounding maternal tissues of the fruit.

2

Fertilisation like other metabolic processes of the organism possesses the property of selectivity. This selectivity is a historically conditioned adaptation which arises under the influence of natural selection. It expresses itself not only in the preference of the maternal organism for particular types of pollen, but also in the actual process of mutual assimilation of the gametes. The degree to which the heredity of one cell is "consumed" by the other does not depend on accidental factors but on the specific nature of the gametes, the previous conditions concerned in their formation, and the conditions in which the new organisms develop.

Many experiments have been carried out by Russian investigators in which mixtures of several kinds of pollen have been applied in artificial pollinations. For example, Babadzhanyan (1938) worked with a number of varieties of readily interfertile cotton, possessing characters which could be easily recognised in the hybrid offspring. One variety was used as the maternal form and was pollinated with different combinations of the pollen of the other varieties, including itself. The pollen components were applied to the stigma simultaneously and also separately at different intervals. The results showed clear evidence of selective fertilisation,[1] with distinct relations for each particular combination. Similar results have been noted in experiments with maize, wheat, tomatoes, flax, and other plants.

Many detailed experiments were carried out by Polyakov and Mikhailova (1949) using varieties of tobacco. Great care was taken to ensure uniformity of experimental conditions and the application of equal amounts of pollen of each kind to the stigma. Large numbers of offspring (hundreds, and in some cases, thousands of plants) were raised. The vitality and growth rate of the various types of pollen was studied on an artificial medium. The results indicated the occurrence of selective pollination (in Lysenko's sense) which could not be ascribed simply to differential growth rates of the pollen tubes of the various kinds of pollen. The authors demonstrate the very interesting

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[1] The Soviet investigators distinguish between "selective" and "elective" fertilisation. The former term refers to the Mendelian explanation of the phenomenon as a statistical effect due to differential growth rate of pollen tubes, etc. The term "elective" is used to denote the greater significance which is ascribed to the process by the Michurinists (see Prezent, 1940). At the risk of some confusion I have preferred to use the term *selective fertilisation* to convey the meaning implied by Lysenko, since the word selectivity has already been used to express the active nature of assimilation which characterises living organisms.

fact that one maternal type shows different selectivity relations to the pollen of another variety when the latter is grown in two different regions.

Some significant results have been obtained by Khachaturov (1939) working with the first generation of hybrid tobacco plants. Some of the plants were allowed to fertilise themselves naturally, whilst a second group were castrated and then self-fertilised in the usual way with a large mass of pollen. These plants formed 250 to 350 fertile seeds per ovary. A third group of plants were castrated and self-fertilised using varying small amounts of pollen, namely, 5, 25, 50, 100 and 200 grains per stigma. The number of seeds per ovary varied from 2 to 200, corresponding fairly closely to the number of pollen grains applied.

The second generation was raised in uniform conditions, the seed from each type of pollination being sown separately. The F_2 plants from the first two groups (abundant pollen) were similar to one another in general character. They were rather uniform in height, earliness, and appearance; most of them resembled the F_1 plants in type. The plants from the low-pollen fertilisation were much less uniform in character, and half of them were of types not found among the normal F_2. The extremes of variation were most marked in plants from fertilisation with the smallest amounts of pollen.

These data are at variance with accepted Mendelian ideas of the "purity of the gametes," and provide striking evidence of the occurrence of selective fertilisation when sufficient pollen is present.

The most numerous and significant group of facts concerning selective fertilisation are, however, derived from the study of natural free pollination (either by wind or insect agency). One of the most important results of this work has been to establish the difference in behaviour between artificial hybrids and those produced by natural free pollination.

These investigations arose out of the technique of intra-varietal crossing introduced by Lysenko for the improvement of self-pollinating lines of cereals. Some reference has already been made to this in an earlier chapter, and to the immediate beneficial effects which were obtained. The basis of these effects was seen to be the renewal of vigour and adaptive capacity by the crossing of plants with slightly different heredities formed by the assimilation of slightly different environmental conditions. It soon became clear, however, that selective fertilisation played the major role in this phenomenon. The first intravarietal crosses were made by castrating the maternal plants and then pollinating them artificially. The effectiveness of the procedure was found to be enormously increased if, instead of artificial pollination, natural wind pollination was employed, and this has become the standard technique.

The significance of selective fertilisation is seen very clearly when comparison is made between the hybrid produced by free pollination and the same hybrid produced by obligate pollination. This is shown, for example, by some experiments at Mironov in which two winter wheats were crossed by artificial and by natural wind pollination (the maternal form being castrated in both cases). In the F_2 of the artificial cross 36 per cent. of the plants were winter-hardy, but of the F_2 of the natural cross 72 per cent. were winter-hardy. The mean yield and number of productive tillers was much higher in the natural than in the artificial cross. These results have been widely confirmed in the course of plant-breeding work in many research stations.

The importance of the selective effect has been shown in numerous experiments, especially with cereals, in which castrated plants are exposed to wind pollination in field conditions. For example, Santrosyan (1938) grew several winter wheats in pots and at flowering placed them (previously castrated) among field sowings of a number of varieties of spring and winter wheats, where they were wind pollinated. In spite of the large amounts of spring pollen available 80–95 per cent. of the offspring were of the winter type. In another similar experiment (Avakyan, 1938) varieties of winter wheats grown in pots were brought into massive sowings of exclusively spring wheats. The ears in this experiment were not castrated but were slit without injuring the anthers so that self-pollination was possible whilst at the same time they were exposed to abundant spring pollen. Only 3–7 per cent. of spring plants appeared among the progeny.

In some other field experiments a particular variety of wheat, Erythrospermum 1160, was pollinated in three ways with its own pollen and that of another variety, Lutescens 062. Some plants of the first variety (castrated) were exposed to wind pollination at the junction between two large plots, one of each variety. Other plants, also castrated, were wind-pollinated in the middle of a large mixed sowing of equal numbers of each variety. A third group of plants had their ears slit so that self-pollination remained possible and were then exposed to wind pollination in a pure sowing of the second variety. In all three cases 60–85 per cent. of the offspring were hybrids, showing that E1160 prefers the pollen of L062 to its own. The hybrid progeny was superior in vigour and rapidity of growth to both parents.

The great importance of selectivity in the process of fertilisation first became apparent in the investigation of intra-varietal crossing of normally self-pollinating plants. But selectivity is observed to be equally significant in cross-pollinators, and this has been amply confirmed in practice.

3

This work has revealed the widespread existence in nature of a special form of heredity in which the maternal type is preserved when crossed. An example is provided by the work of Dolgushin (1941) with a local variety of winter wheat, Krymka, which forms a rather non-uniform population.

Seeds of Krymka were obtained from intra-varietal crossing by castration and natural wind pollination. From the seed were grown ears, the best and most typical of which were harvested and the seeds sown in the nursery by families (i.e. the seeds of each single ear constitute a family).

> In this way plants of the F_2 from the intravarietal crossing of Krymka were grown. Alongside was sown the seed nursery of Krymka with ordinary seeds, in which could be seen such a great diversity of families that hardly two could be found alike in morphological characteristics. In such a case it was hard, of course, to describe what would be obtained in the F_2 hybrids obtained from the castration of individual plants

> from the population, and their pollination by wind by any pollen from the whole diversity of morphologically different forms. One would expect from the examples observed and described in genetic literature to find in every family of the hybrid F_2 extreme diversity of morphological form. For each ovum of the castrated ear will be fertilised by pollen of very differently formed plants. However in the seed nursery of Krymka from intra-varietal crossing exactly the same sharp differences between individual families are seen as in the seed nursery of normal Krymka not from intra-varietal crossing.

Even by the most rigorous standards of examination there was a high degree of uniformity within each family with regard to morphological form and such characters as colour, vigour of growth, size, the form and quality of grain. Certain individual families are especially noteworthy. Thus out of over 400 families only 13 showed some flattening of the ears and in one family this characteristic was very marked. This type must be very rare in the original population, and all the grains of one ear could not possibly be accidentally fertilised by pollen of the same type.

Exactly analogous results were obtained with another variety of wheat. Experiments have also been carried out with rye, which is a cross-pollinated plant. A large number of varieties of rye were grown in adjacent field strips (usually replicated) for 2–8 years (Glushchenko, I. E., 1939; Avakyan and Feiginson, 1946). The plants of each variety were thus exposed to free wind pollination by a large number of other varieties. The results showed that free inter-varietal crossing maintained, and frequently significantly increased, vigour, yield and resistance to disease and unfavourable conditions. Careful analysis showed, moreover, that in almost every case varietal type, including even a number of recessive characters, was almost fully preserved. The only exceptions were three highly inbred lines which lost their maternal characteristics completely, doubtless owing to lack of constitutional vigour. Two of them were in addition derived from another geographical region.

The same general maintenance of morphological type has been demonstrated in buckwheat, under conditions of free crossing (Glushchenko, I. E., 1941). Buckwheat is insect-pollinated and is not self-fertile. Examples of maternal heredity are also found in other flowering plants when naturally pollinated (e.g. poppies). The basis of this type of inheritance is the strength of maternal heredity derived from the fact that (in higher plants) the maternal plant provides the food materials for the early stages of development of the young organism, and is in very close organic connection with it. The natural strength of maternal heredity is increased by the selectivity of fertilisation, by which the maternal gamete assimilates to a greater or less degree the heredity of the paternal sexual cell. It is obvious that in natural conditions this selectivity is of great vital significance and must have been developed under the guidance of natural selection in the course of evolution.

An additional reason for the stability of maternal inheritance in cross-fertilised plants under conditions of natural pollination is believed to be the presence of abundant maternal and especially of paternal pollen on the stigma. There is a good deal of evidence of metabolic effects caused by the presence of pollen which does not directly take part in the sexual fusion from which the zygote arises. Such effects, closely related to the processes involved in selective fertilisation, are sometimes termed "mentor" effects by Soviet workers.

An interesting example is observed in the cross between a variety of winter wheat, Hostianum 0237, and a particular variety of spring wheat, Erythrospermum 1160. Whether this cross is made artificially or by wind pollination, the hybrid (spring) progeny are non-viable and always turn yellow and die at the stage of the second leaf. If pollen of various winter wheats is applied to Hostianum simultaneously with Erythrospermum pollen, then among the offspring a number of Hostianum × Erythrospermum hybrids appear which are viable and which develop and ear normally.

