THE PRODUCTION OF A QUICK-GROWING WALNUT

THE BURBANK ROYAL AND OTHER EXPERIMENTS

MY hybrid walnuts, already known to the reader as the Paradox and the Royal, were first publicly announced in my catalog called "New Creations in Fruits and Flowers", in June, 1893.

The hybrid walnuts themselves were then five or six years old and the Royal had borne fruit, so that a photograph of its large-sized nut could be given. The Paradox, on the other hand, although it had flowered for several seasons, had produced no fruit. It was supposed, therefore, that it would be impossible to reproduce this hybrid from seed.

In subsequent years, however, the Paradox proved its capacity to produce fertile fruit, although it was never a free bearer. And in my supplementary catalog of the year 1898, I was able to offer seeds of the Paradox for sale, and to make a statement as to the manner of seedlings that

might be expected to grow from these seeds. The statement, in view of the date when it was printed, has somewhat exceptional interest in the light of later developments, so I quote it here.

It was as follows:

"The six beautiful specimens of this hybrid growing on my home place have been objects of admiration to all who have seen them.

"Young trees could have been sold at almost any price, but, having no time to raise them, offer this season's crop of nuts which will be a great surprise in producing about one-third of a new type of the broad-leaved Persian walnuts, one-third of a new type of the California black walnut, and about one-third combined, as in the original tree."

The "original tree" in question was, of course, the hybrid called the Paradox, produced by crossing the California walnut and the Persian walnut. So the seedlings, the character of which is predicted in the paragraph just quoted, would of course represent second generation hybrids from this cross.

I make the quotation here, carefully specifying the date at which the original was printed, because there is a certain interest in knowing that tests made prior to this time with the seeds of the hybrid walnut had clearly revealed to me the fact

that "about one-third" of the second generation hybrids would revert toward one parent, while another third would revert toward the other parent, the remainder being intermediate in character, and in this corresponding to the first generation hybrid that was their parent.

This implies a fair understanding of the combination of characters of the two parent species in the first generation hybrid, and the segregation and recombination of these characters in the second generation hybrid. It will be noted also that the distribution of these characters in the second generation (as predicted on the basis of my observation of earlier seasons) was essentially that which has come to be familiar everywhere within recent years as the typical distribution of characters among second generation hybrids in what is now known as Mendelian heredity.

To be sure the figures given are only approximate, nor have I in any of my experiments endeavored to keep accurate count of the precise numbers, the large scale on which I operate making this scarcely practicable—but the close approximation of the rough estimate that I made to the precise figures that have been determined by more recent investigations, sufficiently attests the accuracy of the observations on which the estimate was based.

And, figures aside, the essential principle of the segregation of characters, and their redistribution into three essential groups, one representing each parent, and one combined as in the first generation hybrid, is as clearly stated as can be desired.

The interest of all this hinges solely on the fact that the statement was published in 1898, based obviously on observations made prior to that date; at a time, therefore, when no one living had the remotest knowledge of the discovery made by Mendel more than thirty years before. Mendel himself died in 1884, and the rediscovery of his work was not made until a year or two after the date of my catalog, just quoted.

And I may fairly assume, I believe, that there were few, if any, botanists or plant developers in the world, at the date of this publication, who had any such clear conception of the meaning and interpretation of the prediction contained in the quoted paragraph as my own original observations had given me.

In point of fact, the observation on the seeds of the Paradox walnut, as here quoted, was made quite casually.

I did not put it forward as constituting a new pronouncement in heredity, because it simply represented a specific application of a general truth regarding the tendency of heritable characters to

A Row of Paradox Walnuts

The paradox walnut, it will be recalled, is a hybrid produced by Mr. Burbank, through cross pollenizing the Persian walnut and the California black walnut. The picture shows a row of very young Paradox walnuts growing beside Mr. Burbank's gardens at Santa Rosa.

be segregated and recombined in the second generation hybrids that had come so often under my observation that it had become a commonplace to me many years before the publication of this catalog in 1898.

I have elsewhere stated that the matter had been the subject of controversy with a good many of the leading botanists and horticulturists of the world, and that during the period of perhaps fifteen years prior to the rediscovery of Mendel's experiments, I seemingly stood in a minority of one in the belief that such segregation and redistribution of characters in the second generation hybrids is the usual and all but habitual method of inheritance.

After DeVries and his fellow-workers had come upon Mendel's earlier publication and made it known to the world, the matter was no longer in dispute.

But then the neophytes who had so long refused to listen to my claim were disposed, after the manner of neophytes, to become over-enthusiasts, and some of them at least thought that the principle of the segregation of heritable characters in the second generation was one that must supplant all other principles of heredity, reducing questions of inheritance to such simple formula that the veriest tyro could master them, and having them in

hand, could go into the field and create new forms of plant life at will.

And because I ventured to point out that the essential principles that now came to be spoken of as Mendelian had been the guiding principles of my experiments for at least twenty years before Mendelism was heard of, I was denounced in some quarters as reactionary, the fact being quite overlooked that the essential principles involved had been discovered by me quite independently; exploited by me in connection with many hundreds of species; given publication by me prior to the rediscovery of Mendel's forgotten paper; championed by me against the opposition of all the leading authorities of the world; and that therefore the aspect of heredity in question might with full propriety have been named "Burbankian" instead of "Mendelian", were it not that Mendel's discovery had priority because it was published so long ago as 1863, whereas my independent discovery of the principle was not made until almost twenty years later.

