The Effect of one Plant on Another.

BY

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With three Figures in the Text.

FIG. 3 shows a pot with two mustard plants growing in earth, on the surface of which rested a perforated tray with five inches of earth in it; through this all the water given to the plants percolated. The tray has been removed so as to be more clearly visible in the photograph. The presence of such a tray makes practically no difference in the behaviour of the plants in the pot below. Figs. 1 and 2 show a like arrangement,¹ but with a crop of mustard growing in the trays: in one case (Fig. 1) the effect has been to reduce the plants in the pot to one-hundredth of their normal size; in the other (Fig. 2) there has been no effect. The only difference in the two cases is that in Fig. 1 the washings from the surface growth were allowed to reach the plants in the pot (though the penetration of any roots through the perforations of the trays was prevented by a layer of very fine metal gauze at the bottoms of the trays), whilst, in the other (Fig. 2), no washings passed, the holes in the trays having been blocked, and such water as the plants required was given to them direct. The conclusion is obvious: the leachings from the plants growing in the trays must contain something which is toxic to other plant-growth.

Such a very simple experiment must definitely settle the question of toxin production, and should have been made long ago,² but as a matter of fact it comes only as the (at present) final step in a series which originated in 1895 in observations on the effect of grass on fruit-trees. As so often happens, we start with the more complex problems, and only gradually work down to the simpler ones.

It has now been established with a reasonable amount of certainty that the deleterious effect of one growing plant on another is a general phenomenon. By means chiefly of pot experiments such as those indicated above, the following plants have been found susceptible to such influence: apples,

¹ In Fig. 2 there appears to be only one plant: this is due to a fault in the photograph.

² The details of this, and many of the experiments alluded to below, have not yet been published: a description of the other work on the subject will be found in the Third, Thirteenth and Fourteenth Reports of the Woburn Experimental Fruit Farm, 1903, 1911 and 1914.

pears, plums, cherries, six kinds of forest trees, mustard, tobacco, tomatoes, barley, clover and two varieties of grasses; whilst the plants exercising this baleful influence have been apple seedlings, mustard, tobacco, tomatoes, two varieties of clover and sixteen varieties of grasses. In no case have negative results been obtained. The extent of the effect varies very greatly: in pot

FIG. 1.

FIG. 2.

FIG. 3.

experiments the maximum reduction in growth of the plants affected has been 97 per cent., the minimum 6 per cent., whilst in field experiments with trees, the effect may vary from a small quantity up to that sufficient to cause the death of the tree. The average effect in pot experiments may be roughly placed at a reduction of one-half to two-thirds of the normal growth of the plant, but no sufficient evidence has yet been obtained to justify the con-

clusion that any particular kinds of plants are more susceptible than others, or that any particular surface crop is more toxic than another ; that such differences exist is highly probable, but all the variations observed so far may be explained by the greater or lesser vigour of the plants in the particular experiments in question. Similarly as regards the effect of grass on fruit-trees, though the extent of it varies very greatly, and in many soils is certainly small, we must hesitate to attribute this to any specific properties of the soils in question ; for when soils from different localities (including those from places where the grass effect is small) have been examined in pot experiments, they have all given very similar results ; and this applies equally to cases where pure sand, with the addition of artificial nutrients, has been taken as the medium of growth.

In searching for an explanation of the effect of grass on trees, various possibilities suggested themselves, and these were excluded, one by one, till the only possibility left was that of the formation of some deleterious substance by the growing grass. It would be impossible in this short communication to give any account of all the suggestions which were negated, but these included the robbing of the tree of necessary moisture and food by the grass, alterations in the temperature, alkalinity or physical condition of the soil, and alterations in its carbon dioxide and bacterial contents, the exclusion of all which suggestions is embraced in experiments such as those mentioned above, where the grass, or other crop, is grown in a separate vessel, merely resting on the surface of the ground, without any possibility of it extracting anything from the soil in which the plant affected is growing.

From the outset the behaviour of trees in grassed land suggested the action of some toxin : not only is the growth arrested, but a peculiar alteration in the colouring of the bark, leaves and fruit occurs, unlike that attending other forms of ill-treatment : indeed, the high colour developed by fruit under grass is, in some cases, so great, that expert fruit-growers have been unable to correctly name the varieties after being affected, and if this action of grass could be limited, and suitably adjusted to every tree, it would prove beneficial from the point of view of the fruit-grower, if not from that of the tree itself, especially as a limited check to the growth of a tree generally results in heavy cropping. The extent of the grass action which brings about these notable colour changes is very small, for they are apparent in cases of trees weighing about two hundredweight when only three to six ounces of their roots extend into grassed ground. Such an effect is in itself strongly suggestive of toxic action.