The presence of pollen of barley on wheat has been shown to affect such characters as earliness, vigour, breadth of leaves, in the wheat offspring. The type of segregation of wheat hybrids in F_2 appears to be influenced by barley or rye pollen (Babadzhanyan, 1949). The same author has shown that inbreeding depression in rye is significantly removed by foreign pollen (spring wheat). Most interesting are comparisons over several years of isolated and natural self-fertilisation in a number of varieties of wheat. Isolation of the flowers, i.e. exclusion of all but their own pollen, in every case resulted in a lower proportion of fertile grains. Even a single isolated fertilisation showed its effect in the following year in a reduction in average height of plant and weight of grain (although pollination was open in the second year). Similar results were obtained with tomatoes and cotton. It appears that the habitual presence of foreign pollen may play an important role in natural conditions in maintaining the vigour of self-pollinating plants.

It must not be supposed that selective fertilisation is always or only expressed in the preponderance of maternal inheritance. In certain conditions, although less frequently, the paternal heredity may almost completely consume the maternal. Absorptive paternal inheritance has been obtained, for example, in a cross between two species of *Ribes* by very late pollination at a stage when the ovum was approaching degeneration and its vigour, therefore, reduced (Kuzmin, 1950). In general the degree of mutual assimilation of maternal and paternal heredity depends on a number of factors, the most important of which are the previous history of the parents and their ancestors, and the environmental conditions in which the new organism develops.

This brief account does not exhaust either the theoretical significance of Lysenko's interpretation of fertilisation or the many new facts to the discovery and elucidation of which it has led. A few words will be said in conclusion about the relation between development and reproduction.

The biological function of reproduction is twofold. It is first, to increase the numbers of an organism, and secondly, to begin anew the entire sequence of irreversible phases which constitute the process of development, that is, continually to renew the adaptive possibilities of the organism. For adaptation is inseparably linked with development.

The special importance of sexual reproduction is that by combining two heredities it doubly increases adaptive possibilities and vigour. The significance of hybridisation, and especially of distant hybridisation, in plant breeding is not simply that it leads to new combinations of characters but that it causes a profoundly shaken heredity with a consequent enrichment of the adaptive possibilities in appropriate conditions.

It would be expected that asexual reproduction, which historically preceded sexual reproduction, would also lead to rejuvenescence, that is, to the removal of the readiness to reproduce and the beginning of the developmental sequence afresh. This appears to be the case in some primitive unicellular organisms where asexual reproduction is frequent or is equivalent to sexual reproduction, so that the gametes may either fuse sexually or function as reproductive bodies without fusion. In most higher plants, however, vegetative reproduction has developed secondarily in the course of evolution as an accessory to sexual reproduction. Usually in such vegetative reproduction development continues from the stage which has already been reached, without rejuvenescence. A consequence of this is the frequency of degeneration in many plants propagated repeatedly by vegetative cuttings, buds, or other means.

The question arises whether rejuvenescence is connected with the occurrence of meiosis (reduction division) during the maturation of the sex cells. It is clear that rejuvenescence is not necessarily connected with fertilisation, for many cases are known where the unfertilised ovum develops into a new plant. This question was approached experimentally by Avakyan (1948), who used as material a species of onion, belonging to the family *Liliaceae* in which vegetative organs of reproduction (bulbils) frequently occur in place of the flowers, that is, directly replacing sexual reproduction. Vegetative bulbils also are produced which do not replace sexual organs.

In experiments between 1943 and 1947 Avakyan found that the bulbils which replaced sexual organs also showed rejuvenescence. Like the seed generation they had to pass through the vernalisation stage before they could flower. Vegetative (subaerial) bulbils on the contrary require no vernalisation and are ready to flower. These results indicate that the process of rejuvenescence is not bound up with meiosis but that it takes place in the somatic cells which form the sexual reproductive cells.

These results are still of a preliminary character but their theoretical interest is certainly very great. This work is a good example of the fresh and stimulating attitude which characterises contemporary Soviet biology.

VII

HEREDITY AND NUCLEAR STRUCTURE

I

THE gene theory has long been considered to derive particular strength from the analysis of offspring ratios in breeding experiments and their relation to the detailed behaviour of the nucleus and chromosomes of the cell. The Michurinist criticism of the theory from this aspect must therefore be examined in a little more detail.

The extraordinary subtlety and convenience of the Mendelian scheme as a means of expressing the facts observed in breeding experiments is undeniable. This is doubtless one of the reasons why the gene theory has been so readily accepted by many biologists without serious consideration of its deeper implications. Now it is important to note that the Michurinists do not reject any of the facts which have been established by experiment. It is necessary to emphasise this, since repeated statements have been made wrongly asserting the contrary. The facts are not, in general, in dispute but only their interpretation.

What is denied by Lysenko is the interpretation of the experimental results in terms of hereditary determinants or genes. The gene is rejected because it is a particle with unbiological, unphysiological properties. The denial of the existence of genes does not imply denial of the transmission of "unit characters," or more accurately unit processes, in inheritance. It is a fact of observation that many characters behave as "units" in heredity and that they exhibit the relations of dominance or recessiveness.

One of the tasks of genetics must ultimately be to provide a detailed explanation of these phenomena. Such an explanation must be sought in developmental metabolism, to which the formal description in terms of unchanging genes adds nothing useful, whilst it is, if anything, a hindrance to the investigation of the real problems concerned.

The "Mendelian ratios" between the numbers of different types of offspring are also facts of observation. The observed regularities are obviously genuine and in some cases are so neatly represented by the Mendelian notation that it is possible to make predictions which are not trivial. The existence of these regularities is accepted by Soviet biologists; nor do they hesitate to make use of them in their work when appropriate. What they do not admit are the theoretical assumptions based on the "Mendelian ratios," assumptions which involve the existence of "particulate" heredity in the form of genes.

The extremely unplausible conception of the gene has been dealt with earlier, and it is clearly not made any more plausible by the inheritance of "unit characters." The belief that the fact of the inheritance of "unit characters" is evidence for the existence of genes, hypothetical constructions with remarkable properties, rests on a naïve confusion of thought.

The Michurinists further point to the danger of treating the Mendelian categories in a rigid and absolute manner, as if they were isolated from environmental conditions or at least were only related to the environment in a mechanical way.

Many experiments carried out by Soviet investigators have also shown the extent to which segregation and dominant-recessive relations depend on external conditions (e.g. Medvedyeva, 1946; Martsenitsyna, 1950). Quite different patterns of segregation in F_2 may be obtained by subjecting the hybrid F_1 to different external conditions, and this fact has been widely used in plant breeding work. Dominant and recessive relations may be altered by appropriate changes in external conditions and it is possible for a recessive character to become dominant (Glushchenko, I. E., 1945). These facts and many others sharply emphasise the defects and rigidities of the Mendelian analysis even as a conceptual scheme. They are the symptoms of the unstable theoretical foundation on which the scheme is built.

The mistake which lies at the root of all Mendelian theorising from offspring ratios is the neglect of the developmental history of characters, their isolation from the processes and conditions which contribute to their formation. It is impossible to gain an understanding of the fundamental nature of heredity and its laws from an analysis of the behaviour of *finished* characters in inheritance, no matter how rigorous is the statistical treatment nor how numerous are the experimental facts. Whether heredity is particulate or not, simply cannot be decided from this type of evidence. Only a study of metabolism and the internal and external conditions of its development during ontogeny can reveal the essential nature of heredity. This is the meaning of Lysenko's statement that the study of statistical regularities is no substitute for the investigation of the real laws of biological development. It does not mean, as has been absurdly misrepresented, that Soviet biologists reject the use of statistics in their experimental work.

It is sometimes said that the existence of sharp segregation in the F_2 of hybrid organisms can only be explained by particulate heredity. Michurinist theory is, however, capable of giving a biologically more consistent explanation of hybrid segregation.

According to Lysenko heredity is the property of living systems to require definite conditions for their development. It follows therefore that different cells and tissues of an organism differ qualitatively in their heredity, since they exhibit varying specific requirements in relation to environmental conditions. This statement appears paradoxical from the standpoint of conventional theory and its terminology, but is quite logical and comprehensible if Lysenko's definition of heredity is accepted. It may sound somewhat less startling when one remembers that heredity also includes the internal requirements, and that the various cells and tissues of an organism have, as the basis of their differing qualitative heredity, the common requirement of being part of the same organism. Recognition of qualitatively different heredity, of different specific environmental requirements, in the cells and tissues of a single organism is an important feature of Lysenko's theory. For it provides, in principle, a theory of tissue differentiation, which is what Mendelism is so signally unable to do.

The reproductive cells are distinguished from the ordinary somatic cells by the fact that they complete the whole developmental cycle of the organism and initiate a new one. The reproductive cells concentrate in themselves the hereditary requirements of the whole organism, and this process is inseparably connected with the process of rejuvenescence by which the cycle of phasic development starts again from the beginning. The developmental history of the organism, phylogenetic and ontogenetic, is, as it were, summed up at the phase of rejuvenescence, although how this happens can at present only be stated in the most general way since little or nothing is known of the biochemical processes involved. The hereditary nature of the sexual cells depends on the extent to which the various metabolic activities of the organism participate in their formation.

In a hybrid the selectivity of the organism is strengthened and widened owing to its dual nature, the result of the mutual assimilation of two sexual cells with somewhat different hereditary requirements. The cells of the organism during development can in consequence select their requirements from the environment in several ways. The somatic cells will differ in hereditary quality owing to differences in type of assimilation, and these differences will be reflected in the sexual cells which arise from them.

Thus the result of the destabilised or shaken heredity caused by hybridisation shows itself in segregation in F_2. There is, in effect, a re-sorting of hereditary requirements, but this phenomenon is not random. It is related to environmental conditions and is controlled by natural selection. The origin of segregation in shaken heredity explains why it also occurs in vegetative hybrids and in non-hybrid forms subjected to metabolic disturbance under the influence of changed conditions of life.