Even at that, however, I had had full twenty years priority over any one else except Mendel in the recognition of the principle.

Therefore, as I just intimated, I have found it a trifle disconcerting to be heralded as reactionary and as scouting the essential principles that I

ardently espoused during a period of at least sixteen years subsequent to the death of Mendel, during which they had no other champion.

What I have deprecated, however, in recent years, is the over-enthusiasm of certain alleged followers of Mendel, who have entertained what I conceived to be a misapprehension as to the real significance of "unit characters", and who, misguided by a narrow range of experiments, and lacking the breadth of view that comes with wider experience, have supposed that all heritable characters might be classified as fixed and unvarying entities that are transmitted in accordance with the Mendelian formula.

Fortunately, a good many former holders of this biased and inadequate view have seen its insufficiency, and already there is a tendency to react from it, evidenced in the writings of some of the leading Mendelians; and, coupled with this, the tendency to take a broader view of heredity and to understand that there are countless heritable characters that do not Mendelize in any tangible or demonstrable way; that "unit characters" are themselves made up of subordinated characters; that new "unit characters" from time to time appear, whereas old ones that at one time Mendelized are finally so fixed that they blend with the older structure of heredity and no longer present the

A Twelve-Year-Old Paradox Walnut

An idea of the size of this tree may be gained by comparison with the telegraph poles and with the man standing in the corner. Were it twice its actual age, it would still be a remarkable tree. Observe the attractive and symmetrical form.

phenomena of "dominance" and "recessiveness"—in a word, that heredity is a somewhat larger term than Mendelism, and that the biologist or botanist or plant developer who would gain a really clear conception of the situation must clearly distinguish between the lesser term and the greater, although at the same time recognizing that one is an essential sub-structure of the other.

So Darwinian heredity, which recognizes the heritability of whole coteries of characters that are too profoundly fixed to Mendelize, is again receiving recognition; and the multitude of special studies of the past decade that were inspired by the rediscovery of Mendel's work and by the exploitation of his formula will take their place as interesting additions to the minutia of the scheme of heredity, without being supposed by any one, except here and there a victim of mental strabismus, to represent the full measure of the great mysteries of inheritance.

We have had occasion in successive chapters to present again and again illustrations of the type of hereditary transmission that lends itself to classification under the Mendelian notation. We shall catch further glimpses of it before we are through. Here it seems worth while, in connection with the story of the hybrid walnuts, to attempt a more comprehensive view of the entire field of heredity,

endeavoring to gain a clear notion as to just what are the underlying principles that determine whether or not a certain heritable character or pair of characters shall Mendelize; and in so doing we may correlate our earlier studies, and secure a clearer notion of the underlying principles of evolution, and of the origin and development of species, than could perhaps have been gained without the aid of the illustrative cases that have been presented.

Natural Selection

In the preceding chapter we briefly reviewed the story of the vicissitudes to which plant life has been subjected in the course of recent geological eras. We were concerned there with the elimination of unadaptable species rather than with the evolution of adaptable ones.

But it should of course be understood that the same principle of natural selection applies to the preservation and to the weeding out of species.

In the case under consideration, it was the changed climatic conditions, through which the northern hemisphere was transformed from a region of tropical heat to one of arctic cold, that resulted in the destruction of countless species, leaving only a tithe of the original number to constitute the flora of the temperate zone in our own day.

It is easy to see how the altered conditions of temperature made the struggle for existence unduly hard for many species, because there is a tangibility about the coming of a glacial period that finds an analogy in the coming of winter in the regular sequence of seasons. The fact that a plant which thrives in the summer in northern regions cannot survive through the winter unless protected is so familiar as to give us a concrete example of the destruction of species through changed climatic conditions in the geological eras.

But the struggle for existence that goes on all about us among plants of every species is so much less tangible that it is not so easily visualized.

Not unlikely the climate of the northern hemisphere is changing now year by year as rapidly as it ever changed in any era of the past.

The alteration is so slight within the span of any single life as to be unappreciable. But when we look back, aided by the studies of the geologist, and think of the change of climate that transformed the flora of the Mesozoic time, we see things clustered in perspective, and in our mental vision the picture of the transformation from tropical to arctic conditions corresponds rather to the onset of winter in our annual experience, than to the true picture of a change of climate that required not merely centuries but millenniums.

In the same way we conceive of the evolutionary changes through which new species were evolved in the past as having been relatively sudden. I have already referred to the difficulty with which the average mind can grasp the idea that precisely the same sort of change in animal and vegetable forms is taking place to-day that has taken place in all other stages of evolution.

It was one of the great merits of Darwin's exposition of the "Origin of Species", that he gave detailed illustrations of the struggle for existence, and brought tangibly before the minds of thoughtful people the conception that each race of beings is more or less in competition with every other race, and that the race that is adaptable enough to adjust itself to new conditions is the only one that stands any prospect of survival.

The idea of the progression of the normal increase of living creatures in geometrical ratio and of the resulting over-population of any territory by the progeny even of a single pair, if there were no counteracting factors, was of course received by Darwin from Malthus. But the application of that idea to all races of animals and plants, and the logical deduction from its application which first made possible anything like a clear understanding of the reason why vegetable and animal races have evolved, was due to Darwin.