To some agricultural chemists the mention of a toxin as being formed in the soil by a growing plant is as a red rag to a bull, chiefly, perhaps, because it conjures up the picture of the plant ejecting some virulent poison ; but, though the excretion of toxin from the roots is possible, there is no

need for imagining such an occurrence: all plants in growing leave much root-detritus in the soil, and such disjecta may account for toxic properties, just as well as ejecta. That some forms of organic matter may be highly poisonous to plant-life has been established: soil which has been heated to 125° is very toxic, and there is evidence that toxicity may be produced in it by heating to much lower temperatures ('Journal of Agricultural Science,' iii. 277). In the case of heated soils, the chemical changes are complicated by changes in bacterial character; this may or may not be the case with soil which is growing crops; but there is one feature in common between the two, namely that in both cases the toxin is easily oxidized, and that after oxidation, it acts as a plant nutrient, increasing the fertility of the soil. When in pot experiments such as those mentioned, the leachings from the crop in the trays are kept exposed to the air for about twenty-four hours before being given to the plant, their toxic property is found to have entirely disappeared, and in some cases, indeed, they act beneficially: even a two-inch layer of pumice-stone interposed between the tray and the earth in the pot will admit of sufficient oxidation for a reduction in the toxic effect to be discernible.

A reversal of the effect of grass may also be recognized in field experiments, for in a case where apple-trees were planted and kept clear from grass to a distance of 3 feet from the stems, the trees flourished better at first than those without any grass near them (and, of course, much better than those which had been entirely grassed). But as they grew, and their roots approached the grassed ground, the toxin affected them before it had time to become oxidized, and they began to suffer. Though there are other reasons why land under grass gradually becomes more fertile, the accumulation of the oxidized products of the toxin must constitute an important factor in this enrichment. In certain experiments with apple-trees it was found that soil which had been under grass for ten years induced double as much growth as similar soil which had been under tillage, though, when the turf was replaced on the soil, the trees showed all the bad effects of grass.

From the general character of the action of one crop on another, it follows that the tables may be turned on the grass, and, even in pot experiments, it has been proved that grass in the pots will be adversely affected by apple seedlings in the trays. In practice, of course, it is known that grass and other surface crops are adversely affected by trees. This is generally attributed to the shading effect, and to the robbing of the soil of its nourishment. Doubtless the shading produces bad results in many cases, but it may be questioned whether any serious robbing of the soil occurs, for there is good evidence for believing that ground under trees, even when worked regularly for timber, increases in fertility, just as does ground under grass. At any rate, it has been found that a surface crop

may suffer from trees above it, even in cases where there certainly has been an increase in fertility, and where, also, the shading effect is inoperative, so that the damage to the crop can only be attributed to the toxic action of the trees. Thus, a quarter of an acre of land over which some fifteen apple-trees, twenty years of age, were distributed, was planted uniformly with Brussels sprouts: those under the trees suffered to the extent of 48 per cent. in their growth; but there were patches in the ground where trees had been growing until the preceding winter, when they had been cut down, leaving the roots undisturbed in the soil, and in these patches the sprouts did better than elsewhere to the extent of 12 per cent. In other parts of the ground canvas screens had been erected, at a height of 6 feet above the surface, to simulate, and even exaggerate, the shading of the trees, and under these the sprouts gave exactly the same values as on the unshaded ground. Thus, the trees themselves materially injured the crop, though the soil under the trees was more fertile than elsewhere, and though the shading was inoperative.

Though differences in the toxicity and in the susceptibility of different plants may be overshadowed by differences due to other causes, it is highly probable, as has already been mentioned, that such differences do exist. The only case of differences of a positive character noticed at present in our experiments, is that the effect of a plant on plants of its own kind is generally greater than that on plants of another kind. This may be fallacious; but, certainly, a plant affects its own kind just as much as any other kind; and hence we must conclude that the toxin formed by any individual plant will affect that individual itself. This has been proved by growing plants in pots divided into compartments, so that there was no root interference, and comparing these with other plants grown in similar pots not so divided: in the former case each plant will be affected only by the toxin produced by itself, in the latter it is affected partially by its own toxin, and partially by that of its neighbour, but the amount per plant must be the same in both cases, and, as a matter of fact, the plants all gave the same results, except for a slight advantage in favour of those in undivided pots, due to conditions which can be easily specified.