The Michurinist explanation of segregation is logical and is consistent with the nature of biological systems. It can only be a generalisation, since the real investigation of the complex processes involved has scarcely begun, but it is a fruitful generalisation which opens the path to future advance through the study of these metabolic processes in relation to the external and internal conditions on which they depend. The Mendelian explanation of segregation in terms of the recombination and assortment of maternal and paternal genes is nothing but a formal description which fails to show the essence of the process. It is not even consistent with the facts, since segregation takes place when no gene recombinations occur, as a result of vegetative hybridisation, or of the disruption of metabolic norms by various treatments including removal to a new geographical environment, or of vegetative reproduction in certain cases. On the other hand, as Lysenko and his co-workers have shown, segregation does not necessarily take place in sexual hybrids.

There are a number of examples known (pollen grains, reproductive spores of some fungi) where it is possible to separate the four (sometimes eight) cells produced from a single reduction division and thereby to show that certain characters segregate clearly and precisely, at least in normal conditions, according to the Mendelian laws. The occurrence of this type of segregation is not denied by the Michurinists, any more than they deny the occurrence of other regular Mendelian ratios in given conditions. Can the Michurinists explain such regular segregation?

The question would imply that Mendelian theory does offer an explanation, a claim which can hardly be admitted. All that Mendelism can do is to give a description of the phenomenon in terms of the distribution of hypothetical materials. But the essence of segregation is a redistribution of certain *processes*, and whilst it obviously must include the redistribution of various substances, this is only one aspect of what is fundamentally a complex metabolic process.

The Michurinists are rather more modest and do not pretend to have any detailed explanation of regular segregation. They believe however that their approach to the question will ultimately lead to a solution in biological, not in descriptive, terms. The way to understand segregation is not to treat it as an absolute, but as a metabolic process, and in particular, to investigate the way in which its pattern can be changed by external conditions.

One of the most interesting results of the work on the segregation of reproductive spores in the fungi has been the demonstration that in a number of cases segregation does not take place in a strictly Mendelian way (see Lindegren, *The Yeast Cell, Its Cytology and Genetics*, 1949). Indeed many of the results are not readily compatible with gene theory at all, and cast doubt on the fundamental positions of classical genetics. It is remarkable how the theoretical crisis of Morgan-Mendelism is developing most rapidly in just those fields of investigation which were once thought to provide its strongest support.

The uncritical assumption that the inheritance of unit characters necessitates "particulate" heredity may also be looked at from another point of view. It can be shown from purely physico-chemical considerations that in certain continuous reaction systems involving autocatalytic linked reactions there may be more than one position of dynamic equilibrium (steady state). Such open systems, which are akin to the types of reaction-system found in living matter, possess a number of very interesting properties (for a recent discussion see, for example, Denbigh, Hicks and Page, *Transactions of the Faraday Society*, 1948, 44, 479).

Slight changes in concentration of the reactants or in the rate of particular reactions may cause the system to move sharply from one position of dynamic equilibrium to another. In certain conditions a system of this type will oscillate rhythmically and continuously about the steady state. It is not difficult to postulate systems in which a continuous change in the level of one factor may lead to the formation of either product A or product B but not both.

There is an obvious analogy with the situation in living organisms since complex linked systems of continuous reactions, some of which may be autocatalytic, certainly take part in the organisation of living matter. The formation of a single "character" of an organism is the result of a series of processes and reactions which may be imagined as analogous to such model reaction systems, although qualitatively much more complex. The dominant and recessive forms of a particular character may then be understood as the expression of the discontinuous dynamic equilibria which result from the continuous variation of a dynamic reaction system.

Such a picture, however vague in outline, is not entirely speculative since it provides a reasonable biochemical basis for discontinuous effects based on continuous changes. The application to heredity is clear: consideration of the discontinuous effects by the use of normal statistical technique would inevitably suggest the operation of some particulate cause. Yet this assumption would be incorrect and deceptive, and would conceal the real nature of the underlying processes. These considerations give added point to what has already been said. The mere analysis of statistical regularities in inheritance cannot, in itself, explain the fundamental nature of heredity, which is only revealed in developmental metabolism.

2

A great deal of the evidence for the gene theory of heredity is drawn from cytology, that is, from the study of the structure and behaviour of the microscopic components of the cell, especially of the nucleus and chromosomes. A large number of remarkable facts can be cited which indicate a relation between the detailed structure of the chromosomes and the hereditary behaviour of the organism. It is true that the most recent advances in this field have begun to undermine the theoretical structure which they were expected to sustain, as was discussed in an earlier chapter. Nevertheless the correspondence between cytological features and hereditary behaviour is frequently very impressive.

This correspondence cannot, however, be used to support the proposition that heredity is determined by material particles in the chromosomes, for it would also, and more rationally, result from Lysenko's view of heredity. The nucleus with its chromosome apparatus undoubtedly has important functions in cellular metabolism, and its visible structure and behaviour must reflect the biochemical processes that go on in the cell. Changes in heredity, that is, in the type of metabolism, will find expression in corresponding structural changes in such vital organs as the nucleus and chromosomes. Material structures arise as one aspect of the underlying metabolic process, and it is illogical and absurd to treat a partial aspect of the process as the cause of the whole. Changes in the chromosomes are structural signs of changes in metabolic behaviour, not the cause. Parallels between cytological and hereditary behaviour are not therefore valid arguments for the existence of genes. This does not mean that such parallels are not of great interest and significance in the investigation of heredity if they are correctly interpreted.

Apart altogether from such general considerations arising from the fundamental nature of heredity, the Michurinists believe that the facts of cytology themselves lead to the decisive rejection of the gene theory. Now an essential requirement of Mendelism is the continuity of the individual chromosome (or its basic structure of genes) between successive nuclear divisions. The individual chromosomes only appear when the nucleus divides, and the process of division, which is known as mitosis, leads to the accurate distribution of equal numbers of homologous chromosomes to each daughter nucleus. Between the divisions, in what is termed with singular inappropriateness the "resting" nucleus, the chromosomes cannot normally be distinguished.

But Mendelism must assume that even in the resting nucleus the linear arrangement of the genes in the chromosomes is preserved, for the effect which the genes exercise on the development of the organism depends both on the nature and the precise linear arrangement of the genes. When it is remembered that the nucleus spends the greater part of its time in the resting or non-dividing stage, and that most of the protein synthesis of the cell takes place while the nucleus is in this condition, it is obvious that, according to the gene theory, the linear arrangement of the gene material must be preserved between divisions. The permanence of the chromosomes during the resting stage is the foundation of chromosome genetics. If the chromosomes do not persist then the whole structure of Mendelian genetics and the gene theory fall to the ground.

The evidence for this essential basis of Mendelism is, however, unconvincing in the extreme. Many of the more elementary textbooks simply evade the question and treat it as an article of faith. The evidence which is adduced in proof of the dogma is derived from two main sources. In the first place the chromosomes can sometimes actually be seen in the inter-mitotic nucleus, whilst in other cases they reappear at the beginning of the next division in exactly the same position and coiled in the same manner as when they disappeared at the end of the preceding division. There is no reason to doubt the correctness of these observations in certain cases, especially in rapidly dividing nuclei where the chromosomes begin to form again for the next division before they have completely disappeared after the one before: but they are not very relevant to the more usual condition where the resting stage is more prolonged and the chromosomes are certainly not visible.

An extension of this evidence is the continued appearance, at successive divisions, of chromosomes characteristic in shape and number. This is claimed as proof that the chromosomes must persist as individuals. Yet it is well known that many organisms continually reproduce accurately and precisely structures of astonishing complexity (as for example the elaborate patterns of certain pollen grains, diatoms, etc.) which certainly do not persist unchanged but which regularly reappear.

The second type of evidence for the existence of chromosomes in the resting nucleus comes from the work of Mirsky and his collaborators, who break up and centrifuge animal tissues in such a way as to obtain what is believed to be material from resting nuclei. This material appears in the form of threads which are assumed to be chromosomes since they resemble them in staining reactions and general structure. Even if Mirsky's technique is accepted as really accomplishing what is claimed, this evidence only proves that nuclear material possesses the property of rather readily coagulating to form chromosome-like threads if it is interfered with—a conclusion which is consistent with what is known of the behaviour of nuclear material. The experimental induction of chromosomes by the action of external stimuli has been shown by Makarov (1946, *b*) in the homogeneous nuclei of frog oocytes.

Against these facts may be set many others which clearly demonstrate the absence of any structure (reticulum, nuclear skeleton) in the resting nucleus which might be supposed to represent the mitotic chromosomes. In many cases the resting nucleus can be shown to be quite fluid, as is indicated by the complete coalescence of nuclei in sexual fusion, and by the very low viscosity, equal to that of water, as directly measured. In some animal cells the nucleoli fall freely under gravity within the nucleus, with no signs of the presence of any internal structure. Micro-manipulation detects no trace of a reticulum, whilst the complete contents of the nucleus can be withdrawn by means of a micropipette. These observations leave no doubt that the nucleus may be fluid and structureless. This does not imply that the nucleus is always so; in different conditions it may show varying degrees of aggregation.

The work of Nasonov and Alexandrov (1940) showed that no structure can be seen in normal nuclei either by vital staining or by the use of the ultra-microscope. Various injurious external agencies such as high temperatures, lack of oxygen, narcotics, cause the appearance of structure in the nucleus, and these effects are reversible (unless the cells are seriously injured), so that removal of the toxic agencies causes the nuclear structure to disappear again. Many similar results have been obtained by Makarov and his collaborators with both animal and plant cells (see, for example, Makarov, 1945). This work shows that the nucleus is extremely labile and that its state depends on physiological conditions. Healthy resting nuclei are usually without structure, and the reversible process of formation and disappearance of structure under external stimulus could be repeated several times in some experiments.

Healthy living cells photographed by ultra-violet light show homogeneous nuclei provided the exposure time is short. With longer exposures nuclear structure begins to appear owing to injury by the intense radiation.

The common fixatives used in cytological work cause coagulation of the proteins of the protoplasm. Nuclei fixed in this way usually show a reticulate structure, but this appearance is generally recognised to be a product of fixation. The use of osmic acid as a fixative is claimed to be free from these defects and to preserve vital structures without coagulation of the protoplasm. With this fixative Makarov (1946, *a*) has demonstrated the absence of structure in the nucleus even after staining in various ways, thus disposing of the suggestion that a nuclear skeleton is present but cannot be seen because its refractive index is the same as that of the nuclear sap.