A Sixteen-Year-Old Royal Walnut

The royal is a Burbank hybrid between the California black walnut and the eastern black walnut. It rivals the Paradox in its rapidity of growth, and quite outdistances either one of its parents.

Alfred Russell Wallace conceived the same idea independently, and must always be credited with a share in the discovery.

But of course it was Darwin's exposition that gave the subject general vogue, and the scheme of heredity that it connotes is with full propriety spoken of as Darwinian evolution.

The essentials of this scheme of heredity may be stated in a few words, as follows: Animals and plants tend to increase in geometrical ratio. If unopposed, the progeny of a single pair of animals or an individual plant would soon populate and over-populate the entire earth. Opposition to such over-population comes from the rivalry of other animals and plants. The struggle for existence thus induced puts a premium on the individual animal or plant that is better able than its fellows to seek means of sustenance. Such an individual will, on the average, live longer and produce more offspring than an individual less well adapted to its surroundings.

The preservation of these favored individuals and their progeny may be described in a phrase as "the survival of the fittest."

The natural processes that determine such survival on one hand, and the destruction of the less fit on the other, may be spoken of as constituting "natural selection."

This term, natural selection, has obvious propriety because it connotes a process closely akin in its results to the artificial selection through which man determines that certain races of animals and plants under domestication shall be preserved, and that others shall be destroyed. But artificial selection is after all only a phase of natural selection, in which man becomes an active influence or a deciding element in environment.

Because of man's power to transform the conditions of soil, to supply artificial heat, and to bring together and hybridize plants and animals that would not come in contact in the state of nature, the results of artificial selection, epitomizing within certain bounds the results of natural selection, may be produced with unexampled celerity.

Man, for example, eliminates a species in a few decades, where nature would have found no way of correspondingly rapid elimination. The black walnut, for example, has been almost exterminated throughout eastern America because man prized its wood for the making of furniture. But for the presence of civilized man the black walnut would doubtless have maintained its position for ages to come, just as it had maintained it throughout the ages of the past.

Yet we must not forget that on occasion there

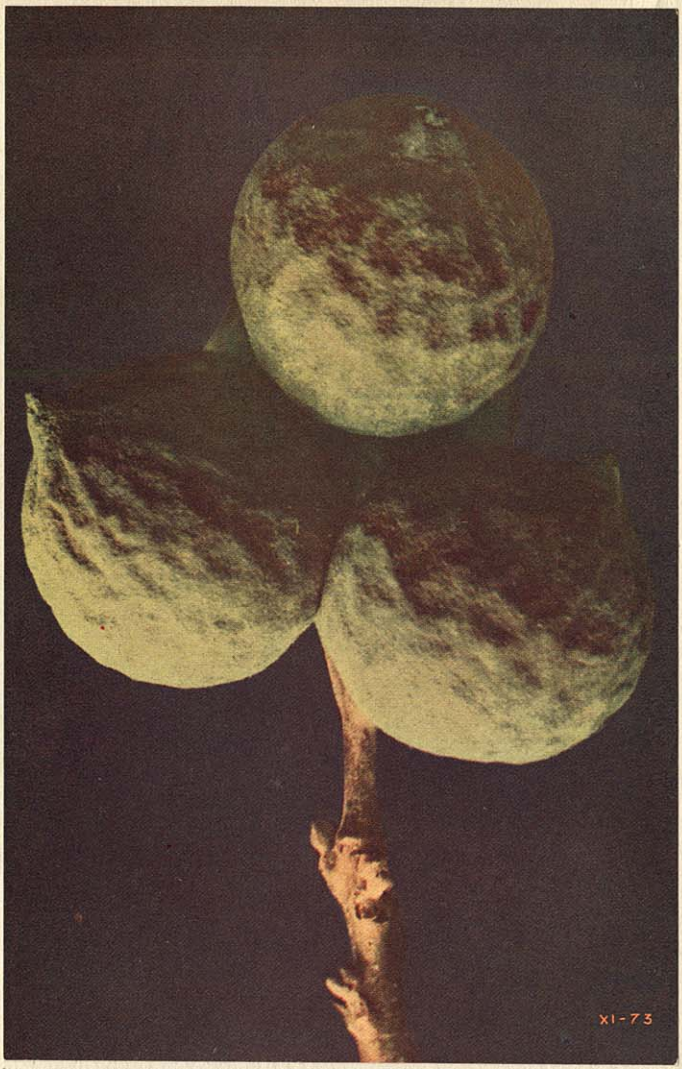
may be natural methods of elimination that will single out a species and destroy it as expeditiously and as certainly as man could accomplish that end.

A case in point is furnished by the chestnut, which, as we have seen in a recent chapter, has been singled out in certain regions of the Eastern United States by a fungoid blight that leaves no chestnut alive in the regions over which it spreads. Yet this blight seems powerless to effect any other species.

Here, then, we have an example of a destructive agency of an unpredicted kind that gives an example of the rapid destruction of a species, through natural selection, because that species could not rapidly enough adapt itself to a new condition.

Given time, the chestnut would doubtless develop immunity to the fungoid pest. But time was not given it, and hence it was destroyed.

