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On the Causes of Failure of Natural Regeneration in British Oakwoods

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ON THE CAUSES OF FAILURE OF NATURAL REGENERATION IN BRITISH OAKWOODS.

BY A. S. WATT.

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INTRODUCTION. VIEWS OF PREVIOUS AUTHORS.

DESPITE the prolific production of ripe acorns in certain years, when the floor of our oakwoods is littered with fruits during the autumn, and when, during the following spring, millions of seedlings may be seen coming up through the surface layer of humus or among the herbaceous plants of the ground vegetation, yet the occurrence of natural regeneration of oakwoods in this country seems to be something of a rarity. If regeneration took the normal course, one would expect to find during the years subsequent to a "fall" a community of young oaks, some of which, sturdier than their fellows, would dominate and handicap the others in the struggle for existence, finally causing their suppression and death. The dominants, we should expect, would ultimately grow up to replace the aged stock. The following is an attempt to solve the problem and is a record of the causes responsible, so far as these have come under my observation or been ascertainable by experiment.

This enquiry is so intimately associated with the larger subject of the degeneration or retrogression of forests, that a brief review of the more important causes assigned may assist us towards a solution.

The reduction in the number of seed parents of both species of oak (*Quercus pedunculata* and *Q. sessiliflora*) due to the great demands upon oak for the Navy and to the encroachments made upon the forests by the peasantry for agricultural and pastoral purposes in former days not only reduced the area under forest, but deprived the woods themselves of the finest trees. Evidences of such are frequent in writings on Natural History or in works of general historical bearing or can be deduced from the Statutes passed from time to

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time ordering the reservation of young oak¹. To repair this loss no adequate planting took place and the oak being a heavy seeded tree was slow in recolonising the land thus laid bare.

Krause² (1892) attributes the limiting of the forest area in North Germany to "errors in sylviculture, especially to the grazing of cattle in the forest," and this may be legitimately applied to this country as cattle and pigs were formerly driven into the woods for pannage. This is generally conceded as a factor responsible.

Degeneration of woods due to the lack of suitable conditions for the germination of the seeds of the dominant species has been laid stress upon by Moss³. Similarly Henry⁴, quoting Schwappach in regard to continental soils, says, "Natural regeneration of the stock is rendered quite impossible on poor soils and more difficult on soils of better quality by the unfavourable modification of the surface covering (hardness, dryness) and by the stunting of the parents." Tansley⁵ also describes this in the case of the Damp Oakwood association of this country. "When the soil is left exposed to the sun and wind by excessive felling of standards or clearing of coppice, the humus layer is destroyed and the soil either becomes very weedy or cakes hard and becomes almost bare of vegetation. Under such conditions the natural regeneration of the wood from self-sown seed is checked or arrested and unless the wood is properly taken in hand it degenerates to scrub and grassland." Schlich⁶ and Forbes⁷ express similar views.

Degeneration has also been attributed to the impoverishment of the soil. A summary of Graebner's account of the degeneration of woodland in North Germany due to this cause is given in *The Woodlands of England*⁸, where we find that by the removal of tree trunks, by the leaching of the soil and by the spread of heath vegetation consequent on the formation of a moor pan, the ground is impoverished and the oaks die out without leaving successors.

Dealing more particularly with causes affecting the natural regeneration of oak, Forbes⁹ states that where acorns "were sown in small patches scarcely any (seedlings) made their appearance, though we could never discover what really became of them." Elwes and Henry¹⁰ and others testify to pigeons and pheasants devouring enormous quantities of acorns.

Regarding the influence of rabbits Percival Lewis¹¹ remarks of the New Forest about 100 years ago, "The rabbit in his pursuit of food did much injury and the cutting of browse wood as it was carried on in former times must have

¹ Cf. Nisbet, *Our Forests and Woodlands*, 1909, Chap. I. where quotations are given from Gilbert White's *Natural History of Selborne*, 1789, Holinshed's *Description of England*, 1577, *Statute of Henry VIII*, 1543, etc.

² Quoted by Moss, *Vegetation of the Peak District*, 1913.

³ Moss, *op. cit.*

⁴ Henry, *Les sols forestiers*, 1908.

⁵ Tansley, *Types of British Vegetation*, 1911.

⁶ Schlich, *Manual of Forestry*, Vol. II. 1907.

⁷ Forbes, *Eng. Arb. Soc. Trans.*, Vol. V. 1902.

⁸ Moss, Rankin and Tansley, *The Woodlands of England*, 1910.

⁹ Forbes, *op. cit.*

¹⁰ *Trees of Great Britain and Ireland*, Vol. II. 1907.

¹¹ Nisbet, *op. cit.* p. 102.

been attended with considerable depredations; the holly and the thorn are often the preservers of the seedling oak." Elwes and Henry also state that mice are the worst enemies of seedling oaks.

Upon the type of seed bed available for acorns Nisbet¹ remarks, "Owing to the want of close cover the soil often gets overgrown with grass or worse still with moss, and then a satisfactory crop of self-sown seedlings cannot be expected." Compare this with the observations of Forbes². "A grassy surface seems the natural seed bed of oak, for very successful examples may often be seen on rough pasture adjoining woods which for some reason or other has been allowed to lie waste or is only slightly stocked with cattle during the summer."

With regard to the supply of light necessary for oaks opinions vary slightly. Nisbet (*op. cit.*) says, "As soon as the seedling crop appears the seedbearers have soon to be removed because the young oak is impatient of even the comparatively light and broken shade cast on it by the parent trees." Warming³, however, remarks that "the common oak is a tree making moderate demands in regard to light."

The above are a few of the various causes assigned in the explanation of the failure of regeneration, and effects observed in particular instances may lead many foresters to attribute all failure to one or two particular causes. So far as I am aware no systematic attempt has been made to ascertain exactly how far each is operative and generally to find out as much as possible about the causes of the observed lack of regeneration.

The enquiry naturally falls into three sections, the first dealing with the fate of the acorn up to the time of germination, the second with the causes inducing the loss of germinative capacity, and the third with the establishment of the seedling and its subsequent history.

PART I.

ENEMIES OF THE ACORN UP TO THE TIME OF GERMINATION.

During the latter part of October, 1914, the floors of the various oakwoods in the vicinity of Cambridge were littered with millions of brown, well-ripened fruits. Visits during the next few weeks revealed a striking change in the number visible and one may account for this either by assuming that the acorns are removed or that they were now in some way concealed from view. Both these causes are in fact operative.

Dealing first with the latter it may be noted that the oak continues to shed its leaves long after the fall of the fruit—and this assists in the concealment of the acorns. Further if the wind has access to the floor of the wood, leaves may collect in certain sheltered spots, and in these the acorns are effectively concealed. Certain types of ground vegetation also are insufficiently closed to

¹ Nisbet, *op. cit.* p. 102. ² Forbes, *op. cit.* ³ Warming, *Oecology of Plants*, 1909.

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prevent the heavy acorn, in its fall, from at once reaching the soil surface, and in the case of a floor covered with humus the impact of the acorn is such as to form a sort of *nidus* which produces at least a partial embedding.

Nevertheless a careful note of the number of acorns on selected areas at successive dates established the fact that many were disappearing, and so complete was the removal in certain cases that by the spring of the following year great difficulty was experienced in finding even a few where thousands had fallen in the autumn. At the same time it was observed that where acorns had fallen among humus and become concealed through the subsequent fall of foliage, the rate at which they disappeared was decreased compared with the quick removal of those which had fallen on bare or comparatively bare areas.

Table I (plots 1-3) shows the rapid disappearance of acorns, when these lie exposed on the soil surface. Plots 4-7 (inclusive) indicate that a certain amount of protection is afforded by a humus covering as evidenced by the acorns' slightly longer survival. The value of protection against all but small animals is shown in plots 8-10 where the removal of all the acorns was somewhat delayed as compared with those completely exposed.

Table I.