The weight of the evidence clearly suggests that the resting nucleus usually consists of a fluid phase of disperse micelles varying in degree of aggregation according to physiological conditions. The difficulties in the way of demonstrating any permanent chromosomal or gene structure in the nucleus have led Mendelists to suggest that the structure sought may be without analogy on a larger scale. This bit of metaphysical obfuscation presumably means that the structure is without analogy to the chromosome structure which it is supposed to represent! It is hard to avoid the conclusion that the Mendelian doctrine of permanence of chromosome structure is a myth, intended to preserve the theory from which it derives.

There is another group of facts which is equally destructive of the whole basis of Mendelism. An essential feature of the theory is that, with rare exceptions, every cell is provided with a complete set of genes, and the purpose of mitotic division is to ensure this by accurately distributing the chromosomes as a complete set to each daughter nucleus. There is, however, another form of nuclear division which occurs much less frequently and which is known as amitosis, because in this case there takes place direct division of the nucleus into two daughter nuclei without the formation of chromosomes.

Many observations of amitosis were made at the beginning of the century, especially in embryonic tissues; and in various cells, including those which later gave rise to sexual cells, it was found that amitotic divisions were followed by normal mitotic divisions. Thus two nuclei, produced by amitosis without orderly and precise division of the chromosomes, each subsequently form a complete and regular set of chromosomes which divide in the normal manner. These results are so damaging for Mendelian theory that they have been either ignored or explained away by a hypothetical process of "endomitosis" in which a form of regular mitosis is assumed to occur within the nucleus in such a way that it cannot be seen.

The occurrence of amitosis followed by mitosis has been observed more recently by several Soviet investigators. In the regeneration of muscle cells the nuclei were found by Zavarsin to divide initially by amitosis and later change over to mitosis. Evidence that various types of amitosis and aberrant mitosis in regenerating tissues can give rise to viable cells is given by Frelov (1949). The demonstration of Revutskaya (1950) that amitosis may alternate with mitosis appears particularly convincing. These facts are inconsistent with orthodox theory and point to a more rational conception of chromosome behaviour.

It follows from the evidence that has been outlined that the chromosomes normally disappear in the period between nuclear divisions, and that there is no sign of any corresponding structure in the resting nucleus. The chromosomes must therefore be formed afresh at the prophase of every nuclear division. The process of dissolution of the chromosomes at telophase and their reappearance in prophase has been followed in detail by Makarov (1948). Observation shows a gradual aggregation of micellar material into scattered droplets or threads which then begin to come together in groups and ultimately form themselves into chromosomes. The process gives no indication of any antecedent sub-microscopic structure. The chromosomes are thus transitory structures which are formed *de novo* at each cell division and which then disappear again. They are an example of the property of regular organ formation which is characteristic of living matter.

The way in which a chromosome gives rise to two daughter chromosomes at each nuclear division is a problem which is also being intensively studied by Soviet cytologists. They are inclined to the view that a second chromosome is formed *de novo* alongside the first chromosome, rather than that one chromosome divides longitudinally, but the question cannot be regarded as settled.

Recently the extremely important work of O. V. Lepeshinskaya has been published (*The Production of Cells from Living Matter and the Role of Living Matter in the Organism*, Academy of Medical Sciences, Moscow, 1950). As a result of many-sided researches over a number of years by herself and her collaborators, Lepeshinskaya claims to have shown that in animal organisms organised cells with complete nuclear apparatus arise from living but non-cellular material (yolk globules in eggs of birds or fishes, inter-cellular material in the process of wound healing in adult organisms). The writer has not yet had the opportunity of studying this work and cannot therefore do more than mention it. The evidence was presented at a special meeting of the Soviet Academy of Sciences where it was discussed and accepted. The far-reaching implications of this work for current conceptions of cellular organisation in relation to heredity and development are very great. It is certainly consonant with the Michurinist view of chromosome formation which has been outlined.

The basic facts of cytology are thus inconsistent with the requirements of the gene theory, and the process of mitotic division cannot have the function which Mendelian theory assigns to it, namely, the division of hereditary material. Nevertheless it is clear that the complex and highly regulated mitotic mechanism of division which has arisen in the course of evolution fulfils some very essential function. The nature of this function future investigation will decide. Undoubtedly the accurate division of certain materials between the dividing cells is an important feature. It may be that desoxyribosenucleic acid is one of the substances involved in this equal division. This substance is believed to be closely associated with growth, and one of the biological functions of mitosis may therefore be to ensure that the daughter cells grow at related rates so that the integrated organisation of the tissues is preserved. The full significance of mitosis certainly involves a great deal more, however, and many studies along different lines will be required to elucidate it.

The Michurinists believe that abandonment of the fallacious preconceptions of gene theory opens the way for a more objective and effective investigation of the intricate field of nuclear structure and behaviour. They point with some justification to the unsatisfactory state of cytology at the present day, which they consider arises from the attempts to fit facts into an arbitrary and formal theoretical mould. Certainly the simple, rigid cytological schemes, repeated from one elementary textbook to another, bear no resemblance at all to the complexities actually found in reality. The number of the chromosomes in the somatic cells is now known to vary not infrequently, both within one tissue and in different tissues. Various degrees of polyploidy may occur quite commonly. Even the number of chromosomes in the sexual cells is not always constant in a particular organism. The form of the chromosomes may vary considerably in different parts of an organism and also in response to external conditions.

An array of facts, discovered by Mendelian cytologists themselves, now stands outside the theoretical Mendelian scheme, which is incapable of assimilating them. At the same time there is acute disagreement among orthodox cytologists about the factual details of just those features of nuclear division which play so essential a role in their genetic theories. This unsatisfactory position is not accidental but is a reflection of the theoretical confusion inherent in the gene hypothesis itself.

Because the Michurinists reject the view that the chromosomes are the "organ of heredity," they do not thereby deny that the chromosomes play a very important part in heredity, the nature of which has to be determined by observation and experiment. Interest in cytology has been greatly stimulated in the Soviet Union in consequence of the theoretical developments in genetics. A very great volume of work in cytology is now in progress directed to the elucidation of the details of chromosome structure and behaviour, the formation of sexual cells, the course of events in fertilisation, the nuclear and cytoplasmic changes accompanying the development of drought- and frost-resistance, and many other problems.

VIII

MICHURINISM AND AGRICULTURE

I

ONE of the principal reasons for the rejection of Mendelism by Soviet biological science was its failure in practice. Because of its theoretical defects it proved in practice to be incapable of solving the most pressing problems of collective agriculture, those connected with seed production and the raising of new varieties, and was becoming an actual barrier to their solution. The report of the decisive session of the Lenin Academy of Agricultural Sciences brings out this point again and again. Directors and workers of various research institutes showed how Mendelian theory had shown itself sterile in relation to the practical problems in their own special field, and how going over to methods based on Michurinist theory had led to fruitful results.

No biological theory has ever been tested on so large a scale, with such unlimited opportunities, as Mendelism has been tested in the Soviet Union, and the evidence against it from the experience and conviction of so many scientific workers is all the more impressive. It has, of course, been recognised that in capitalist agriculture Mendelian genetics has had very little impact. The practical methods used in plant breeding and especially in animal breeding are largely empirical and derive little that is positive from genetical theory. A leading British geneticist has remarked:

> The progress of genetics has not yet led to the marked advances in plant and animal breeding which has been so confidently expected in the past (Mather, *Nature*, 1944, 153, 780–3).

It is significant that the production of hybrid maize, the one technique which is usually presented as a triumph of Mendelism in practice, is founded on very anciently known practices, and depends for its efficiency on a phenomenon which Mendelian theory is peculiarly incapable of explaining, whilst the prolonged inbreeding associated with the technique has been shown to be unnecessary and inessential both by American and Soviet investigators (Salamov, 1950).

The lack of application of Mendelian genetics to agriculture could always be attributed, with considerable justification, to the restricting influence of capitalist social conditions. However, its failure when applied on a large scale to socialist agriculture shows that the cause lies deeper, in the theoretical inconsistencies on which it rests. The decisive test of a scientific theory is in its practical application.

There can be no doubt of the practical triumph of Michurinism when measured by its services to Soviet agriculture. It has given a new direction to seed production, breeding and research, which is bearing fruit in increased yields and efficiency. In these developments Lysenko has played a considerable personal part, about which it is appropriate to say a few words in order to correct the ignorant nonsense that has been written of him. His own practical achievements are very impressive and it is not surprising that they have gained him the presidency of the Lenin Academy of Agricultural Sciences and the triple award of the Order of Lenin, the highest decoration which the Soviet Union can bestow. Reference has already been made to the results of his work on vernalisation and summer planting of potatoes in the Southern Steppes. In addition he created a variety of spring wheat suitable for the same region, which was until recently the standard variety; he brought about phenomenal increases in the yield of millet, which played an important part in feeding the Red Army during the war; he increased the yields of kok-sagyz by cluster-planting; solved the problem of over-wintering wheat in Siberia by sowing in the autumn stubble; developed a branched wheat of great promise; laid down the principles and practice of seed production, which are now having revolutionary effects in raising yields: these are only a few of the practical developments in which he has played a leading and inspiring part. These achievements have won him the respect and affection of the Soviet people.

To regard Lysenko merely as a brilliant practical man but scientifically negligible is quite incorrect and can only be based on lack of acquaintance with his work and writings. All the practical achievements just mentioned (which are sometimes sneered at by his opponents as "not genetics") are inseparably connected with the fundamental theories of biology and genetics which he has propounded, with phasic theory, with the study of the specific requirements of a plant as the basis of its heredity, with the connection between organism and environment in metabolism. Nothing is more striking than the way Lysenko's thought and action go hand in hand.

As a "pure" scientist Lysenko undoubtedly stands in the first rank, as even those who do not agree with his theories could hardly fail to admit if they take the trouble to study his work. His observations on plant development, generalised in his phasic theory, are the most brilliant contribution to developmental physiology in the last thirty years. His theoretical intitiative and, in many instances, his practical guidance are behind the discovery of a host of new facts which any genetic theory will have to take into account. There is no doubt that he has inspired thousands of Soviet scientists of the younger generation. The significance of his ideas I shall discuss later, but I hope that the earlier chapters have already made it clear that his theories are a serious contribution to biological thought which cannot simply be dismissed with abuse or ridicule.