This present-day illustration perhaps gives as vivid an impression of one of the more tangible ways of the operation of natural selection as could be desired. But we must suppose that such drastic measures as this are rather exceptional and that in general the processes through which species are eliminated are more subtle in their operation, although their ultimate results are no less striking.



Nuts of the Royal Walnut

The Royal hybrid, unlike the Paradox, bears nuts in extraordinary profusion. Moreover, these nuts are of very large size, far surpassing those of the parent forms, as is illustrated in the succeeding picture.

All this has to do, however, with the destruction, rather than with the evolution of species.

I have already said that the principles of natural selection apply with equal force, and seemingly with entire impartiality, to the destruction and to the preservation of species.

But it is obvious that mere preservation of species does not necessarily imply also the evolution of species. Natural selection might give a dominant position to a particular species, and preserve it for indefinite periods without essential change.

But this could only occur in case the conditions of environment themselves remained essentially unchanged.

It is fundamental to a clear understanding of evolution to realize that in a changing environment, under natural conditions, no species could be preserved unless it proved adaptable.

Indeed, the more perfectly adjusted the species might be to its environment at a given period, the more certainly must that species be destroyed should the essential conditions of the environment change.

The great penalty of specialization is the danger that attends it from this source. It is held that the species that were eliminated when the great climatic change occurred to which we have

more than once referred were those that were the most highly specialized.

But, on the other hand, a species that is able to change in such a way as to adapt itself to new conditions stands at least a chance of being preserved, however widely the environment may be altered. And, in point of fact, most species in a state of nature have a considerable measure of adaptability. Individual variation is the universal rule, and such variations are accentuated by natural selection very much as the plant developer accentuates them by artificial selection. So the plants and animals in a state of nature are plastic material, and under changing conditions of environment which represent probably the usual and normal condition of things, they are constantly, even if slowly, being modified. And of course such modifications, when they have been sufficiently added to, alter the character of the species altogether.

Which is only a detailed and roundabout way of saying that species are evolved and transformed into new species under the influence of natural selection.

But whoever considers this matter attentively will come presently to realize that in any such analysis of the operation of natural selection in the evolution of species as that just suggested,

there is an underlying assumption to the effect that the various modifications of the individual are transmitted to the offspring of the individual.

Unless such is the case, it is clear that there could be no such thing as the evolution of new species. It would avail nothing for the progeny of an individual that this individual was well adapted to its surroundings, unless the said progeny inherit the characteristics that made such adaptation possible.

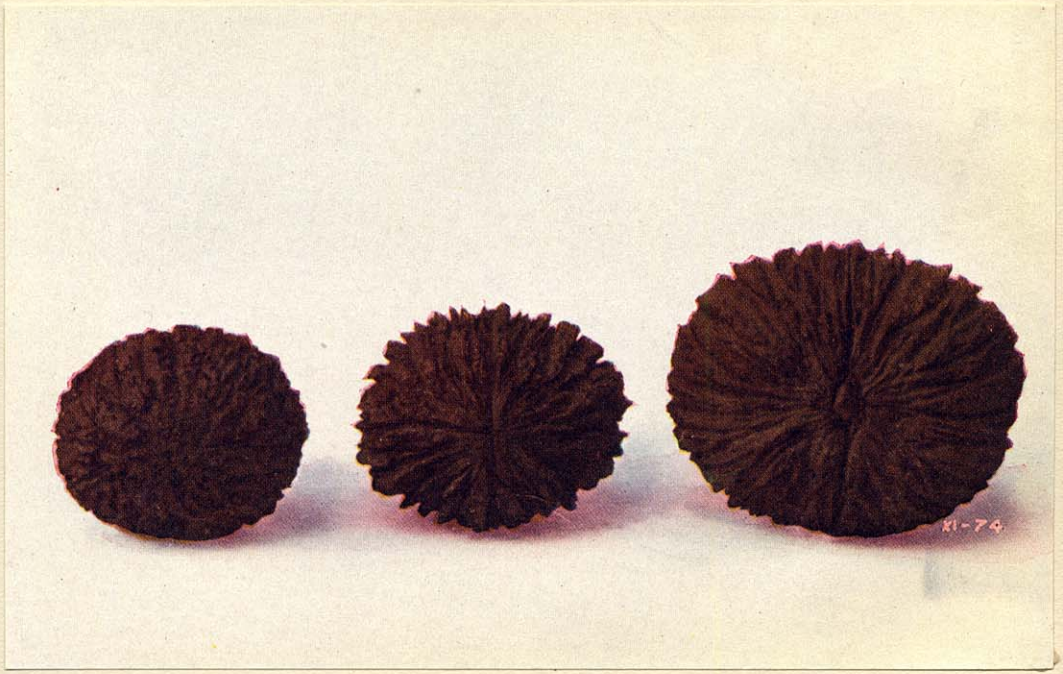
There is no logical escape from that conclusion. Whatever our conception of the mechanism of heredity, or of the exact manner in which the transmission of variation occurs, no one can be an evolutionist who does not believe that acquired characters are transmitted through heredity.

There was a school of biologists who gained great prominence a few years ago, who denied the possibility of the transmission of acquired traits. Throwing logic to the winds, they based their denials on a metaphysical interpretation of certain observed microscopic structures within the germ-cell. These same biologists, while denying that acquired traits could be transmitted, were at the same time ardent upholders of what they called Darwinian evolution.