No. of Plot	Type of soil covering	Oct. 22nd	Oct. 30th	Nov. 9th	Nov. 14th	Nov. 21st	Dec. 1st	Dec. 5th	Dec. 10th	Dec. 16th	Jan. 16th
1	On Humus ...		50	1	0						
2	On Moss ...		20	13	6	3	0				
3	Sparse covering of dry leaves ...				45	21	0				
4	Under 1 in. of humus ...	30	16	4	2	0					
5	"		25	0							
6	Under 2 ins. of humus		50	26	4	0					
7	"			25	25	24	13	0			
8	On Moss ...		30	13	6	3	0				
9	In Grass ...		25	17	16	11	1	1	1	0	
10	"			16	9	8	6		4		0

In the course of these observations evidences were not wanting of some of the agents responsible for the heavy mortality. Sometimes, where there had been once an abundance of acorns there remained later only pieces of broken pericarps. In others there was found among the humus a large number of acorns in all stages of mutilation, while the coincidence of the disappearance of a number of acorns planted below a humus covering 2 ins. in depth and the appearance of mice burrows in the area was suggestive. But a very large number of acorns must have been removed *in toto* as no traces of them had been left.

Foresters are generally agreed that rabbits eat large quantities of acorns, so plots temporarily protected against them were established. Nevertheless in due course all the acorns disappeared.

The foregoing observations suggested the following experiments which were carried out on light sandy soil in an open oakwood at Didlington near Brandon (Norfolk).

1. An area of about 144 sq. yds. was enclosed with wire netting of $1\frac{1}{4}$ in. mesh so as to exclude rabbits and mammals of similar size. The ground was prepared, about two bushels of acorns sown, and the whole then raked over so as to conceal the seed.

2. An area of about 16 sq. yds. was similarly surrounded and also covered over with netting to prevent attacks from birds, 50 acorns being sown on the surface and 50 planted below.

3. An area of 1 sq. yd. was enclosed by a wooden frame, the lower part of which was sunk 9 ins. into the ground. Over the top a double layer of netting of $\frac{1}{2}$ in. mesh was fixed. 50 acorns were sown on the surface and 50 below.

4. At the same time 30 acorns were planted below the surface unprotected in any way.

The results are set forth in Table II.

Table II.

No. of Plot	Number of acorns sown on 11th Dec.	18th Mar.	29th Mar.	30th June	8th Sept.
1	2 bushels				8 seedlings
2	50 on surface	0			
	50 below surface				35 seedlings
3	50 on surface	50	50	50	
	50 below surface	50	50	50	
4	30 below surface	30	1		

Near the above experiments the gamekeeper was in the habit of feeding the pheasants. From the testimony of both the gamekeeper and the forester of the estate, plot 1, with its newly turned loose sandy soil, was a great attraction for the birds, with the result as shown. Out of 2 bushels of acorns, only 8 seedlings appeared.

With regard to plot 2 all those acorns placed on the surface disappeared the following day, but of those below 35 germinated. Of the 30 planted under the surface without any protection only 1 remained. Nor does the pilfering cease after the seedling is established, as in an area protected from rabbits and birds 23 out of 24 had their acorns stolen.

The value of complete protection from animals is obvious from the results of plot 3 where all the acorns remained intact.

That burying in the soil by itself lessens the mortality is not apparent from the experiments. Where the soil is loose and easily turned over to be searched, the chances seem less favourable to survival than where they are embedded in hard soil. The success of regeneration after the pigs were driven into the forest for pannage in former days, may have been in part due to the concealment afforded by burial of the acorns. Also in woods where the work-

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men in felling operations have trodden the acorns well into the soil regeneration at least in its initial stages has more chance of success. Mice cannot penetrate and search the surface 2 ins. of hard soil so completely as they would a layer of humus of equal thickness. In fact, the presence of the woodmen may have acted in two ways, by scaring the mice from the area of operations and by making the ground unsuitable for their occupancy for some time to come, thus diminishing the enemies of the acorns in the particular locality.

The foregoing experiments clearly demonstrate the value of protection against the attacks of animals. Exactly the share taken by the various agencies in the disappearance of the acorns in any given locality seems to depend a good deal on local circumstances, e.g. birds such as pheasants may be an important factor in one place and quite negligible in another. Further it is well known that rabbits tend to abound on light sandy soils so that they are ordinarily much more prevalent on soils such as bear the Dry Oakwood and Oak-birch-heath associations than on the clay of the Damp Oakwood. But mice seem more evenly distributed and are certainly a powerful factor militating against successful regeneration by their consumption of large quantities of the seed.

The following is a list of animals known to eat acorns¹:

Cattle, Red Deer, Fallow Deer, Roe Deer, Wild Pigs, Rabbits, Squirrels, Dormice, Forest Mice, Voles, Pheasants, Wood Pigeons, Jays, Rooks. The principal offenders are: Rabbits, Mice, Voles, Pheasants, Wood Pigeons, Jays.

PART II.

CONDITIONS AFFECTING THE POWER OF GERMINATION.

During the latter part of the year some acorns seem to escape the attention of those agents previously mentioned—acorns which look unhealthy, having lost their brown colour. Upon examination they are found to be the hosts of a weevil larva, which feeds on the kernel and ultimately destroys the acorn. Fabre² from observations on woods in France says, "More than the jay, more than the field-mouse, the elephant-beetle (*Balaninus elephas*) has contributed to reduce the superfluity of acorns." The beetle found in this country, viz. *Balaninus glandivum*, is not so prevalent and the damage done is not extensive.

During the summer of 1915 in the course of visits to various oakwoods in the South of England, I found certain acorns which evidently had escaped the marauders, but which had not germinated. For the most part they lay

¹ Schlich, Nisbet, Elwes and Henry, *opp. cit.*

² *Social Life in the Insect World*, 1912.

among a litter of pieces of pericarps upon a soil surface, in places devoid of vegetation. The soil itself was light and sandy such as is characteristic of the Dry Oakwood or the Oak-birch-heath associations and characteristically flat and even, compared with that of the Damp Oakwood, where beneath the humus the soil is extremely uneven on a small scale, owing to the animals present in the soil piling it up in one place and leaving furrows or depressions in others. The surface was devoid of humus, except where the latter had collected in rabbit burrows, under the shelter of protecting brambles, in the lee of a fallen log, or in the sheltered parts of the wood. In areas such as these acorns were found lying, 10 months after their fall, still ungerminated. Nor do they after this lapse of time present the almost stony hardness or chocolate brown colour of the kernel such as is exhibited in most acorns exposed for a similar length of time in a room, the pericarp is whiter and the kernel seems quite fresh and capable of germination though somewhat shrunk, tougher and less brittle in texture than in a freshly ripened acorn. Such areas, devoid of humus and with sometimes a sparse vegetation of bracken or low growing mosses, were devoid of seedlings, in strong contrast to those places, perhaps a few feet distant, where the fallen leaves had collected. Considerations dealt with in Part I will partly explain the reason for this, but these do not explain why certain acorns overlooked by the despoilers did not germinate.

That such acorns did not represent the ungerminable portion of the crop, the following experiment will show. 25 acorns were placed on a surface devoid of vegetation and 25 below and the plot enclosed. Of the latter all germinated, but of the former none. The following experiments were undertaken to find out what essential factor was lacking from the germination requirements in the case of the acorns lying on the surface.

In these experiments carried out in a glasshouse where the temperature was that of an ordinary heated room, acorns obtained from Brandon were utilised. They were sent to me towards the end of October and, until I should require them for experiment, I kept them in a well-stoppered glass bottle. Of the exact interval which elapsed between the fall of the acorn until my receipt of them I have no precise information, but during that time there must have been a slight loss of moisture.

The experiments were divided into three sections, treating of:

- A. The relation of the micropyle to water absorption.
- B. The relation of the position of the micropyle to the soil surface and germination.
- C. The relation of water supply to germination.

A. *Relation of micropyle to water absorption and loss.* The method employed to find out if there was any relation between the micropyle and water absorption or water retention was simply to seal up the micropyles of a number of acorns and to compare the loss or gain under different conditions with those unsealed.

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6 acorns, 3 sealed and 3 unsealed, were exposed to the atmosphere of the glasshouse for 34 days. The following were the results:

3 acorns unsealed and exposed had an average loss of 19.6 per cent. of the original weight.

3 acorns sealed and exposed had an average loss of 21.6 per cent. of the original weight.

At the same time 6 acorns, 3 unsealed and 3 sealed, were planted.

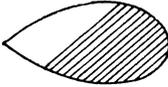
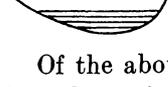
3 acorns unsealed and planted for 34 days gained 5.4 per cent. of the original weight.

3 acorns sealed and planted for 34 days gained 5.1 per cent. of the original weight.