It seemed necessary to make these remarks at this point since some of the ill-informed attacks which have been made on Lysenko have created a false impression of the man and his work and of the position he occupies among the Soviet people. This false picture has had the effect of confusing many people and making it more difficult for them to understand his work and ideas.

2

In addition to the many old-established research institutes which are concerned with plant breeding and genetics there are 72 State Selection Stations more recently established, which play a major part in the application of genetics to the problems of agriculture. These Stations are situated in all the main soil and climatic zones of the Union, and most of them are not less than 4,000 to 5,000 acres in area. They were created as an important link in the system of seed production for the use of collective farms.

The main tasks of these Selection Stations are the following. In the first place to produce new, improved, high-yielding varieties and in the second place to produce élite seeds of local varieties in sufficient quantity to satisfy the needs of the collective farms. They also study the most suitable agronomic methods to secure high and stable yields. In connection with this work research is carried out in genetics, agrochemistry, physiology, plant protection, and in some stations also in animal husbandry and farm mechanisation (Varenitsa, 1949).

The distinctive feature of plant breeding and genetical work in the Soviet Union is thus not only its close integration with all other aspects of agronomic research, but also its linkage with seed production. In capitalist conditions the work of plant breeding and genetics is isolated from seed production, which is controlled by private capitalist firms, as well as from the practical problems of agriculture. This is no doubt one of the reasons for the failure of Mendelian geneticists to appreciate the real significance of the new genetical principles which have arisen in the Soviet Union.

The basis of seed production in all the State Selection Stations is now that recommended by Lysenko on Michurinist principles. The foundation of the method is the intra-varietal crossing of self pollinators (by castration and wind pollination) in order to increase the vigour and adaptive possibilities of the progeny. This is accompanied by cultivation (training) of the plants in conditions of high agricultural technique and the selection in these conditions of those plants and families which, whilst preserving the varietal type, incline in their agricultural and biological characteristics in the desired direction. Thus the production of élite seeds is linked with constant ameliorative selection in the seed nurseries.

Comparative trials on a large scale on the collective farms demonstrated the considerable increases in yield resulting from the use of élite seeds produced by intravarietal crossing and accompanying measures in this way. Thus trials with three varieties of winter wheat over three years in the Odessa region showed a mean increase in yield of 7·5 per cent. in favour of élite seed (Kirpichenko, 1949). Results in many other regions and with various crops show increases in yield of 3–15 per cent. from the use of élite seed in comparative trials.

Selective fertilisation by free wind pollination of both self- and cross-fertilised plants has been shown to ensure high vitality and adaptability and in consequence high yield in those plants in which agriculturally valuable characters coincide with those that are biologically useful. Lysenko therefore recommended *inter*-varietal crossing by free pollination as one of the best ways of improving the productivity and biological qualities of existing varieties. The best local variety is used for crossing by wind pollination with other varieties adapted to the region in question. In this way hybrid seed is obtained which gives very much higher yields than normal, especially in unfavourable years. Hybrid seed of different varieties of wheat in various regions gave yields varying from 10–40 per cent. above those of normal seed, and similar results have been obtained with rye and other crops.

It should be noted that in most cases maternal type is fully preserved; the hybrids do not differ morphologically from controls and show no greater diversity. A few types, especially recently introduced non-local ones, lose their varietal type to a significant degree (16–18 per cent.), but even these usually show increased vigour and yield (Dolgushin, 1941, *a*). The essential basis of inter-varietal, as of intra-varietal, crossing is selective fertilisation in conditions of free wind pollination.

These methods of seed production were laid down by the All-Union Conference on this subject in 1939, and were based on Michurinist principles. The practical evidence in favour of the correctness of these ideas has thus proved overwhelming, and was a considerable factor in deciding the outcome of the genetic discussions. The widespread development and extension of these methods by the State Selection Stations is leading to phenomenal increases in the productivity of collective agriculture.

Another aspect of the work closely integrated with seed production is the breeding of new and better varieties. Great stress is laid on the development of locally adapted varieties suitable for each particular region. In this work the greatest possible use is made of the Michurinist methods: selection of the pairs for crossing by phasic analysis, distant hybridisation, the use of free (selective) pollination, and training of the hybrid progeny in appropriate conditions.

The production by Lysenko of a spring wheat suitable for the Southern Steppe region, Lutescens 1163, is now well known. In 1946 this wheat was replaced as a regional variety by a superior type Odesskaya 13 which, like Lutescens, was produced by the selection of parental forms after phasic analysis. The maternal form was a local spring variety well adapted to the required conditions but limited by the photo-stage which it passed more rapidly in longer days. This was crossed with a Central Asian variety possessing drought resistance and other desired qualities and well adapted to short days at the photo-stage, but requiring vernalisation. By sowing vernalised seeds of the latter the two varieties were successfully crossed. By the selection of suitable families from the progeny, followed by training and selection for several years, and making use of intra-varietal crossing, Odesskaya 13 was developed. Prolonged trials established the superior qualities of the new variety, which gave average yields 20–30 per cent. higher than the standard variety Lutescens (Dolgushin 1941, *b*; Kirpichenko and Shumakova, 1949).

A new winter wheat for the Southern Steppes is Odesskaya 3, adopted by the Government Testing Commission as the basic variety for the Odessa and Nikolaev regions in 1946. The difficulty in creating this variety did not lie in selecting the parental forms, which were local varieties, but in transforming the hybrid in the required direction by the influence of environmental conditions. This variety yields 4–5 centners per hectare more than the standard variety Ukrainka in normal years, but in bad years it yields 7–9 centners per hectare more. It is already sown on more than two million hectares, so that the increase in wheat production resulting from the adoption of this variety is at least a million tons per year.

Another winter wheat, Odesskaya 12, produced in a similar way was accepted as the standard variety for the middle zone of the Odessa region in 1947. These examples illustrate the vitality of plant breeding work in the Soviet Union under the impact of the new principles and methods, and the great importance attached to the creation of locally adapted varieties for every region. The new varieties are always very thoroughly tested by trials over several years before they are accepted, but once their value is clearly established there is no delay in introducing them into production on a very large scale.

The examples quoted from one region can be matched in many others. At Krasnodar the new high-yielding and rust-resistant winter wheat Novoukrainka was produced by Lukyanenko, using the method of crossing distant geographical races, and it is now sown on more than 1½ million acres. A number of new grain varieties have been bred by Gromachevsky in Azerbaidzhan, which are sown on more than a million acres and yield 30–40 per cent. more than the original local varieties. At Narymsk in the extreme north where very severe conditions prevail, several new varieties of winter rye, wheat, and of oats, millet, and other crops have been developed and are undergoing government varietal trials. Altogether in the dozen years of their existence the State Selection Stations have produced some 650 new varieties, among them 105 winter wheat, 112 spring wheat, 54 oats, 75 leguminous crops. Of the new varieties 280 have been officially adopted as standard local varieties.

In all this work Michurinist theory and practice are widely and fruitfully used. In hybridisation the technique of free wind pollination is very frequently adopted, and has been repeatedly found to give more favourable material for selection work than artificial crossing. The transformation of spring into winter cereals, and the reverse, has been used in the creation of new and valuable forms. Extremely winter-hardy types have been created in this way, whilst at Almatinsk Selection Station a spring form of Ukrainka (wheat) has been produced which yields 3–4 centners per hectare more than winter Ukrainka and is highly resistant to fungal attack and lodging.

Among spring forms of Voroshilov wheat, produced from the winter form, Lukyanenko found that 26 per cent. were highly rust-resistant, although among thousands of lines of the original Voroshilov tested each year in the nursery not a single rust-resistant plant was ever found. This indicates the importance of external conditions in the first phase of development for forming the character of disease-resistance in plants (in this connection see Lukyanenko, 1941).

Grafting is widely used for various purposes. In some cases difficult crossings may be accomplished by the aid of vegetative approximation, that is, the preliminary grafting of one parent on the other. This technique has been used for example by Zvereva (1946) to make certain difficult *Solanum* crosses in attempting to breed for frost resistance in potatoes. Similarly an apple-pear hybrid, which gave a small amount of fertile seed was produced by grafting cultivated pear on the Siberian apple (*Malus baccata*), and later fertilising the apple with the pear pollen. Varieties of melon have been produced by Alekseeva (1948) which can be grown and ripened in open ground in the Moscow region. The method employed was to graft the melon at the cotyledonary stage on to marrow or pumpkin (*Cucurbita Pepo*, *C. maxima*, *C. moschata*) in order to get ripe seeds. The melon seed from these grafted plants was sown, and by training and selection of the seedlings varieties of melon were obtained which would ripen on their own roots without preliminary grafting. These melons are now grown on a commercial scale around Moscow.

Grafting is also used to produce vegetative hybrids for use in plant breeding. At the Byelorussian Selection Station vegetative hybrids of cultivated buckwheat with *Fagopyrum tataricum* have given high-yielding forms which are valuable material for the development of new varieties. Mikhailov at Mordovsk grafted local buckwheats on to wild forms and obtained vigorous vegetative hybrids with large grains, which are now being reproduced.

Vegetative hybridisation of spring wheat by transferring the embryo (scion) at various stages of its development into the grain of another variety (stock) has been carried out by A. S. Pushkin at Kamalinsk Station. This remarkable work is actually carried out in field conditions. Several valuable forms

MICHURINIST METHODS OF CHANGING THE NATURE OF PLANTS

Paths of Transformation

Action of environmental conditions at critical phases of development.

Sexual hybridisation (crossing).

Vegetative hybridisation (grafting).

Stages of Work

(1) Definition of aim of work; selection and thorough study of starting material.

(2) Operations with starting material.

(3) Production of organisms with shaken heredity.

(4) Training of organisms with shaken heredity.

(5) Fixing the heredity; reproduction of new varieties.

Methods of Work

Methods of directing dominance of required properties by training prior to crossing or grafting. Use of phasically young plants to overcome difficulty in crossing, etc.

Difficulty of crossing removed by repeated pollination, pollen mixtures, method of intermediary, etc.