But such a paradoxical contention must of necessity fail to maintain itself for any consider-

Hybrids and Parents

At the left, a nut of the California black walnut (Juglans Californiaca), the staminate parent; in the center a nut of the eastern black walnut (Juglans nigra), the pistillate parent; at the right a nut of the Royal hybrid, all shown in natural size. It will be seen that the hybrid nut is fairly intermediate between the parent forms in its general appearance, but that it greatly surpasses either of them in size.



able period. In the last analysis, people are able to put two and two together and discover that the result is four. And in the course of time even the most illogical biologists were forced to see the elemental truth of the proposition that new characters acquired by an individual organism must be transmissible, else there could be no such cumulative change as that which results in the transformation of a species in new adaptations to its surroundings.

In other words, if acquired characters are not transmitted, there can be no organic evolution.

But a good many of the former adherents of this paradoxical view have abandoned their illogical position unwillingly, and even now are only willing to admit that such acquired characters are transmissible as are imprinted first on the germ plasm, and not on the body of the parent organism.

The contention really reduces the entire matter to a question of definition. It is virtually a distinction without a difference, when we reflect that, at all events, in the case of the plants, germ plasm and body plasm are everywhere associated, so that we must suppose that if there is really a distinction between the two, it is a distinction within the substance of the individual cell, as the plant body contains both body plasm and germ plasm. Our earlier studies have shown that we are forced to

this conclusion; and obviously if this interpretation of germ plasm be accepted, it is a mere quibble as to whether the change or modification of an individual plant involves primarily the germ plasm or whether it involves the body plasm of the same cell as well.

Of course such mere incidental modifications of an individual as have to do with injury of its parts, the laceration of tissues, or the like, cannot be supposed to have any influence in heredity.

If such accidental modifications are heritable, the entire scheme of inheritance would become chaotic.

The modification that *is* heritable must be one that involves the constitution, so to speak, of the plant; such modification as would be brought about by changed conditions of nutrition, or by an altered temperature. A certain amount of experimental proof is already in hand that such modifications as these may be inherited. And if the opponents of the theory of the transmission of acquired traits can get any comfort out of the claim that such modifications directly effect the germ plasm, we need not wish to rob them of that cold comfort.

Details as to the special manner of inheritance aside, we may accept it, I think, as the only logical conclusion from a wide survey of the facts of her-

edity and evolution, that all modified characters that effect the constitution of the individual are heritable. Even the slightest modification of structure due to altered nutrition, to changed temperature, or the like, probably makes its influence felt on the next generation in exact proportion to its value in the great complex scheme of characters with which it is associated.

But this statement must not be misinterpreted. It must not be supposed that any minor modification of an individual can influence, except in an infinitesimal way, the inheritance of the offspring of that individual.

For the new modification will be, in the nature of the case, only as an alien drop or two in an ocean of hereditary tendencies.

Or, stated in somewhat more modern terms, the hereditary factor that represents the new modification will be as one minor factor among thousands or perhaps millions of pre-existing factors.

If we revert to an earlier illustration, in which we thought of the germinal nucleus as a piece of architecture made up of multitudes of factors of heredity, we may think of the new factor as one added brick in a structure of palatial proportions, made up of thousands of bricks.

Yet it is by the cumulative effect of such minor modifications, we may well believe, that evolution

has been brought about, and that in the long lapse of ages, the highest forms of existing plants have been built up by successive stages of inheritance from the lowliest single-celled organisms.

The Status of Mendelism

In the large view, then, whereas it will be recognized that all acquired traits have their influence in heredity, yet it will also be recognized that the vast sum of qualities that are of less recent origin has preponderant influence, and that the racial characteristics as a whole are overwhelming in their power as against any individual modifications.

Yet, to complete our picture, we must recognize also that nature is not conservative, as she is commonly said to be, but is highly progressive. It could not be otherwise, in a world in which the natural environing conditions are constantly changing.

The basal law of evolution, as we have seen, is that the unchanging, the conservative organism, is doomed. It is only the progressive, the changeable, the plastic organism that can hope to maintain itself and perpetuate its kind indefinitely.

The price of specific life is that the species shall not maintain its identity.

And this interpretation of the situation gives a clew, so it would seem, to that important and inter-

A Typical Specimen of the Royal Walnut

This splendid tree grows beside a fence in Mr. Burbank's experiment garden at Sebastopol. Note the symmetry of form, the wide spread of limbs, the luxuriance of foliage, and the general aspect of vigor.

esting aspect of heredity to which we referred at the beginning of this chapter—the phase commonly spoken of as Mendelism. The essential characteristic of this aspect of heredity, as we have pointed out over and over, is that heritable characteristics are transmitted in a sense independently one of another, in such a way that they may be segregated and put together again in new combinations in successive generations.

The detail within this scheme of transmission, with which Mendel himself was chiefly concerned, and which absorbed the attention of his followers until it was found that there was need of taking a wider view, was involved in the phenomena of dominance and recessiveness. Mendel found, for instance, as we are aware, that when a tall pea vine was crossed with a short one the hybrids of the first generation were all tall, because, as he said, tallness was dominant and shortness recessive. And in the second generation one-fourth of the vines were short because the factors for shortness were segregated, according to the theory of chances, and one-fourth of the vines were pure recessives.