From these results we find that by sealing the micropyle the retention of water is in no way assisted, whilst similar action does not impede the imbibition of water.

B. *Relation of position of micropyle to soil surface and germination.* Experiments were carried out with acorns which were partially buried in the soil to different depths, and whose long axes were placed at various angles to the horizontal. Table III shows the positions of the acorns, the shaded portion representing the amount buried, while the dividing line between the shaded and unshaded parts being horizontal *in situ*, shows the position of the acorn in the experiment.

Table III.

Position of acorn	Order of depth	Weight in grams		% Loss	Fate
		3.11.15	17.3.16		
	1 (deepest)	6.32	6.28	.60	Germ. ¼ in. then dried up
	2	6.97	6.94	.44	Germ. to seedling
	3	5.98	5.77	3.6	„ „ „
	4	7.28	6.67	8.2	No germination
	5	8.67	8.20	5.3	„ „
	6	6.77	5.82	14.0	„ „

Of the above 6, 3 germinated but only 2 developed to normal seedlings, the 3rd germinated ¼ inch then ceased to grow. It will also be seen that there

is a definite relation between germination and the percentage loss of water—the average per cent. loss of the 3 which germinated being 1.55, whilst the average loss of those which did not do so was 9.2 per cent. Further only those two whose micropyles were embedded in the soil developed to seedlings.

12 acorns were next inserted in the soil with varying amounts of each projecting, the first 6 having the micropyles pointing vertically downwards, the second 6 having these pointing vertically upwards. The results are given in Table IV.

Table IV.

	Height of part exposed	Weight in grams 2.11.15	Final weight in grams	Date of final weighing	% Loss or Gain	Fate
Micropyle vertically downwards	12 mm.	6.15	6.01	9. 3.16	- 2.3	All germinated to normal seedlings
	„ „	6.38	6.28	9. 3.16	- 1.5	„ „ „
	11 „	5.52	5.65	21.12.15	+ 2.2	„ „ „
	6 „	7.70	7.78	21.12.15	+ 1.0	„ „ „
	5 „	6.96	7.07	25. 1.16	+ 1.56	„ „ „
	3-4 „	6.38	6.58	21.12.15	+ 3.0	„ „ „
Micropyle vertically upwards	19-20 mm.	8.67	8.22	9. 3.16	- 5.2	No germination
	17-18 „	8.94	8.60	3. 2.16	- 3.8	Germ. $\frac{1}{4}$ in. then ceased
	15 „	6.75	6.45	3. 2.16	- 4.4	„ „
	10 „	6.17	6.29	25. 1.16	+ 1.9	Decayed
	8 „	6.26	6.36	18. 2.16	+ 1.6	Germ. $\frac{1}{4}$ in.
	Deepest	6.16	6.49	1.12.15	+ 5.3	Decayed

Especially in the case of those acorns whose loss was small, the decrease was not continuous. Sometimes in the course of the weighings, the weight on a given date was greater than on the one preceding, owing no doubt to variations in the moisture of the air; and especially in the case of the last 6 there was difficulty in obtaining reliable data, as the basal ends soon began to decay. The general result, however, is clear that in the case of the first 6, planting with the micropyles downwards ensures success, while in the case of the second 6 even if a commencement of germination was made, this soon ceased. No doubt there was too much evaporation from the young radicle in the warm atmosphere of the room, and the supply of water not being rapid enough, it wilted and died. There would not, of course, be the same rapid evaporation in the open, where the temperature would be lower and the relative humidity higher.

C. Germination and the Moisture Supply. First an experiment was carried out to determine how much water an acorn can lose before its capacity to germinate disappears. According to Guppy¹ an acorn reaches a stable weight after it parts with 60 per cent. of its weight. After such a loss has taken place, however, many kernels assume a brown colour and a stony hardness and when supplied with all the requirements of germination fail to respond. Table V gives the amount of water lost up to date of planting and the acorns' subsequent fate.

¹ *Studies in Seeds and Fruits*, 1912.

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Table V.

Weight on 2.11.15	Weight when planted	Date of planting	% Loss	Average %	Fate
5.59	5.24	23.11.15	6.3	7.3	Germ. and developed
7.82	7.27	"	7.0		"
7.73	7.06	"	8.6		"
5.66	5.16	15.12.15	8.8	11.8	Decayed
7.88	6.64	"	15.7		Germ. and developed
6.98	6.22	"	10.9		"
9.11	8.39	23.12.15	7.7	11.4	"
9.08	7.60	"	16.2		Decayed
7.16	6.42	"	10.4		Germ. and developed
6.83	5.41	1. 2.16	20.8	27	"
6.85	5.34	"	22.0		Decayed
7.83	5.49	"	29.8		"
9.94	6.73	"	32.3		"
6.61	4.59	"	30.6		"
7.27	5.78	"	20.4		"

Attention is here drawn to the individual differences among acorns in the amount of water they give up in a given time. We find that the average loss in weight of those acorns which failed to germinate even when a suitable environment was provided was 27 per cent. Taking the individual acorns it appears that 20 to 21 per cent. represents the critical loss of water, but this figure may be too low owing to the likelihood of a certain loss of water before my receipt of the acorns.

Again, 5 acorns were placed in a bottle containing some calcium chloride. After losing 26.8 per cent. of their weight they were planted and subsequently weighed one month afterwards. While these were in the soil they gained 30 per cent. in weight yet no germination ensued, the previous loss of water evidently destroying the viability of the seed.

Another experiment was started to find out whether acorns would germinate in an atmosphere of higher relative humidity, but with only a small part of their surface in contact with the soil. To this end depressions were made in the soil by packing the earth round a specimen tube 1 in. in diameter. Five such were made of varying depth and the acorns placed at the bottom, one to each depression. The following table gives the results.

Table VI.

Depth of depression in mm.	Weight on 1.11.15	Weight on 16.3.16	% Loss	Fate
35	6.23	5.98	4.1	No germination
25-30	6.01	5.75	4.2	"
20	6.84	5.38	21.3	"
18	6.99	6.57	6.0	"
15	7.89	6.85	13.2	"

So that in spite of the diminished loss of moisture no germination ensued.

A comparison of the loss of water in the preceding experiment with the loss from acorns lying on the surface of the soil, and acorns lying on paper entirely exposed to the atmosphere of the glasshouse is instructive.

Average loss of water from acorns in depressions during 19 weeks = 9·7 per cent.

Average loss of water from acorns on soil surface during 19 weeks = 22·5 per cent.

Average loss of water from acorns on paper during 19 weeks = 36·5 per cent. This at least shows the value of even contact with the soil in lowering the net loss, while an atmosphere of greater relative humidity assists still more in that direction. In no case, however, did germination occur.

We have seen that after the acorn has lost a certain percentage of its water even if it be thereafter placed under suitable conditions for germination there is no response beyond the merely mechanical imbibition of water. Further that even if the amount of water lost is much reduced by simply placing the acorns on a soil surface or still more so by placing them in depressions in the soil there was no attempt at germination on their part.

In these experiments we are dealing with acorns which have in part at least entered the resting stage so that there can be no question of vivipary as is noted by Guppy¹. While therefore the acorns in the above experiments which lost on the average less than 27 per cent. of water germinated normally when planted, those which lost a very much smaller amount, but placed under different circumstances as regards water supply, did not do so, and there seems ground for believing that conditions suitable to the germination were not provided in the latter case. Again the above-mentioned author gives the case where acorns germinated whilst actually drying but adds, "that in most cases the loss of water is too rapid and the tendency to proceed at once to germinate is suppressed." In the above experiments the temperature was the same in all, the supply of oxygen was sufficient, so that *ceteris paribus*, one is led to the conclusion that the inhibiting factor has some relation to the supply of water.

Under the soil surface the seeds are in direct contact with a film of water, and under these circumstances they absorb water mechanically. Now in the case of an acorn lying on the soil surface, either in a depression or on level ground, there is only a small part of its surface actually in contact with a film of water, the remainder being surrounded by an atmosphere with a relative humidity varying according to circumstances. The problem resolves itself, therefore, into an investigation as to whether acorns can utilise this atmospheric moisture for germination. In the experiment with the acorns in depressions one of the acorns gained 1·9 per cent. in weight, a percentage which closely approximates the hygroscopic figure given by Guppy, viz. 2–3 per cent. about a mean.