Method of preliminary vegetative approximation to overcome difficulty of crossing.

Influence of changed conditions on early seedlings stages: method of sowing gradually farther north, etc.

Hybridisation of forms distant (*a*) geographically, (*b*) systematically.

Vegetative hybridisation to cause shaken heredity.

Training of young hybrid seedlings by regulation of food supply, etc.

Method of repeated crossing.

Use of mentors.

Vegetative reproduction by rooting.

Reproduction by seeds.

Reproduction by grafting.

Selection of pairs for crossing or grafting and selection of starting material for raising new varieties by the influence of changed conditions.

Selection of hybrid seedlings and seedlings produced under the influence of changed conditions, etc.

Selection of the best seedlings for reproduction, use of suitable stocks for grafting.

Selection

of spring wheat have been obtained which are now being widely studied and tested. A new variety of winter wheat was produced by grafting wheat on rye at a very early stage of shoot development. This variety appeared promising in 3-year trials, and is now undergoing Government varietal tests.

The examples which have been quoted give some idea of the extent to which Michurinist theory has reanimated and transformed every branch of plant breeding and seed production, and contributed to the rapid development of socialist agriculture. It must be emphasised that Michurinist theory and practice as applied to plant breeding form a fully integrated system. The diagram on page 143 reproduced from Grushvitsky (1950) provides an interesting summary of its leading features.

3

A very important agricultural technique directly connected with Michurinist theory is that of additional artificial pollination. This procedure which is now used on a very large scale in the Soviet Union was first investigated and developed by Musiiko (1939, 1949). He showed that the yield of many cross pollinated plants was very considerably increased if measures were taken to increase the amount of pollen reaching the stigmas at the time of fertilisation. Simple technical methods were devised suitable for different crops in order to increase the amount of available pollen at the critical period. Thus cereal crops such as rye and hemp are agitated by means of string or wires early in the morning at the time of mass opening of the flowers. In this way a very high concentration of pollen is created in the atmosphere at the time of flowering. In the case of sunflowers the operator proceeds down the line of plants transferring pollen from one to another with a special glove which is wiped over the surface of the flower. Slightly different but equally simple techniques are used for other crops, and will not be described in detail.

Tests of the method were made in 1936, 1937 and 1938 on some 20 collective farms. The yields from sunflower, maize, hemp and lucerne from parallel plots with and without additional pollination were recorded. The total area of the tests was over 800 hectares. The increases in yield due to additional pollination were very considerable, ranging from 25–50 per cent., lucerne (seed only), 120 per cent.

Since that time additional pollination has become a standard agricultural technique, used on areas of hundreds of thousands of hectares on the collective farms. It has been extended to such crops as buckwheat and millet. The average increase in yield per hectare is 4 centners for maize, 2·3 for sunflowers, 1–3·5 for rye, 1–3 for buckwheat, 1·5–5·0 for millet. The effectiveness of this procedure is very striking when measured in terms of labour expended. Thus for maize the number of labour-days required to carry out additional pollination is only 1·1 per hectare and this leads to an increase in yield of 4·21 centners per hectare (16–20 per cent.). Comparable figures are obtained for other crops.

The significance of additional pollination is not merely to ensure that the maximum number of seeds are pollinated, although this is naturally an important contribution to the increased yield. There is, however, also a considerable effect on the quality of the seed. The seed from extra-pollinated plants is larger than from control plants and is richer in food reserves as the following figures show:

Experimental Area (ha.)	Plant	Absolute weight (g.) of 1,000 "seeds"	
		Extra-pollinated	Normal
60	Maize	295·26	239·18
150	Hemp	20·30	17·25
27	Sunflower	79·0	69·0
8	Ricinus	276·46	224·08

Analysis of Grain of Maize (as per cent. dry matter)

	Extra-pollinated	Normal
Fat	5·42	4·59
Total Nitrogen	2·17	2·04
Phosphorus	0·726	0·648

Of even greater theoretical interest is the definite effect of extra-pollination on the yield in the following year. Many experiments have established that seed from extra-pollinated plants gives a higher yield than control seed when compared in uniform conditions, and that the plants of the extra-pollinated seed are in general less susceptible to fungal attack. Figures are given by Musiiko for large-scale experiments on a number of collective farms as well as for institutional trials, in which comparison was made between the yield (without additional pollination) of seed from additional pollination and seed from normal pollination of the same variety of maize. The extra-pollinated seed gave yields at least 18 per cent. higher than the controls, frequently 30–40 per cent. higher, whilst the proportion of plants attacked by fungal disease was about half that in the controls.

Similar beneficial effects of additional pollination on seed quality have been shown for winter rye (Krasnyuk, 1946) and other crops. The results of comparative trials with rye were as follows:

Year	Winter rye variety	Yield in centners/hectare	
		Extra pollinated seed	Normal seed
1941	(*a*)	25·5	22·0
	(*b*)	21·9	18·7
1942	(*b*)	16·1	13·2
1943	(*a*)	17·5	16·6
	(*b*)	17·4	16·1
1944	(*b*)	34·4	33·0
		22·1	19·9 Mean

The technique of artificial additional pollination has become a potent means of directly increasing the yields of many agricultural crops. By 1940 it was being used on an area of over 1½ million acres, giving a total increase in yield of the order of 170,000 tons of agriculture products (chiefly maize and sunflower seed). Since then the use of this technique by collective and state farms has extended rapidly. The significance of additional pollination in improving seed quality is also very great, and it is therefore also used as a standard operation in seed production and breeding work.

Michurinist theory has led to important developments in the organisation and practice of stock breeding. Some of these questions were touched on by Lysenko in an address to a session of the Lenin Academy of Agricultural Sciences in May, 1949, devoted to the advancement of animal husbandry. The position is somewhat different from that in plant breeding since stock breeders have always worked on traditional lines without paying much attention to Mendelian theory, which has been largely inapplicable to their work. Nevertheless Lysenko pointed to a number of ways in which the formalism of Mendelian theory has an adverse effect on animal breeding, and showed how Michurinism is not only consistent with the work of the best practical breeders but provides also a real theoretical basis for solving the practical problems encountered. Great attention is directed to creating local breeds of agricultural animals adapted to the conditions of each region as well as to particular types of production.

It should be noted that seed production and plant breeding, like the other activities of the Selection Stations and the work of stockbreeding, are carried out within the framework of the "travopolye" system of agriculture. This is a system of grass-arable rotation in which all the processes of agricultural production are integrated so as to develop and maintain maximum fertility of soil and the highest possible yields of crops and animals.

4

A brief note about the man whose name has been given to the new trend in biology may be usefully included here. Michurin was one of those remarkable individuals who stand out so surprisingly against the grim background of Tsarist Russia. As a youth he was fired with the idea of remedying the lamentable state of Russian horticulture, particularly in the central regions, and he deliberately set himself

> two bold tasks: to augment the assortment of fruits and berries in the central regions by adding high-yield varieties of superior quality, and to extend the area of southern crop cultivation far to the north (Michurin, 1949).

The whole of his life was devoted to this selfless work, which was carried out under conditions of appalling difficulty for over forty years under Tsarism. Only his patriotism, self-discipline, and enormous industry enabled him to create more than 350 new varieties of fruit plants and to gather together one of the richest plant collections in the world. His attitude is revealingly expressed in his own simple words in a request to the Sixteenth Party Congress (in 1930) to pay attention to fruit growing:

> We must break with the past and cease living for our own sake only—something that has unfortunately become too deeply rooted in each of us. We must all work for the good of all and the consequent general improvement in the standard of living will afford better conditions to every one of us. Throughout my life I firmly adhered to this idea and strove to the utmost to overcome all difficulties. I attempted to improve all that came my way: I have worked in various branches of mechanics and electrical engineering, perfected various instruments, studied agriculture. . . . But best of all I loved the work of improving cultivated fruit-plant varieties.

Owing to the impoverishment of his family—petty land-owners whose mortgaged inheritance had to be sold—he had to renounce his intention of going to the university, and take a job on the local railway. For twelve years he worked on the railway, first as goods clerk and then as inspector of clocks and signals. In order to supplement his meagre pay he set up a watch-repairing business in his spare time, devoting his extra earnings to buying horticultural books and journals, catalogues, and plants for the small nursery which he was establishing. By this incredible industry he was finally able to make the nursery self-supporting and to give up his job on the railway. But his life continued to be one of poverty and privation, made harder by the attacks of religious obscurantists and the utter indifference and even hostility of the Tsarist ministry of agriculture. Only the coming of socialism relieved him of material worries and made possible a tremendous extension of his work and its application in the service of society. Michurin supported the Soviet Government from the first, and it shows the quality of his mind that he not only saw the vast possibilities of advance inherent in collective agriculture but that he linked the further development of his own work closely with the collective farms.

The practical success of Michurin's methods is undoubted, and it is interesting to learn that the United States Department of Agriculture were so impressed that in the years 1911–13 they tried to induce Michurin to emigrate to America, or at least to sell all his varieties on favourable terms. However, he preferred to devote himself to serving his own people. Lenin recognised the importance of Michurin's work, and with the establishment of the Soviet Government, which Michurin unhesitatingly welcomed, funds were made available to support his work. Laboratories were set up, and in 1931 the nurseries became the Michurin Central Genetics Laboratory, with Michurin as director and with a large staff.

The practical results of Michurin's work are a large number of new varieties of fruit plants which are now widely grown in the Soviet Union, and the northward extension of the area of cultivation of various species, including the vine (see Isaev, 1940, for details).