The fact of such dominance and recessiveness between pairs of heritable characters is too obvious to escape attention of any careful practical experimenter, now that attention has been called

to it. But it is equally obvious that there are vast numbers of other heritable characters regarding which no such clear matching as to dominance and recessiveness is observed to take place.

And so the early enthusiasts were led finally to see that Mendelian dominance and recessiveness apply only to a certain small number of hereditary factors in the case of any individual plant or animal.

They came presently, after much heated argument, to admit that dominance and recessiveness constitute after all only a minor aspect of Mendelian heredity.

Yet this aspect of the subject, even if not all-important, has obvious interest. And the question naturally arises as to which ones among the numberless hereditary factors in the case of any given organism will "Mendelize" in this sense, and why these factors will thus Mendelize while others fail to do so.

The answer is found, apparently, in the simple assumption that the factors that show the phenomena of dominance and recessiveness are those that are relatively new acquisitions in the germ plasms of the species under observation. Traits that have been the common heritage of the ancestry for untold generations, constituting the fundamental structures of the organism, do not Mendelize. They

have proved their merit, and are accepted as part of the necessary equipment of the plant, not subject to the testing process that Mendelism essentially constitutes.

Such fundamental structures are, for example, the root and stem and leaves and stamens and pistils of a flowering plant. As to their broad essentials of form and structure, these fundamental organs are inherited *en bloc,* and never jeopardized by being weighed in the Mendelian scale.

But the newly acquired characteristics, such as details of leaf form, or color of petals, or size and quality of fruit—these are matters that are subject to modification because they have not as yet established themselves as fundamentally necessary in any detail of form or color to the species. These fall within the scope of Mendelian testing.

For hundreds of thousands of years, doubtless, the progenitors of plants that now have flowers were provided with roots and stems and leaves, and with essential reproductive organs, but had no blossoms. In comparatively recent times the blossoms were developed. And the modifications of color of the blossoms in the case of any given species are, as we have found reason to suppose, of still more recent origin.

These modern details, then, and their like, are the ones that are subject to variation and that are

still matter for change and adaptation; still in the experimental stage, as it were. And precisely because such is their status, these are the things that are subjected to the Mendelian test when they are brought in juxtaposition, through hybridizing, with forms that differ as to these details.

And as only the relatively new structures Mendelize, so it is the newer member of any pair that assumes prepotency or dominance. Contrariwise, the older member is recessive.

Students of different examples of Mendelian heredity, as applied to animals and plants, have puzzled long to discover the underlying principle that determines which character shall be dominant and which recessive. But this simple principle appears to furnish the explanation.

The new trait or characteristic is dominant over the older one precisely *because* it is new.

By making it dominant, nature gives it the best possible chance. It will reproduce itself in all the immediate progeny of the individual that possesses it. Thus nature shows anew that she is progressing. She accepts the new characteristic and gives it more than an even chance.

But at the same time she is not so foolish as to renounce the old character without full testing. She allows it to be subordinated for a generation, but in the next generation it reappears, isolated, to

The Royal Walnut in Winter

This is the same tree shown in the preceding picture, photographed after it had shed its leaves. Observe the size of the trunk, in comparison with the man's body, and the straightness of trunk, indicating a large quantity of lumber. The wood itself has the good qualities of the black walnut, being hard and durable, and susceptible of taking on a fine polish.

compete with the dominant character. And whether in the end the new dominant character will prove itself and prevail, or whether the recessive character will re-establish itself, depends entirely on the value for the species of one character as against the other.

Mendelian heredity, then, is a testing out process for new characters. It is, as it were, the skirmish-line of the advance guard of evolution. So long as a character is subject to Mendelian transmission, showing the phenomena of dominance and recessiveness, it is a relatively new and unfixed character still on trial.

And in proportion as any character has proved itself and has passed the trial stage, it becomes blended with the hereditary factors that have more stable position, just as conscious acts of the individual become instinctive or reflex when often enough repeated.

In this view, then, the so-called unit characters that Mendelize are, as was said before, merely the fringe to the great fabric of heredity. They serve the plant developer an admirable purpose, and, indeed, it is with their manipulation that he is chiefly concerned. Their relative insignificance is evidenced in the fact that the plant developer cannot possibly produce major modifications in the organisms with which he deals.

He does not attempt to make squash vines into oak trees, or blackberry briers into tomatoes.

He recombines those newer, and hence less important, structures and qualities of which the fact of their Mendelizing is adequate proof of their newness and relative unimportance. If he would get beyond this and create really new forms, adding something to the plant that no ancestor of the plant ever had, he could hope to do this only if a term of life were granted him that would be measured not in mere years but in millenniums. For evolution is a slow process, and the history of the development of natural species is measured in geological eras.

Selection and Mendelism

Perhaps it may be worth while to illustrate this matter a little more in detail, that we may make clear precisely what manner of thing the plant developer is doing when he produces a new race by selection.

We have stated over and over that the process of hybridizing and the process of selection are complimentary. One supplements the other. In hybridizing we make possible new combinations of the hereditary factors, and in selecting through successive generations we isolate certain definite combinations, and thus produce what we call new varieties. Now it is frequently stated by the ex-

perimenters who have paid attention only to a few conspicuous characters that Mendelize, that all possible combinations of characters will occur among the second generation hybrids, provided only enough of these are produced.