¹ Guppy, *op. cit.*

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A brief consideration of the occurrence of vivipary in acorns as dealt with by this author will assist us to understand the results of the experiments given later. He clearly shows that acorns freshly detached hold more water than is actually required for their germination and can proceed at once to germinate without any external supply. "In fact we have seen that such acorns will germinate without a rest period after losing a good proportion of their weight by drying. Any check to the drying process of the fresh detached nut would directly aid the seed in proceeding continuously with its growth and dispensing with the usual period of repose." Further, "we may infer from Berthelot's principle that hygroscopicity being associated with the water which the seed, living or dead, holds in maintaining its equilibrium with the air, has nothing to do with germination," and thereafter he states that the germination observed where the atmospheric moisture was apparently utilised was in reality due to the fact that the acorn used its own excess water for this purpose. In this case the acorns were kept in the atmosphere of an unheated room in Devonshire, where the conditions are very humid and may have imposed a check on the drying process. The percentage germination under these circumstances was in one case 20, and in the other 23, so that $\frac{1}{5}$ to $\frac{1}{4}$ of the acorns concerned were able to utilise this excess water—an excess which he estimated at about 10 per cent. of the original weight of the acorn.

Owing to my inability to procure fresh acorns of either *Quercus pedunculata* or *Q. sessiliflora*, acorns of *Q. Cerris* were utilised in the following experiments in an endeavour to show that after a percentage of water is lost, acorns cannot absorb sufficient from the atmosphere to enable them to germinate.

Table VII shows the results of suspending over water, in a corked bottle, freshly collected acorns.

Table VII.

Original weight	Weight after one week	% Loss	Fate
2.812	2.728	2.9	Germinated
2.215	2.106	4.9	„
2.857	2.751	3.7	„

The acorns were presumably utilising their excess water for germination—a process which continued in spite of the loss of moisture.

Table VIII.

	Original weight	Weight before suspension or planting	% Loss	Greatest weight during next 6 weeks	% Gain	Fate
Suspended	3.112	2.820	9.3	2.897	2.7	No germination
	2.592	2.350	9.3	2.375	1.6	„
	1.727	1.550	10.2	1.606	3.6	„
Planted	3.652	3.194	12.5	3.580	12.8	Germinated
	2.392	2.158	9.7	2.415	11.9	„
	3.215	2.800	12.9	3.246	15.9	„

In the next experiment (Table VIII) 6 acorns were exposed in a room until about 10 per cent. of their original weight was lost. 3 of these were then suspended over water and 3 planted.

These results show that while the planted acorns absorbed the quantity of water lost and proceeded to germinate, those suspended in an atmosphere saturated with water vapour absorbed a small percentage only while no germination ensued.

From a consideration of Guppy's experiments and of those described above, one is led to the conclusion that an acorn has two chances of germinating, either, if conditions are suitable, proceeding with germination straight away before it has lost 10 per cent. of its weight (Guppy's estimate), or if the amount lost exceeds 10 per cent. but does not exceed 27 per cent.¹ that germination will take place only if the acorns come in contact with a film of water such as is provided for them in the soil. If the latter is not provided and the seed can absorb from the atmosphere only the water of hygroscopicity, then germination will fail.

A comparison of the method of storing acorns for spring sowing in this country with that in vogue on the continent, will show to what practical application the above information may be put. Among some foresters and seedsmen in this country the method employed is simply to collect the acorns in sacks and leave them there until required. Energy is set free in respiration and the acorns "heat." A large proportion make use of their excess water and proceed to germinate, with the result that the percentage germination in spring is very low. On the continent much greater care is taken. The authors of the *Neudammer Förster Lehrbuch*² give the following directions. "If the acorns....are to be kept until next spring, they must first dry. To that end they are piled up on a floor, about 20 cms. high, and turned over once or twice daily, until they are no longer moist externally. Nevertheless the drying must not go so far that the kernel becomes loosened from the pericarp, and the latter becomes wrinkled. Further storage results best in a (specially constructed) shed, less well on house floors in 30 cms. deep layers, mingled with dry sand. The fruits are turned over perhaps every three weeks, and also as soon as they show signs of 'heating'; thus especially at the beginning of and during unusually damp weather, caution is recommended." Here we have the precaution taken first to initiate the drying process to prevent the acorn utilising its excess water, and secondly to ensure that this drying process does not go beyond the "death point" of the acorn.

This check to the drying process mentioned above is brought about in nature by the provision of a seed bed which has an atmosphere more or less saturated with water vapour. Conditions vary in different woods and in different parts of the same wood and those necessary for successful germination may be brought about in a variety of ways.

Whether in the Damp Oakwood, Dry Oakwood or Oak-birch-heath as-

¹ Or perhaps 21 per cent., see p. 182.

² 1902, p. 148.

sociations, wherever there is a covering of humus over the acorns, there germination is successful. In depressions in the soil where a few leaves can collect and form humus, there are often found many seedlings, e.g. in the entrances to disused rabbit burrows. Further in the lee of fallen branches or where the leaves have been caught, when urged by the wind, among the stems and branches of low growing shrubs such as Hawthorn (*Crataegus monogyna*), Blackthorn (*Prunus spinosa*), and Brambles (*Rubus* spp.), among the stems and fronds of bracken (*Pteris aquilina*) or among *Vaccinium Myrtillus* and *Calluna vulgaris*, there do we find numerous seedlings coming up. Again among grass such as meadow grass, acorns germinate in great numbers—a fact noted by Forbes¹ and also by Warming² who says, “If we were to leave these (meadows and pastures) to themselves, in time they would certainly give way to forest.” A carpet of *Sphagnum* spp., or *Polytrichum commune*, provides also locally a suitable seed bed for germination, as I have observed in the New Forest and elsewhere.

The above data appear quite sufficient to show that in all the cases cited, conditions are such that the necessary environment is provided to inhibit the drying process, to allow the acorn to proceed at once with germination or prevent the removal of too much moisture before it can do so. During the autumn in such situations thousands of acorns are in fact found germinating.

Regeneration is often successful after felling has taken place; for this reason probably, among others, that the acorn becomes embedded in the soil and even if it has lost a certain percentage of water it can absorb sufficient for germination. In the old days, also, when pigs were driven into the woods for pannage those acorns which escaped their voracious appetites were either trodden into the soil or buried by the upturned turf, thus concealing them and providing a suitable seed bed³.

Let us review briefly the situations upon which acorns were found ungerminated. They were found upon soils characteristically flat, almost devoid of vegetation, without humus and of a light sandy nature. The evaporation from such a bare surface is much greater than from a surface where leaf mould is present. The following figures are taken from Schlich⁴ quoting Ebermayer.

Evaporation of water from soil in the open placed at 100 parts.

„ from forest soil without leaf mould = 47 parts.

„ „ „ with a full layer of leaf mould = 22 parts.

So that from a bare surface the evaporation was more than twice as much as from a soil covered with leaf mould. Should acorns fall on such a surface their drying process would immediately commence and their germination would be inhibited. These acorns, once they have lost a certain proportion of their moisture, cannot then absorb sufficient from the atmosphere to induce ger-

¹ See p. 175.

² *Oecology of Plants*, p. 323, 1909.

³ Nisbet, *British Forest Trees*, p. 207, 1893.

⁴ Schlich, *Manual of Forestry*, Vol. I. p. 40, 3rd Ed. 1906.

mination and unless they come in direct contact with a film of water which can be imbibed mechanically, there is no hope of their germination.

Whilst I have not found upon bare areas on a clay soil any acorns lying ungerminated during the summer, where the general evenness of the surface and lack of vegetative covering, either living or dead, identify it with the above, I have found small seedlings 1–1½ ins. high projecting from small cracks in the soil and upon closer examination it was found that the acorns which had lodged there had been afforded concealment and conditions suitable for germination. It is not that the soil is too hard for the penetration of the radicle, requiring to be “wounded” on this account, but that under these circumstances the acorn does not find a suitable haven where its moisture can be conserved, and tilling of the soil and covering of the seed are necessary either to provide this or supply the acorn with the necessary water if it has parted with too much. Not that “screefing” or “wounding” is not a desideratum for the better growth of the seedling but it is unnecessary to ensure physical ability of the radicle to penetrate the soil.