The basic principle of Michurin's operations was the changing of heredity by means of environmental changes acting on the early developmental stages of the organism. It is this conscious use of the adaptive capacity of plants in order to change them in a desired direction which is the new and distinguishing characteristic of his methods. Michurin makes it very clear that he was not a selectionist: he never denied the importance of mass selection in appropriate circumstances but considered that selection is not a sieve but a positive method of using the variability of organisms in order to transform them. Selection must be linked with the "shaken" heredity caused by hybridisation and with subsequent training of the seedlings. Thus Michurin worked with only some tens of seedlings at a time and he complains with reference to Burbank (whom he nevertheless greatly admired) that some writers had placed his own work "in an extremely false light by placing it on a par with the work of the late Burbank, an advocate of planting many thousands." Michurin's methods which he applied almost exclusively to fruit plants have been widely and successfully used in the Soviet Union in plant breeding. The work of Lysenko and his collaborators on the transformation of spring and winter forms of cereals represents an extension of Michurin's methods and a striking confirmation of the correctness of his theoretical standpoint. Furthermore, the conception of heredity and of the organism-environment relation which Lysenko puts forward can be seen as a clarification and deepening of conceptions which are already contained in Michurin, although it is not suggested that there was any direct derivation. In this connection it is interesting to note the penetrating observations which Michurin made on the specific environmental requirements of plants. Such observations foreshadow a line of investigation to which Soviet biologists have paid considerable attention and which has culminated in Lysenko's phasic theory of development.

Just as the environment plays an active role in the transformation of plants by man, so Michurin considers that it plays a similar active role in natural evolution. Organisms are changed under the influence of environment, but only in the course of development, by the assimilation of new conditions through metabolism. The creation of new plants and animals in agriculture does not differ in principle from their creation in nature, except that the process is controlled and directed by man.

Michurin's manner of work was vigorous and unconventional, and firmly directed to practical aims. His theoretical ideas emerge quite clearly from his writings, although often cast in the form of practical instructions or descriptions of methods. But he was always conscious of the need for a correct theory on which to work, and like Darwin, he based his ideas on the closest observation of nature. He made great use of grafting as a means of influencing and improving immature plants, showing that a plant can be altered by grafting if in a sufficiently early phase of development. To secure hybridisation he employed a number of interesting techniques, including the use of mixed pollen, vegetative approximation of the parents, repeated fertilisation, the use of an intermediary. The necessity of producing locally adapted forms for every region, and careful selection of parental forms on the basis of their environmental history, are repeatedly stressed by Michurin.

His extremely interesting methods of selection of young plants for breeding have considerably influenced plant breeding work in the Soviet Union.

These methods of Michurin have not only affected Soviet practice in plant breeding but have opened up new lines of research which have led to the discovery of many facts of great theoretical significance. The appellation Michurinist for the new biological trend is not therefore inappropriate. It expresses both the origin of this trend in the solution of practical problems and its continuity with the great materialist tradition of Darwin.

IX

THE SCIENTIFIC AND SOCIAL SIGNIFICANCE OF THE NEW THEORY

I

THE history of science provides many examples of theoretical advances which resulted from the unorthodox but effective experiments of technologists and practical men, intent on solving immediate problems, and satisfied if their methods worked, even though contrary to accepted theory. The men who gave theoretical formulation to the new knowledge were often themselves outside strict academic tradition and more closely in touch with the experience which challenged it. The strength of Darwin was not drawn from academic sources but from his own observations of nature in different parts of the world and from his intimate acquaintance with the practices of stock breeding and agriculture.

Michurin began his work as a follower of the accepted ideas of Grell on acclimatisation and he only abandoned them when they proved useless in practice. In attempts to introduce various fruit plants into Central Russia and to breed more suitable varieties he developed novel methods and techniques. The practical success of these methods was the stimulus to a critical reconsideration of accepted theory, and the new ideas grew up, incomplete but vital, out of the soil of experience.

What happened in the breeding of fruit plants was repeated on a larger scale, and with more profound results, in agriculture under the impact of the great social changes following the October Revolution. The establishment of socialism brought about a rapid increase in the forces of production, an increase which did not take place once for all but which continues year after year. The advance of the productive forces in every branch of economy creates an ever wider technical basis for the many sided development of science. At the same time the technical needs of socialist society raise new and more complex problems, requiring a profounder understanding of the scientific laws of the universe for their solution.

It has already been explained how the rapid development of collective agriculture provided the foundation for a great expansion of biological science, simultaneously giving rise to urgent problems for biology to solve, problems which differed both in scale and in kind from those which arise in the restrictive conditions of capitalist agriculture. But socialism not only created greater opportunities and wider problems for biology: it also created people with a new outlook and with capabilities commensurate with the tasks before them. The generation of Soviet scientists which has grown up during the years of active construction of socialism differs in origin and training from the older generation of scientists. Drawn from the whole of the working people, closely acquainted with the technical problems of industry and collective farming, they bring to the theory and practice of science a boldness and confidence which respects but is not hampered by tradition, either in thought or action. This freshness of outlook is combined with the conscious use of the scientific principles of dialectical materialism as a guide in experiment and interpretation.

The close link between the working scientist and the collective farms, exemplified by co-operative experimentation and the constant interchange of advice and experience, continually enriches agronomy. It has been a primary cause of the vitality of Soviet biology and of the emergence of new leading principles. The statement of these principles in a coherent form owes much to Lysenko and his remarkable ability both in experimental work and theoretical generalisation, an ability which derives from his complete mastery of the dialectical method. But the new biological trends are much more than the results of one man's labours. They are the product of the socialist transformation of society, and of the creative initiative of thousands of ordinary men and women which socialism liberates.

2

When making an estimate of the value of rival scientific theories it is important to bear in mind that a decision can rarely be made on the basis of one or two critical experiments alone. Even those historical experiments which we now think of as decisively establishing some particular theoretical advance were rarely considered so decisive by contemporary thought. The process of clarification of scientific theory is more complicated in actuality than it appears in retrospect, and the new only establishes itself in the course of a more or less prolonged struggle with the old.

All this applies with special force to biological questions in which the complexity of the systems involved and the magnitude of our ignorance create particular difficulty. Lysenko's ideas are not established, just as Mendelism is not rejected, by any single fact or experiment. The decision has to be made by consideration of a general body of facts and experiments, by the effectiveness of the theory as a guide to practice and investigation, and by its consistency with the general laws of living organisms. Furthermore it is necessary to approach a new theory in a positive way: to make an effort to understand it and to see what advantages it offers in interpretation and as a stimulus to further experiment. To reject an idea because it is strange, without any attempt to see what it can do and what illumination of known facts it can provide, is to abandon constructive inquiry.

Some biologists have considered Lysenko's theories as nonsense because of his use of a number of terms in an unusual and unfamiliar sense. But this extension of the meaning of an older terminology is something which has been characteristic of almost all theoretical advances in the past. Indeed, it would be true to say that any new theory which makes a fundamental change in our conceptions is likely to sound like nonsense at first acquaintance. As I have shown in the course of this book, Lysenko's ideas are quite clear and comprehensible and require serious attention, although they do not fit into the categories of Mendelism. It is useless, however, to approach them in a spirit of blind prejudice, as some Mendelian geneticists have unfortunately done, especially in the United States of America. A recent article by Sonneborn, for example, in *Science* is as remarkable for its unquestioning acceptance of Mendelian theory as for its ludicrous misstatements of Lysenko's position, which show that the author has not taken the elementary precaution of studying the man he seeks to criticise.

The complacency of some advocates of Mendelism is rather astonishing in view of the extreme vulnerability of the fundamental tenets of this theory. For the gene theory has never been universally accepted by biologists, and has been repeatedly criticised because of the obvious weakness of its philosophical basis. Yet this doctrine is now being surrounded with an almost religious respectability, simply because it is the Russians who have carried to its final conclusion the criticism already begun from the materialist standpoint by philosophers and biologists in the West.

Probably many biologists, who have not considered the question very deeply, support the gene theory because of a confused identification of chromosome segments with genes. But genes are not simply parts of the chromosome, for according to Mendelian theory they are much more. They are bits of chromosome endowed with a set of properties which analysis shows to be self-contradictory and inconsistent with the known laws of biological systems. The gene is thus an entity which is contrary to the materialist basis of science. The existence of "units" in heredity in no way requires or implies the existence of genes.

This criticism goes to the root of Morgan-Mendelism. The essential point is explained with pungent clarity by Lysenko.

> The Morganists present the heredity of organisms as a special substance. This substance, like any other, they divide into separate particles. But in fact the hereditary substance in something invented by the Morganists, it does not exist in nature. This supposed hereditary substance is placed by the Morganists in the chromosomes of the cell nucleus in linear order. These particles of hereditary substance they have endowed with the property which no particle of a living organism possesses—the property of not developing and of not changing. In other words, they ascribe to these invented hereditary particles the miraculous property of growing and reproducing whilst remaining unchanged. But we know that no living organism and no part of a living organism can grow or reproduce without changing and being transformed. Without change and transformation there is no development (Lysenko, 1938).

The fictitious character of the gene, this up-to-date and particulate version of the vital force, is the cause of the numerous difficulties of Mendelian theory which have been discussed in an earlier chapter. Starting from the gene concept it is impossible to construct an adequate theory of development, capable of even beginning to embrace the facts of embryology, tissue differentiation, and the ordered progress of ontogeny. It is in dealing with the central problem of genetics that Mendelism has proved most unsatisfactory.

It might be argued that Mendelism, although unsatisfactory as a fundamental theory, should be preserved because of its convenience as a representation of many facts in sexual inheritance. A theory cannot be wrong in its basis, however, and right in details at the same time. Moreover, there is real danger in preserving an arbitrary theory for heuristic reasons, since it is bound to lead to neglect of significant facts and to false isolation of related phenomena. The apparent success in representation becomes an actual barrier to investigation of the laws of movement of the underlying processes.

3

The question that must now be considered is therefore the extent to which Michurinism overcomes the weaknesses of Mendelism and is able to provide the basis of an adequate genetic theory. Before dealing with this point the leading features of the new theory may be briefly recalled.

Michurinism is based on the unity between every organism and its conditions of life, a unity of continuous mutual interaction expressed in the process of metabolism. The characteristic property of a living organism is development, its passage through a series of qualitatively distinct, irreversible phases, at each of which it has definite requirements with respect to external and internal conditions. This property of having definite requirements and responding in a definite way to the environment constitutes the essential basis of heredity. Thus heredity is looked on as a metabolic process of the organism as a whole, in which the internal and external meet and interpenetrate. The environment therefore creates heredity through its effect on metabolism, and heredity may be considered as the summation of environmental influences assimilated by an organism in preceding generations.

According to this view variation and evolutionary change take place in response to external environmental conditions. If external conditions cause a decisive change from the normal type of metabolism then the selective requirements of an organism, that is, its heredity, may be changed. The heredity of plants and animals can therefore be directed through their conditions of life, provided their specific requirements have been studied and understood.