Possibly this statement is correct. But it is not susceptible of demonstration because it would not be feasible to produce enough individuals in a single generation to put it to the test. For the number of possible combinations increases in geometrical ratio, as we have seen, with the increased number of characters under consideration. And a really penetrating view of the situation reveals to us hereditary factors in the germ-plasm of each individual plant that would be numbered, could we isolate them, not merely by tens or scores; not merely by hundreds or thousands; but rather by hundreds of thousands or millions.

Such a statement probably will not surprise any one who has read the various preceding chapters in which we have viewed various aspects of heredity. But to those experimenters who have been prone to think of "unit characters" as few in number, such a statement will perhaps seem anomalous. Yet there can be no question that it is fully justified.

In point of fact, what the present day student of heredity usually speaks of as a unit character

might better be referred to as a "unit complex," or by some allied term that would suggest its complicated character. The word "gene-complex" has been suggested in a similar connection.

It would appear that the real purpose of selective breeding through many generations is to remove one after another of the factors that dominate or mask other factors, so that subordinate or recessive factors may make themselves manifest.

No one who has experimented widely will doubt that it is possible by a series of selections extending over several generations to accentuate a given character, say to bring out the crinkled formation of the poppy petal, or the corrugations in the leaf of a wild geranium, or an added row of petals in a balloon-flower. And it goes without saying, that, according to the modern terminology, the character thus isolated must be represented by an hereditary factor which was present in each successive generation utilized in our experiment, but which for some reason was not enabled to make its influence so potentially felt in earlier generations as it was in later ones.

And the only logical explanation appears to be that in each successive generation of the plants carefully selected and inbred, there was a new redistribution of factors, always along Mendelian

Another Fine Specimen of the Royal Walnut

This magnificent tree, one of the first seedlings of the Royal walnut, stands in a dooryard beside the Sebastopol road, near Santa Rosa. It bears mute but eloquent testimony to the success of one of Mr. Burbank's early experiments in hybridizing forest trees.

lines, which isolated, in the case of the individual we selected, the particular character which we had under observation more and more completely.

Whereas, in a simple case of Mendelian heredity, where one pair of factors is in mind, there is complete isolation of the recessive factor in one case in four; in this complex case there is isolation of groups of factors, and in one case among thousands there may occur such relatively complete isolation of the factors for quality we are seeking as will serve our purpose. Such isolation might occur in the second generation, but it cannot be counted on to occur until we have tried again and again, in each successive generation, using material that is a little less complex because a certain number of disturbing factors have been segregated and removed.

We may perhaps illustrate the meaning of all this a little more clearly if we suggest that each so-called unit character with which Mendelian heredity deals is in reality made up of a thousand factors. I do not mean to imply that the number is just that; it is merely that a thousand is a convenient round number for purposes of our computation.

There would be, then, a thousand factors for color combined to make up what we commonly speak of as the unit factor for color; there would

be a thousand subordinate factors for form of flower; a thousand others for texture of petal; a thousand others for odor; yet another thousand for hardiness; and so on for each and every patent characteristic of flower and twig and stem and root of the plant. In the aggregate, let us say, there are a thousand different "unit characters," each made up of a thousand minor factors, so that the total number of hereditary factors stored in the germ-plasm and fighting for recognition, in the case of a single plant, is a round million.

Each of these million factors has been developed in the long slow process of evolution, one after another added, generation by generation, or era by era, beginning with the time when the remote primordial progenitor of the plant was a single-cell organism.

In the course of the ages, development has taken place along divers lines, and it has come to pass that certain combinations of hereditary factors have been grouped into systems that have so long been working in harmony together that they cannot be separated. The members of one such group determine the architecture of the root; the members of another group determine the architecture of the stem; and so on for each of the patent characters.

But there are other groups of factors that are

Foliage and Fruit of the Royal Walnut

The foliage of the eastern and western black walnuts is very similar, and the foliage of the Royal hybrids may be said to bear close resemblance to that of both parents. It is grown in extreme profusion, however, as this picture shows, in keeping with the very great vigor and fecundity of the tree.

less ancient in their origin. There were some that made their way into the germ plasm of the ancestors of the plant so recently as half a million years ago. There are others that are more parvenus of perhaps ten thousand years. And there are yet others that are upstarts of literal yesterday.

Each one of these hereditary factors is striving for recognition and endeavoring to make tangibly manifest the condition or quality or form or constitution of tissue that it specifically represents.

And, according to the view just presented, the thousand factors that make up any given complex stand in such sequential relation to each other that each successive one controls in a measure its predecessor in point of time, and is controlled by its successor. The very newest factor that has been admitted to the coalition has a more powerful influence than any other *single* member of the coalition.

But meantime this most powerful individual is after all only one among a thousand.