A similar result to that occurring on bare soil may be caused by a rank growth of herbage, which may prevent the acorns from reaching the soil and expose them to desiccation. “All foresters are agreed that in felled areas, invaded by a thick carpet of tall grasses such as *Molinia caerulea*, *Poa nemoralis*, *Poa sudetica*, various *Festucas*, etc., regeneration does not take place and one is obliged to break this carpet by ‘screefing’ so that the seed can fall on the damp soil, there to germinate and take root. Otherwise the seeds suspended on the vegetation are desiccated and lose their germinative capacity¹.”

Again where such species as *Deschampsia flexuosa* and *Festuca ovina* form a mat on the soil surface, acorns readily lose moisture, the brown colour of the pericarp becoming white. Although on such situations I have found no seedlings, the cause may readily be assigned to those factors mentioned in Part I, but the change of colour of the pericarp has been noted before the acorn’s disappearance. On this subject Moss² writes, “A matter which is not sufficiently emphasised is that in a closed plant association seedlings especially of plants with large seeds like the oak are rarely found. Now as time goes on the ground vegetation of a wood tends to become closed; and this simple fact in itself is one of great importance in the question of the rejuvenation or degeneration of forests. Some foresters make use of their knowledge of the fact and go to great trouble in keeping the ground vegetation open by removing the woodland weeds.”

With regard to the effects of a grassy covering of the soil, however, there does not seem to be a consensus of opinion. For the natural regeneration of the oak under proper sylvicultural methods, preparation of the ground is advocated³. In a contribution to the Société Centrale Forestière de Belgique⁴

¹ E. Henry, *op. cit.*

² Moss, *op. cit.*

³ Cf. Schlich, Nisbet, Forbes, *opp. cit.*

⁴ *Soc. For. de Belgique*, 1909, p. 633.

entitled "La Forêt de St Michel," the author says, "Do we not often exaggerate the difficulty and the uncertainty which the sowing of acorns, whether natural or artificial, presents? I confess for my part, to have seen this carried out with complete success in Prussia under conditions which formerly had appeared to me purely utopian. Among the undergrowth (prés-bois) of the forest of Bramvald, the oak regenerates itself to perfection on a soil, superficial, degraded, and covered with thick grass. There is produced by natural and artificial sowing in the forestry canton of Salmünster (Spessart) admirable stocks of oak on soils invaded by *Calluna* and *Vaccinium*. Far from condemning these two plants, which, however, receive scant consideration in the forestry world, the forester of Bramvald looks upon their presence, but not their superabundance (that goes without saying) among the trees to be regenerated with satisfaction. If they are harmful inasmuch as they produce acidic humus, they conceal the acorns and young plants from forest animals especially from game."

These two expressions, seemingly contradictory, may be harmonised if we consider the type of ground flora more in detail. Undoubtedly where the acorns fail to reach the ground and are desiccated, or even if they germinate and the radicle fails to find a suitable medium before that occurs, regeneration will not take place. Or even if they do reach the soil and germinate normally but the seedlings are quickly overtaken by tall herbaceous species the chances are very much against their establishment. Now in pastures where grazing occurs and the acorns lie on the soil, germination is good and the establishment of the seedling seems assured if such grazing ceases and the seedlings grow up amidst grass which is not tall enough to cut off the supply of light. The determining factor seems to be whether the ground association is absolutely closed throughout the year, preventing the germination and establishment of the seedling, or, if not closed, the constituent species of this association forming a rank growth sufficient to cut off the light supply if germination takes place. From an examination of the list of species (v. *Types of British Vegetation*, p. 81) to be found in the ground flora of a Damp Oakwood, and from my own observations on a wood of this type, the herbage does not form an association close enough nor of such rank growth as to prevent the germination and establishment of the seedling. Undoubtedly from a strictly sylvicultural point of view the removal of any rank growth is a desideratum, but where there is a plentiful crop of acorns, regeneration need not cease to take place solely on account of the presence of such. Such regeneration may be patchy but there would certainly be enough seedlings to ensure the continuance of the forest, or in other words to ensure successful natural rejuvenation.

Further, there seems to be no inherent difficulty in the recolonisation of scrub or neutral grassland by the oak, if other factors such as the grazing of animals were eliminated. In this connection the reader should compare Warming's remarks, previously quoted, on the invasion of pastures and meadows.

A study of the plant formation of the older siliceous soils, while presenting a ground flora in the damper parts of the oakwood association similar to that of the Damp Oakwood of clays and loams, and consequently not unsuitable to the germination of acorns, does not indicate the same suitability as a seed bed for these in the scrub and grassland associations to which the highwood may degenerate. From a comparison of the lists of species characterising the ground flora of the woods of *Quercus sessiliflora* and of the associated scrub (for lists see Moss, *op. cit.*) we find that in the latter, plants of the wiry type, e.g. *Deschampsia flexuosa*, *Festuca ovina*, etc. predominate, tending to form a mat on the ground surface. Acorns falling upon such springy turf would tend to bounce upwards and then lie loosely on the surface. Were such grasses to form a closed association, and in consequence be the only seed bed available for acorns from the occasional oaks, the conditions are such as to expose the acorns to the desiccating action of the wind, and as we have seen they cannot regain sufficient moisture from the atmosphere. This may be a partial explanation at least of the lowering of the altitudinal limit of oak on the Pennines. Other factors such as the "indiscriminate felling of trees and the grazing of quadrupeds" may in part initiate such a degeneration from the typical oakwoods to scrub, but once the ground association becomes closed by such grasses as the above it is difficult to see how regeneration can take place. The initiation of this process of retrogression may also take place in those drier parts of the wood where acidic humus is present in good quantity—a surface layer which is very favourable to colonisation by *Deschampsia flexuosa* (noted by Moss and Woodhead) whose "dense dry wiry tussocks" would present an unfavourable medium for the germination of acorns. The difference in the water content of the soil, correlated with the formation of acidic humus, by favouring the growth of these grasses, prevents successful regeneration of the oak.

The Dry Oakwood association presents a rather varied ground flora according to the character of the soil and the supply of light which reaches the ground. The soil of this association is characteristically poorer in humus than that of the Damp Oakwood but wherever we find the leaves collecting, there do we find germination normal. Also in those parts of such woods where the ground flora consists of herbaceous species which do not form a springy turf, and which do not impede the acorn in its fall from reaching the soil, seedlings appear in normal numbers. Similarly a *Holcus mollis* society, the intervals between the constituent members of which are occupied by humus, furnishes seed beds favourable to the germination of acorns, as I have observed in oakwoods in Suffolk. Parts of such woods are, however, often occupied by *Deschampsia flexuosa* and where this forms a close mat, the conditions are similar to those previously mentioned in the case of scrub on the Pennines. Bracken is also locally abundant in such woods, but its influence will be discussed later.

After explaining Graebner's account of the degeneration of oak forest to

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heath by impoverishment of the soil, the authors of *The Woodlands of England*¹ go on to say that the replacement is much accelerated by the felling of trees. "This tends to rapid deterioration of the soil through destruction of the mild humus by sun and wind, and on suitable soils enables certain mosses and other plants of the heath association to find an entry. Not only does the felling of mature trees considerably diminish the supply of seed, but there can be no doubt that the occupation of the soil by a heath vegetation with its accompanying layer of acid peat, checks or altogether arrests its recolonisation by such a tree as the oak. This is perhaps due to unfavourable conditions of germination." On account of the open character of the wood, far more light is allowed to reach the ground and where exposed to the action of the wind the ground is swept clear of all the fallen leaves. Conditions are suitable for the propagation of *Deschampsia flexuosa* which is the characteristic grass of the Oak-birch-heath association, and where bare areas occur, or areas with only sparse bracken, as under isolated oak trees, the conditions for germination prove unsuitable and regeneration becomes impossible. Where *Vaccinium Myrtillus* or *Calluna vulgaris* has stayed the flight of the leaves, acorns, if they fall among these, germinate quite normally.

A general review of these associations of oakwoods leads one to the belief that areas unsuitable for acorn germination become increasingly frequent as we pass from the Damp Oakwood to the Oak-birch-heath, and even supposing the acorns to be left intact we should expect seedlings to diminish numerically as we pass from the one association to the other, not only because of the decreased number of parent trees, but also on account of the considerations mentioned above.

PART III.

ESTABLISHMENT AND FATE OF THE SEEDLING.