When a stronger and weaker plant, or an older and younger one, are growing side by side, we find that the latter rarely picks up, and generally gets more and more behind its stronger brother. This cannot be due to the stronger one monopolizing the food-supply; for if it exhausted this supply, both plants would suffer at the same time, and, till that supply is exhausted, both would flourish equally. The inadequacy of any such explanation is demonstrated by taking a pot of soil capable of growing, say, six plants, sowing the seed for three of them first, and that for the other three a certain number of days later. In the case of mustard, when the difference of date is only four days, it is found that, at the end of

growth, some two or three months later, the last sown plants are 60 to 70 per cent. smaller than the others. It is evident that three four-day-old seedlings could not have exhausted the nourishment in $7\frac{1}{2}$ kilos of rich soil so far as to leave insufficient food for three other seedlings; nor can a difference in age of four days in a total life of several months account for such a difference in the weights of the plants. But the results become clear if we take into account the toxic effect of one plant on the other, for the later planted individuals have to start growth under toxic conditions which were absent in the case of those first planted, and throughout their existence their inferiority in size will make them suffer more than their stronger brethren, though the actual amount of toxin in the soil is the same for all. Yet it is found that they are not altogether without their revenge, for the toxin formed by them affects to a certain extent the older plants, and this effect may be traced, even when the feebler plants are only about one-tenth the size of stronger ones. The importance in practice of having seed which will germinate uniformly at the same time, or in having plants of uniform growth in a bed, is demonstrated by these experiments; for a difference of only four days in the germination of one-half of the seeds in the case of mustard reduces the total weight of the whole crop eventually obtained by as much as 20 per cent.

The divided pots have been utilized to ascertain what the effect of crowding in a plantation is when there is no root-interference. In appearance the results were remarkable, for with mustard and tobacco plants at distances of 4, 6 and 9 inches apart, the plants were considerably smaller as the distances between them were greater, the deficiency in their height extending up to 30 and even 50 per cent., and they appeared to be in every way inferior. But these appearances were entirely misleading, for it was found that the weights of the plants were the same at whatever distance they were planted, and at whatever age they were lifted; moreover, this equality held good throughout the plantation, even including the outermost rows: thus interference of the above-ground portions of plants does not affect the amount of growth, but only the quality of that growth.

The results are very different, however, when there is root-interference, as when a number of plants are grown together in one pot, or in one plot in the field; and when the crowding attains to a certain magnitude, the limiting factor is the amount of soil available for each plant: the result of which is that the weights of the plants are inversely proportional to the bulk of soil available (which with soil of uniform depth is synonymous with the area), or, in other words, the total plant-growth is the same, whatever be the number of plants. Thus, in pots containing $7\frac{1}{2}$ kilos of rich soil the total crop was the same with from sixty-four down to sixteen mustard plants (the latter number representing plants at a distance of

1·8 inch apart), or with from sixteen down almost to one plant of tobacco ; whilst in unmanured ground in the field, the equality holds good within a wider range, even to plantations with more than 6 inches between the plants in the case of mustard. At the same time, also, the outside rows of plants are very much superior to the inner plants.

This latter superiority is one which is continually noticed in field experiments, though the reverse, judging by mere appearances, sometimes obtains. Whether, when the outside plants appear the worse, they are so in reality, may be doubted ; at any rate, in all the cases which have been investigated by weighing, it is a superiority which has existed. But appearances would never have led to a correct estimate of the magnitude of this superiority, for these outside plants are often 100 to 200 per cent. greater in weight than the inside ones. The row next to the outside one generally shows some superiority, but the effect of an external position extends to only about 6 inches from the edge of the plot.

The extra vigour of the outside plants is generally attributed to the extra manure which they have to draw upon ; but another factor must now be reckoned with, in the extra facility offered for the oxidation of the toxin at the edge of the plot ; and this appears to be an important factor. The question is being investigated on three lines : manure beyond a certain limit does not benefit, and even injures a plant ; if, therefore, in a plot where the manure has already attained such a limit, we still find that the outside plants show a superiority, this cannot be due to any further surplus of manure. Such a superiority, we find, still exists in ground manured with 100 tons of dung to the acre, and the superiority is little less, if less at all, than in unmanured ground. But these experiments require repetition and extension before definite conclusions can be drawn from them.

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