It has already been seen that Michurinism provides a general explanation of the facts which is quite as satisfactory as that given by Mendelian theory and which embraces a wider range of phenomena. In addition, Michurinism possesses certain positive features which make it at least a beginning for an adequate fundamental theory of genetics. It is in the first place firmly based on metabolism, and attempts to explain the phenomena of heredity in terms of real biological processes which can be investigated as problems of physiology and biochemistry. Thus the completely non-biological conception of a special organ of heredity is abandoned, and heredity is correctly treated as a property of the total organisation of living matter. The Mendelian organ of heredity with its constituent genes is a false abstraction, only possible because cell metabolism is emptied of its actual content. There cannot be an organ of heredity just as there cannot be an organ of growth, for both heredity and growth are general properties of living matter. Analogies between the alleged organ of heredity and the organ of thought or the organ of insulin secretion are misconceived, since thought and insulin-production are not universal properties of living systems.

Having divested itself of the special heredity substance, Michurinism is able to give a biological explanation of various phenomena which Mendelism can only deal with in formal terms. Thus the relative stability of heredity in normal environmental conditions is seen by Lysenko as an expression of the active selectivity of the organism, a universal biological property of metabolism. Selection is not just a neutral sieving out of less viable forms: it represents a creative effect of external conditions, actively moulding new forms. Adaptation results from systematic changes in the balance of various biochemical processes, impressed on the organism by its conditions of life. The fusion of male and female cells in fertilisation is revealed as a special type of metabolism, mutual assimilation, the specific features of which have arisen in the course of evolution in relation to the vital biological role of the sexual process.

Heredity is defined in simple, precise and fundamentally biological terms as the specific metabolic requirements of an organism at every phase of its life cycle. Development is seen to consist of a series of obligate phases each with its own specific external and internal requirements which are open to experimental investigation. Thus Michurinism not only provides a theoretical basis to account for differentiation and development, which Mendelism with its unchanging genes is incapable of doing, but it indicates exactly the kind of experiments which are required to elucidate the complete course of individual development in any particular organism. A whole range of phenomena are opened to experimental attack on fruitful lines. In fact, Michurinism directs renewed attention to what is after all the central problem of genetics, the explanation of ontogeny. This problem has been neglected by Mendelists, because of the incapacity of gene theory to tackle it, in favour of the important but less fundamental questions of inheritance of differences in sexual crosses.

The ability of Michurinism to offer the basis for an epigenetic theory of development is the most powerful proof of its consistency with materialism and of its right to replace Mendelism as the working theory of genetics. In this connection Lysenko has justly said,

> Our theory of plant development is far from being perfect; but, all the same, it is truer and more effective than the knowledge of the laws of plant development possessed by many who call themselves geneticists (Lysenko, 1936d).

The great merit of the new theory is that it relates all the phenomena of heredity to actual biological processes, recognising that the permanent quality of living organisms is expressed in metabolic activity, not in unchanging substances. For this reason it is able to reveal the essential unity of a number of apparently diverse phenomena and throw fresh light on them, as is seen, for example, in the treatment of the common metabolic foundation of shaken heredity and segregation, following sexual crossing, vegetative hybridisation, or physiological disturbance caused by external conditions. The directing of heredity through the action of physiological processes represents a new weapon of attack in genetical investigations which is already leading to important advances in knowledge.

The Michurinist analysis of adaptation and of the active role of the environment in the formation of heredity links the development of the organism with the process of evolution. As Lysenko says, "Organisms, and hence also their nature, are created only in the process of evolution." The relation between ontogeny and phylogeny is clarified and brought within the scope of experimental study, whilst the whole content of genetics is deepened by the inclusion of evolution as an organic part, instead of as a more or less fortuitous adjunct.

A brief reference may be made at this point to Lysenko's assertion of the absence of intra-specific competition, that is, of competition between individuals of the same species. In his view the idea of struggle within a species is a Malthusian conception falsely applied to biology. Thus he considers that the conceptions of competition or, on the other hand, of mutual aid have no meaning when transferred to the relations between members of the same species:

> Intra-specific mutual relations of individuals cannot be brought under the conceptions of either struggle or mutual aid, since these relations are only directed to maintaining the existence and success of the species, to increasing the number of its individual representatives.
>
> In nature there is not and cannot be either struggle or mutual aid within species (Lysenko, 1949).

It must be noted that what has been said refers only to the situation within a species. The existence of competition and of mutual aid between species is, of course, clearly recognised.

Lysenko believes that intra-specific competition due to over-population does not normally occur in nature, owing to the operation of natural selection. The establishment of adaptation for intra-specific competition could not be of advantage to an organism and could only be injurious. Hence the reproductive rate of organisms in nature is so adapted that it does not in general lead to over-population and competition within the species.

Whilst this is the general rule, it may happen that on occasion local over-population occurs. Such a condition can also be produced experimentally, by sowing plants too closely, for example. In these cases Lysenko would not apparently deny the existence of competitive effects. But he considers that such intra-specific competition is unusual in natural conditions and that it does not play a significant role in evolution, since the effect is a general weakening of the vitality of all the individual organisms.

There cannot, on the other hand, be mutual aid between individuals of the same species, at least of the type of symbiosis which occurs between different species, since they all possess the same specific requirements with respect to external conditions. The aim of Lysenko's formulations is evidently to give a description in biological terms of the relations within a species. I shall not attempt to discuss this matter more fully since, in spite of its importance in relation to evolution and species formation, it is not essential to an understanding of the basis of Michurinist theory. Furthermore, it is a question to which very great attention is being paid in the Soviet Union at the present time and which will certainly be further clarified. Enough has been said to indicate the serious character of Lysenko's thought on this subject and to show that his views cannot be dismissed as absurd.

Michurinism is thus not the mere negation of Morgan-Mendelism nor the crude re-hash of earlier theories, as it is sometimes represented by those who have not taken the trouble to understand it. Michurinism is a qualitatively new, serious scientific theory of a really profound character. It is not by any means a finished or complete theory, for it is being actively developed and clarified in the course of practical experimentation all the time. Anyone who has followed Lysenko's writings at all closely must be struck with the way his formulations of theory have increased in clarity and generality as new facts have come to light. Thousands of Soviet biologists are working under the guidance of this theory, accumulating new facts which will deepen and doubtless modify it. But already Michurinism represents a serious and workable genetic theory as well as a very important contribution to biological thought. Most Soviet scientists are convinced of the substantial correctness of the new genetic theory, and they have at least sound factual, scientific and philosophical reasons for their belief, as I have tried to explain in this book.

4

The triumph of Michurinism has undoubtedly led to a very great stimulus to biological and genetical work in the Soviet Union. This is seen not only in practical agriculture and in the researches connected with plant and animal breeding. Work on various aspects of cytology is very active; mention may be made of investigations of the process of fertilisation in plants and animals (e.g. Ellengorn and Svetozarova, 1949; Kostryukova, 1949; Kushner, 1949) which show a number of significant features, either new or previously neglected, especially the frequent occurrence of fusions (sometimes including nuclear fusions) between male reproductive cells and cells of the maternal tissues. There is an important school of biochemistry working on the dynamic biochemical changes which occur in organisms at different stages of development, in genetically different tissues (e.g. Rubin *et al*, 1950), or as a result of fertilisation (Lesik, 1949), whilst others are concerned with the changes in biochemical character following hybridisation or hereditary change caused by disruption of metabolic norms (e.g. Sisakyan *et al*, 1950). These researches are producing very interesting results which unfortunately cannot be summarised here.

The general picture of Soviet biology and genetics to-day is one of extraordinary vitality and activity, with applied and fundamental research closely connected and opening up many new and important fields. Soviet investigators are enthusiastically following the advice which Michurin gave to a young worker, "Experiment fearlessly. Let no old canons stop you. The harder the task, the more interesting."

Above all, the Soviet people are convinced that Michurinism has completely justified itself in the hard test of practice. It is because of their firm belief in the effectiveness of the theory that they attach so much importance to its universal adoption and why so much effort is made to ensure that its principles are widely and thoroughly understood. The scientific and social significance of the new theory cannot be separated.

As was explained in an earlier chapter, the fully socialist form of society which exists in the Soviet Union to-day is now preparing for the passage to a higher form of society, that of communism. By the socialisation of all the means of production the basis has now been laid for a very great increase in production. In 1946, immediately after the fascist invaders had been driven out, the Soviet Government began to make plans not merely to raise production to prewar level (which has already been more than accomplished) but in the course of several Five-Year Plans to raise production to at least three times its present height both in industry and agriculture.

Particular importance attaches to agriculture as the supplier of food and primary products to society. Detailed and fundamental plans were drawn up to transform the productivity of socialist agriculture. In the first place the travopolye system of grass-arable farming, a completely integrated system of progressive agronomy, was universally adopted. This was combined with measures for large scale irrigation, the planting of forest shelter belts, the conversion of desert areas to cultivation, and a general extension of cultivation beyond its present limits.

In order to carry out this tremendous programme of humanitarian advance there are two main requirements in addition to the energy, enthusiasm and co-operation of the Soviet people. The first requirement is the possibility of developing these great schemes in conditions of peace. This is why the Soviet Union has taken the lead in international affairs to secure a reduction in armaments and a return to co-operation between the Great Powers in the prevention of war. The second requirement is the most thorough utilisation and application of scientific principles to the increase in production of material goods.

It is believed that a great role in the development of agricultural productivity will be played by the new biological theory of Lysenko. The existence of an effective materialist biological theory in the hands of the masses of producers is a revolutionary event in the history of the world. The Soviet people therefore look forward with confidence to a rapid advance in general wellbeing, and an abundance of all material and cultural goods of society such as the world has not yet seen. They believe that their own efforts are all that is required to bring about that state of affairs, of which the nobler spirits of mankind have long dreamed, in which society can at last inscribe on its banners

> From each according to his ability: to each according to his needs.

They regard Michurinism as a triumph of socialism and as a weapon in their advance to the future.

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Note. Some Russian journals (e.g. *Agrobiologia*) have no volume number (apart from the year of publication). In these cases the number quoted before the page number refers to the monthly or bi-monthly issues.

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