In spite of the vast mortality among acorns and the failure to germinate on certain areas, we find in certain places during the following spring thousands of seedlings pushing their way through the humus or soil. Yet, in 3 or 4 years' time, or less, nearly every one of this large number has disappeared. We have now to deal with the causes of this disappearance.

To find out whether the type of soil inhibits germination in any way 100 acorns (50 *Q. pedunculata* and 50 *Q. sessiliflora*) were planted in each of the following three kinds of soil, viz. loam, chalk, and acid peat bearing *Calluna*. The germination varied between 96 per cent. and 100 per cent. and was therefore normal in all cases.

Another experiment was carried out to ascertain whether depth of planting in humus had any inhibitory effect. A control plot where ordinary garden soil was used was also planted. 15 acorns were planted at successive depths of 3, 6, and 9 ins. in each. The results are given in Table IX.

¹ Moss, Rankin and Tansley, *The Woodlands of England*, 1910.

Table IX.

	In Humus			In Soil		
	ins.	ins.	ins.	ins.	ins.	ins.
Depth of planting ...	3	6	9	3	6	9
No. planted ...	15	15	15	15	15	15
No. germinated ...	11	9	12	8	10	10

The poor germination may be accounted for by the fact that out of every 15 in each layer, 10 were from acorns kept in a room for some time and the remaining 5 were collected in woods in the neighbourhood of Cambridge, where by that time (March) they were extremely difficult to get, so effectively had the agents mentioned in Part I diminished the supply. Nevertheless so far as the experiment goes it shows that planting in humus to a depth of 9 ins. did not interfere with germination.

The conditions under which acorns may proceed to germinate are described in Part II and even on bare soil the acorn, by utilising its excess supply of water, may germinate, especially if the surroundings are humid enough to impose a check on the drying process, as e.g. in a society of *Mercurialis perennis*, which Salisbury¹ has shown occupies the damper soils. Among grass many germinate and establish themselves, but on bare soil, while some may do so, a certain percentage, depending on the conditions, die either from the effects of frost or simply from desiccation through the exposure of their radicles.

Given that the seedlings establish themselves we have still to account for their disappearance later. With a view to identifying the causes of disappearance, I marked in 1915 certain areas in woods at Midhurst in Sussex and in Staffhurst Wood, Surrey (on the Kentish border) and visited them periodically. Certain areas were chosen where rabbits were known to be absent, others quite exposed to animals were marked and a few were enclosed. By utilising a method similar to that adopted to establish the fact of the disappearance of the acorns (Part I) the same was ascertained to be true of the seedlings.

The following results (Table X), compiled from a selection of a number of plots, give the fate of the seedlings up to January, 1916, i.e. 8 months or less after their germination. The third column gives the number of seedlings at the commencement of observations, the last the number in Jan. 1919.

In the following compilations it is necessary to point out that difficulty was experienced in relegating certain of the seedlings to their respective groups, e.g. the amount of shoot absent distinguishes the "cut off" from those with "tips off," and clearly such a division is an arbitrary one. Further difficulty was experienced in distinguishing certain seedlings, whose tips had withered through the agency of a fungus and subsequently fallen off, from those with their tips off through the action of herbivorous animals, the uppermost part

¹ "The Oak-Hornbeam Woods of Hertfordshire." *Journ. of Ecology*, 6, p. 33, 1918.

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Table X.

On sandy soil, exposed and left to natural agencies.

No. of Plot	Description of plot	Initial No. 1915	No. in January, 1916					No. in Jan. 1919	
			Normal	Dead	Diseased	Cut off	Tips off		Missing
1	1 in. humus. No vegetation, dense shade	39	5	14	5	7	6	2	0
2	Under dense shade of Rhododendron	18	2	3	5	8			0
3	1 in. humus among some brambles	255	31		2		50	172	0
4	Open association of grass with thin carpet of leaves	17	6		10			1	3
5	1 in. humus. Light canopy. Bracken present but fronds removed	250	32		6	87		125	0
6	Among brambles, soil with some leaves but mostly bare	17	5			1	4	7	0
7	Deep humus. Light canopy. No vegetation	23	5		1	12		5	3
8	Among humus. No vegetation	25	7	1	3	1	10	3	—
9	Bare soil, afterwards shaded by bracken	17	1			3		13	0
Totals ...		661	94	18	32	119	70	328	6
% Totals ...			14.2	2.7	4.8	18	10.6	49.6	less than 1

Table XI.

On sandy soil, enclosed against rabbits or where rabbits were known to be practically absent.

No. of Plot	Description of plot	Initial No. 1915	No. in January, 1916					No. in Jan. 1919	
			Normal	Dead	Diseased	Cut off	Tips off		Missing
1	In deep humus. No vegetation	91	65	6	16		1	3	0
2	Area in part bare, exposed to full sunlight	12	10				2		5 (av.)
3	Among grass. Light canopy	127	84	1	7	13	16	6	14
4	1 in. humus. No vegetation	57	5		1	27	4	20	1
5	„ „	24				17		7	0
Totals ...		311	164	7	24	57	23	36	20
% Totals ...			52.7	2.2	7.7	18.3	7.4	11.5	6.4

Table XII.

On sandy soil, enclosed from all animals.

No. of Plot	Description of plot	Initial No. 1915	No. in January, 1916					No. in Jan. 1919	
			Normal	Dead	Diseased	Cut off	Tips off		Missing
1	Area mostly bare. In full sunlight	130	126	1				3	116
2	1 in. humus. Bracken present but removed	17	16	1					14
3	2 in. humus. Dense shade. No vegetation	333	65	21	243	3?	1		0
Totals	480	207	23	243	3?	1	3	130
% Totals		43.1	4.8	50.6	.6?	.2	.6	27

Table XIII.

On clay, unenclosed.

No. of Plot	Description of plot	Initial No. 1915	No. in January, 1916					No. in Jan. 1919	
			Normal	Dead	Diseased	Cut off	Tips off		Missing
1	1 in. humus. Under shade, no vegetation	36	14		1	14	4	3	2
2	1 in. humus. Open ground floor	95	62	4		14		15	3
3	" " "	7	7						0
4	Beech and Oak canopy. Open <i>Scilla nutans</i>	26	13	3		2		8	0
5	Open association of vernal species	36	9	4	2	8	3	10	0
6	Open canopy. Varied ground flora	48	44	2		2			16
Totals	248	149	13	3	40	7	36	21
% Totals		60.1	5.2	1.2	16.1	2.8	14.5	8.5

of the remaining shoot then withering up and presenting a similar appearance. Also, during the course of early summer young seedlings appeared in certain plots, thus creating a difficulty in separating those previously observed from those coming up later. Where this occurred a conservative attitude was adopted and the data on that account may not represent the full ravages of the marauders. Further I have included in the column of "normals" those plants, which while the leaves were attacked by a fungus, yet had not then reached the dying or badly diseased condition, for as will be explained later most of the seedlings observed showed the presence of a fungus. On account of the above and of certain minor difficulties the percentages may be elastic to the extent of 2 or 3 per cent.; but this does not affect the main result.

The Effect of Animals.

Omitting those which are classed as "missing" and grouping those which are "normal," "dead" and "diseased," and comparing the results with the combined "cut offs" and "tips off," under varying exposure to animals, we arrive at the following percentage results (Table XIV, compiled from Tables X, XI and XII only) of seedlings surviving in January, 1916.

Table XIV.

	Exposed to animals	Protected from rabbits	Completely protected
Normal	14.2	52.7	43.1
Dead	2.7	2.2	4.8
Diseased	4.8	7.7	50.6
Totals	21.7	62.6	98.5
Cut off	18	18.3	.6?
Tips off	10.6	7.4	.2
Totals	28.6	25.7	.8

These figures are very significant, as showing in the first place the relative percentages which remain in the exposed, partially protected and completely protected plots, 22, 63 and 98.5, respectively. Secondly there is a decreasing percentage of those whose shoots are cut over as we pass from the exposed to the fully protected.

If we examine the columns of those "missing" we find a similar diminution as we pass from one series to the other, there being 49.6 per cent. classed as such in the exposed, 11.5 per cent. in the partially protected and less than 1 per cent. in the fully protected—a decrease which suggests a certain relationship between protection and those agents which such protection excludes.

In this way we get a series of figures which definitely show the value of protection against those agents which are responsible for the disappearance or for the cutting over of the seedlings.