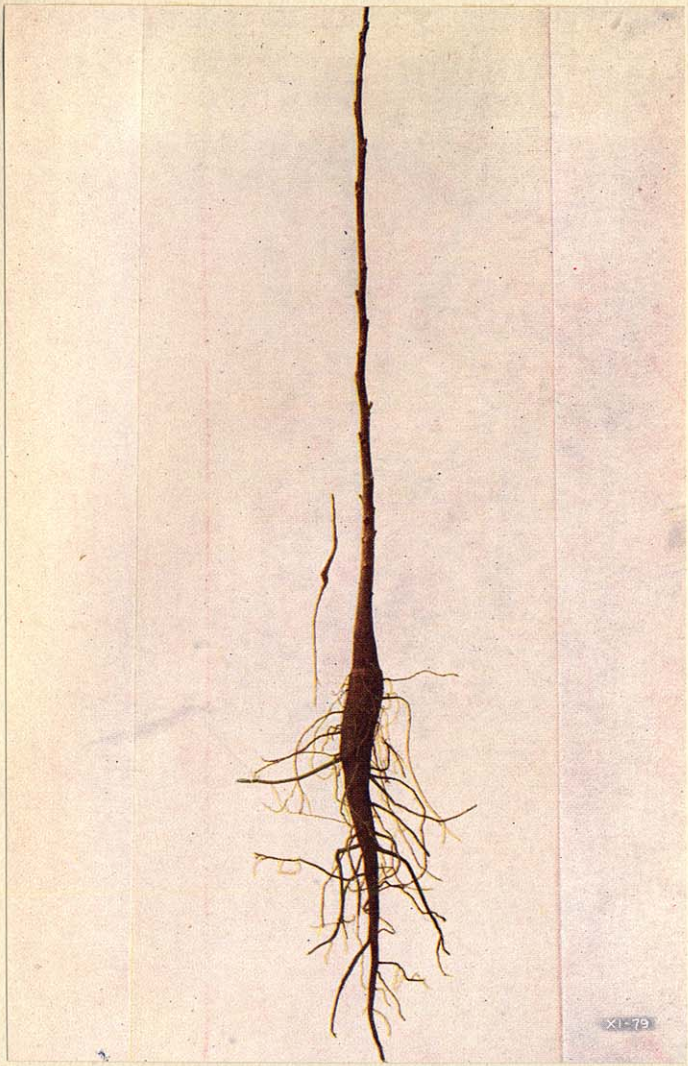
In a company of a thousand men, some one man is stronger than any other. But this strongest individual would be infinitesimally week in comparison with the combined strength of the other 999.

This is the important thing to bear in mind. The newest member in each of the thousand or so

hereditary "complexes" that we speak of as unit characters is the most powerful individual factor. But, inasmuch as the great body of antecedent factors are using their influence in unison in another direction, it is inconceivable that the influence of the single new factor should greatly change the aggregate result.

In this view, what we term a species is a company of organisms in the germ plasm of which the groups of factors for each main characteristic have become purely and unqualifiedly recessive, so that they act as a unit in producing a given character. They thus determine the chief characteristics of heredity in the Darwinian sense, which finds its popular expression in the phrase "like produces like."

Meantime, there are always minor groups of newer characters that are fighting for recognition, and while these are relatively insignificant because of their newness and small number as compared with the whole, yet they are conspicuous and important in the eyes of the plant developer because they represent precisely those modifications of form and constitution and color that mark what we speak of as variations from type; and because they are so matched against one another in heredity—in the manner that we call Mendelian—as to make it possible for the plant developer to segregate and



A Striking Contrast in Seedlings

Here are two seedling hybrid walnuts of the same age, grown from nuts of the same tree, and having had precisely the same care. They are second-generation hybrids, hence the wide variation in size and vigor of growth. One of these plants will grow into a gigantic tree; the other will remain dwarfed always. Obviously there are fine opportunities for selection among the seedlings of the hybrid walnuts.

recombine them variously by hybridizing, and thus to develop new races from the old stock.

When, however, the plant developer, through his hybridizing experiments, brings together groups of characters in which the old guards, so to speak, that have control over the fundamental characters are in conflict, no union is possible.

Either fertilization will not take place, or the offspring will be sterile. Only within narrow limits, and as regards the new and relatively unessential characters, can there be diversity or, at most, the accentuation of old characters.

Such an accentuation, for example, occurs, we may suppose, in the case of the hybrid walnuts, which take on gigantic growth. Both Persian walnut and California walnut have in their germ plasm the hereditary factors of large groups of remote ancestors of the Mesozoic era, when gigantism was the fashion, but these factors have for long generations been subordinated by newer ones born in a less favorable era. Now, however, hybridzation brings the two strains together, and the two dominant groups of factors for slow and relatively dwarfed growth, in some way mask or neutralize each other, enabling the earlier groups to make their influence felt.

And here, as we have seen, the factors for growth that have thus been rudely disturbed as to

their hitherto harmonious coalitions, are reassorted in the second generation, as united groups acting along Mendelian lines, so that part of the progeny of the second generation are giants, and part of them are dwarfs, and that all manner of intermediate forms find recognition in the case of different individuals.

In no other way known to us could such a disturbance of the coalitions of hereditary factors have been brought about. So the plant developer who thus brings together racial strains that have been long separated introduces a disturbing element that in its practical effects may produce such modifications as could only be produced otherwise through the aggregate influences of environment for almost numberless generations.

But let it be repeated that even when the hybridizer effects such a disturbance as this, he can do no more than to enable subordinated hereditary factors to make themselves manifest.

He is dealing with material that has been brought together through age-long experiments, and even though the new combinations that he effects may be striking ones, he may rest assured that even his most spectacular achievement is but a feeble replica of plant developments with which nature has experimented thousands of times over in the course of the long evolutionary ages.