During the course of these observations I repeatedly found seedlings which had been cut off about $\frac{1}{2}$ –1 in. above the surface of the ground, leaving a short stump, and the remainder of the aerial part either removed or lying near. Further in humus I often came across seedlings remaining in the upright position, with the leaves wilted and dry but still attached. Upon my pulling the seedling, I found it to come away quite easily and upon further examination discovered that it had been cut through below the surface level of the humus. Such areas were also undermined with numerous tunnels of small burrowing animals. The supposition naturally suggested itself to me that in the latter case at least, voles and mice in the course of their burrowing through humus found a shoot or radicle of a seedling in their way and simply gnawed it through. Such an explanation, however, did not account for those seedlings which had been cut over above the ground surface. I therefore watched a particular plot,

and after I had waited a short time a mouse made its appearance from a burrow in the area marked, and after a preliminary circumspection went to a seedling and gnawed through the shoot. It then proceeded to another and did the same again, the shoot toppling over and lying on the soil. No attempt was made in this case to look for the seedlings' acorns. I presume the explanation is that mice, being rodents, require some suitable material to gnaw in order to wear down their continuously growing incisors and evidently the shoot of the seedling oak is to their liking from this point of view.

As a result of these observations I made a separate column in the above data for those "cut off."

It is the unanimous testimony of foresters, whether expressed orally or in the literature of forestry, and also of workers in ecology, that rabbits do extensive damage in woods, and by eating the seedlings impede or wholly prevent natural regeneration. I have never actually seen rabbits thus engaged, but the opinion is so unanimous and so well established that we may assume they eat oak seedlings. Now the damage done to seedlings may be exactly identical with that done by mice except that in the former case no shoot remained by the side of the stump (although this is by no means invariable in the case of mice) the leaves and shoot evidently providing the rabbit with provender. The more woody parts of the seedlings are, however, seemingly unsuitable, as on several plots many bits of shoots were found. In other cases only the leaves and tips of the shoots were taken, and in still others only the leaves, short parts of the petiole with sometimes parts of the blade remaining attached—a distinction which is of value in distinguishing the stripping of the shoots through the agency of rabbits from stripping due to the fall of the leaves after their death has been brought about by disease. In many cases after this cutting off or stripping occurred, latent buds produced new shoots, which in turn were cut over and in some cases even a third shoot was put forth. Against such attacks the seedlings cannot hold out indefinitely.

The relation between the number reported missing and the degree of protection afforded has already been noted. If we discount the percentage missing in the enclosed areas (a percentage less than one) and deduct those missing through other agencies than rabbits from the percentage thus reported in exposed areas we get (49·6—11·5) 38·1 per cent. still unaccounted for. The explanation of this may be that not only do rabbits nibble seedlings but may gnaw them off so close to the ground that on subsequent visits there were no subaerial parts left on which to base observations.

The actual damage done by rabbits varies of course in different places according to the attitude assumed towards them by the owners, bailiffs or gamekeepers of the different estates. When preserved in unfenced warrens their presence in neighbouring vegetation is naturally at its most severe pitch. These rodents, however, prefer a sandy soil, in which they breed, and if left alone, multiply rapidly. A clay soil on the other hand is unsuitable for their

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colonisation and rapid multiplication. In this connection it is interesting to compare the damage done by rabbits on the sandy soil at Midhurst, with that caused by the same agents at Staffhurst Wood on clay and loam (Tables X and XIII). For this comparison I shall include those with "tips off" and those "missing" as being largely due to rabbit agency. The total for the Midhurst plots is 60.2 per cent. and for the Staffhurst plots 17.3 per cent., figures which in a general way show the greater efficacy of rabbits as destructive agents on sandy soil than on a clay soil.

The percentage lost through the agency of birds is not large. In their case evidence of their pecking in the soil in search of the acorn reveals the agent responsible, and I have known jays peck out acorns in this way. If the root has a firm hold of the soil, the acorn will be detached, leaving the seedling behind.

The above data clearly show the efficacy of animal agency in reducing the number of seedlings. These tables are compiled from observations made up to January 1916. Owing to absence abroad I was unable to visit the plots again until January 1919. The last column shows the number of seedlings then alive on plots which did not coincide absolutely with the original ones, as the stakes, which were utilised for marking off the areas and were chosen so as to minimise as far as possible any interference from outsiders, had all decayed and were indistinguishable from fallen branches. But in every case an area as nearly as possible coinciding with the original one was examined, with the results as entered in the last column. In the exposed areas on sandy soil only 1 per cent. remained, in the partially protected 6.4 per cent. and in the fully protected 27 per cent. On clay, unprotected, 8.5 per cent. remained. These figures represent the remnant after nearly 4 years from all causes operating against the seedlings' establishment. On account of my absence no data could be obtained as to the fate of these now missing, but the data available are quite sufficient to prove the efficacy of animals as agents militating against successful regeneration of oakwoods, especially on sandy soils.

Supplementary evidence as to the value of protection from animals was patent from observations made in the New Forest towards the end of August. Among such spiny plants as *Ilex Aquifolium*, *Prunus spinosa*, *Crataegus monogyna*, etc., usually near the periphery of clumps of these, saplings of various heights were found growing up among the protecting branches. Their demands for light led them to incline their stems to the outside of this protection but rarely did I find any protruding twigs which would be liable to be nibbled by the cattle, ponies, sheep, deer, etc., which roam through the Forest, or if they do project they are promptly eaten back. Once these branches emerge from this protection sufficiently high up to escape the browsing animals, the future of the tree is assured. It is no uncommon thing to find a large oak standing in the centre of such a clump—an oak which has grown up with the thorny species, the latter affording it the necessary protection. This

phenomenon has been recorded by numerous observers¹ for trees in general and undoubtedly the protection thus afforded was the salvation of the oaks in question. There were also in the Forest some oaks with a stem about $\frac{3}{8}$ in. in diameter and a bushy crown, growing among heather and whose height was the same as that of the surrounding vegetation. The small stature and bushy form were no doubt due to the continual browsing of animals upon the young shoots which projected above the level of the surrounding vegetation. Further, under the protection of spiny plants oaks may colonise new ground in progressive scrub². At Petworth on a piece of waste land, overgrown with tall gorse, there are a few oaks coming up, their foliage adequately safeguarded against animal attacks, whilst the acorn may also have escaped the smaller animals owing to the spiny medium of fallen thorns not being conducive to their comfort. Pounded gorse has been recommended³ as a protection against these.

When natural regeneration is found in certain areas the absence of some of the animals above mentioned usually accounts for it. One of the most successful examples of natural regeneration in the South East of England may be seen at Petworth, where on a particular estate rabbits are treated as vermin. Part of an oakwood was felled and enclosed against the roe deer present on the estate. No greater testimony to the value of protection can be had than to compare the part enclosed with the unenclosed. In the former regeneration is proceeding normally, while in the latter no saplings are seen at all or if so they are small and kept down. Here as in other places the presence of the workmen for a period may have helped to frighten away the animals and the general absence of vegetation which may attract them, for a year or so, probably also assisted towards the preservation both of the acorns and the seedlings.

The effect of a fungus (Oidium quercinum?).

In the above tabulated data there are columns set aside for the "dead" and "diseased," but as already remarked the vast majority of the seedlings, no matter where examined, showed the presence of a fungus. This fungus is one of the mildews provisionally called *Oidium quercinum*, as so far perithecia have not been found. More recent examinations⁴ of the conidia do not identify this fungus with the *Oidium quercinum* of Thümen, but as the matter is still unsettled I shall adhere to the provisional name given above. Attention was called to this fungus during the last quarter of the preceding century and more recently in Britain. The disease was observed on oak seedlings in woods throughout the South of England from Kent to Dartmoor and in the Forest of Dean. It occurred on plants on all varieties of soils and under all conditions as to light, e.g. from the heavy clay of the Weald to the light sandy soils at

¹ E.g. **Adamson**, *Proc. Linn. Soc.*, 1911, p. 339, **Tansley**, *op. cit.*

² **Adamson**, *op. cit.*

³ **Elwes** and **Henry**, *op. cit.*

⁴ **Griffon** and **Maublanc**, *Bull. de la Soc. Myc. de France*, 1910.

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Midhurst and in the New Forest, as well as in those oakwoods degenerating to heath. It occurred likewise on seedlings exposed to full sunlight and on those under dense shade. The apparent effects of the fungus differed, however, in the various situations, but, as from my experiments it was impossible to determine what contribution the diminished supply of light paid and what the fungus paid towards the death of the seedling, in dealing with these two factors separately, this must be borne in mind.

Comparing the plots enclosed from animals (Table XII) where the somewhat heterogeneous column of "missing" is reduced to a minimum, we find that in plot 3 out of a total of 333 seedlings under dense shade, 266 are classed as dead or diseased, whilst in the other two plots there are only 2 reported dead. It may here be recalled that the column "diseased" includes only those which were suffering badly and were likely to die, whilst so long as the leaves remained turgid, the plants to which they belong are classed as "normal." Both the latter plots were exposed to full sunlight during 1915. Further, of those plots fully exposed to animals Nos. 1 and 2 were under dense shade. Out of the total number of seedlings in these two plots (57) 27 are classed as dead and diseased (= about 47 per cent.), whilst of the remaining seedlings in the other plots (604) only 23 are so classed (= about 4 per cent.). Further, in plot 1 of those protected, after 3 years the seedlings were from 2-3 ft. high, while in plot 2 they were only 9 ins. high; and here it is necessary to explain that bracken grew up uninterrupted during those years and shaded the seedlings. So that seedlings even although diseased can withstand the effects of this fungus and grow normally when supplied with sufficient light. How much of this diminished growth was due to the deficiency of light supply and how much was due to the disease acting more powerfully on a plant rendered less vigorous by growing in shade, cannot be determined from the above. Further experiments in this direction are required.

If we compare the seedlings under an open canopy on heavy clay soil with those on light soils under similar conditions the plants on the former seem of darker colour and more healthy than those on the latter. Yet a comparison of the exposed plots on sand with those on clay does not at first glance bear out this observation, for in the former 7.5 per cent. were dead or diseased while in the latter 6.4 per cent. were in a similar condition. If however we take into account the heavier mortality that has taken place in the former through animal agency, and consider those which are still exposed to the disease by comparing the normal with the diseased in both sets we arrive at the following:

On Sand. 7.5 per cent. dead and diseased while 14.2 per cent. remain normal.

On Clay. 6.4 per cent. dead and diseased while 40.1 per cent. remain normal.

This shows that up to my last observations the disease had more effect on seedlings growing on sand than on clay.

The fungus first appears on the leaves, which, upon the attack spreading, ultimately wilt. It thereafter attacks the shoot itself. Diseased leaves usually fall off so that in many cases where at first no seedlings are apparent, a closer examination reveals them quite stripped of their leaves with nothing but the shoot left, and even of this the tip is often diseased. Such seedlings, drawing on their reserves, often put forth new shoots, but the young leaves are immediately attacked and quickly succumb. This cannot continue, so the plant dies.

The effect of light.

For lack of exact experiments and data, opinions may differ as to the amount of light required by young oaks, but all agree that it is a "light demander" throughout its whole life history. Gordon¹ conducted a series of experiments where "an attempt is made...to determine more or less accurately the conditions most favourable to the development of advance growth (i.e. oaks from the seedling to the pole stage growing in association with the parent trees), in other words to determine approximately the optimum conditions for natural regeneration"; and his conclusions are in agreement with the generally established idea. "Long experience has shown that for the oak the lightest possible shade of seed bearers is compatible with most successful natural regeneration."

Now it has been recorded by Woodhead² that bracken often marks the site of degenerate woodland and ecologists testify to the frequency of this fern on sandy soil especially in the opener parts of woods. If we neglect the effects of the fungus and base our conclusions on the above established principle, then it seems clear that where bracken colonises the floor of a wood, the light supply will be cut off from the seedlings. Those seedlings I have observed under bracken were, at 4 years old, from 6-9 ins. high, while the last 2 or 3 years' growth was limited to $\frac{1}{2}$ in. or thereabouts in each year—seedlings which put forth their leaves and probably assimilated enough food to keep them alive before the bracken fully expanded its fronds (early June in S. of England) and cut off the supply of light. In these experiments there was no question of toxic action³ produced by the decaying fronds overlying the seedlings, as the fronds, becoming entangled in the wire netting overhead, remained suspended. Under such conditions the seedlings cannot survive indefinitely and eventually die. Where the bracken is very sparse I have seen in an enclosed area the seedlings 18 ins. to 30 ins. high during a like period.

Bracken, however, may act in another way. If the crop is dense the heavy rains and winds may cause it to become "lodged," when the bracken drags

¹ *Trans. of Scot. Arb. Soc.*, Vol. xxv. p. 147, 1912.

² *Journ. Linn. Soc.*, 1906, p. 333.

³ H. Jeffrey, E. P. Farrow, *Journ. of Ecology*, 5, pp. 145 and 165 respectively, 1917.

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down any young growth that still persists. Seedlings thus treated lie flat on the ground and under such conditions regeneration is impossible. An example of this may be seen at Petworth where in the enclosure (previously mentioned) part of the area shows saplings 10–12 ft. high while the area with a dense crop of bracken reveals few plants and these have assumed the attitude above described. In this case bracken may have had a toxic effect in reducing the number of seedlings, but, as previously pointed out, it can cause the death or dwarfing of the latter by simply cutting off the supply of light.

Where little or no bracken was present, as in Staffhurst Wood on clay, the supply of light which reached the ground was evidently insufficient to induce normal growth, for there also the surviving seedlings were only from 6–10 ins. high.

The effect of a leaf-eating agent.

On the majority of the seedlings observed in certain plots and on many in others, the leaves were observed to be eaten. Either pieces were taken from the edge of the leaf or holes were cut from its surface. The seedlings attacked worst in this way occurred either among humus or among grass, but this is not invariable, as under both conditions in some plots the leaves either remained entire or were scarcely touched. Plants under dense shade appeared to suffer less in this way than those under an open canopy. For example 2 plots, where records were kept of the numbers of plants thus affected, showed 25 per cent. attacked under dense shade, while two others under an open canopy showed 75 per cent. Further, out of a total of 248 seedlings in the plots at Staffhurst Wood on clay 42 (= 17 per cent.) were recorded as having their leaves eaten, a much smaller percentage than the average with leaves thus attacked on sand. On the plots fully exposed to light, where the parent trees had been felled the previous year, the seedlings were characteristically unaffected in this way. Generally speaking, for all the plots examined do not bear out the above deductions, the agent responsible apparently occurred in greater numbers where vegetation was present and was also more prevalent on sandy soil than on clay, being almost entirely absent where the soil had been consolidated by the woodmen in both felling and planting operations.

The damage done is similar to that of the earwig on Dahlias; and although I have examined numerous seedlings for any animals likely to cause this I failed to discover any. Most probably the agent, whatever it is, is nocturnal in its habits, retreating during the day into the soil. Few deaths can be assigned to this cause, but, by a reduction in the manufacturing parts of the vegetative tissue, effects reacting upon the seedlings' vitality are undoubtedly caused, e.g. the fungus previously mentioned would be more deadly on a plant whose vitality was thus impaired, where the full benefit of the available light supply could not be taken advantage of on account of the reduced leaf surface.

The influence of other factors.

Other causes undoubtedly affect the plant's welfare in this way, e.g. the occurrence of galls both on the leaves and the roots, and the presence of a coccid on the shoots must reduce the capacity of the seedlings to resist the attacks of disease, or to hold out where the light supply is none too abundant. But the occurrence of these is not general and at the most only a very small percentage of deaths can be attributed to these causes compared with the mortality due to the causes mentioned previously.

INTERFERENCE WITH THE BALANCE OF NATURE.

In the present investigation it is pertinent to ask why regeneration was successful in former days and successful now only in isolated places. Were acorns devoured in such wholesale quantities then as now and did as many seedlings disappear?

Apart from those factors considered in Part II, and apart from disease, the chief causes of the failure of natural regeneration of the oak are herbivorous animals. Has there been an increase in the number of these since primeval days, especially of rabbits and the smaller animals? We have no exact statistics of the animal population of any wood, but that there has been a general increase in the number of rabbits, mice, voles, certain birds, etc. may be gathered from the following considerations.

Carnivores feed on various animals, including herbivores, and herbivores feed on vegetation. Man, when he became a stock breeder, a keeper of herbivores, or of fowls, found it necessary for the more rapid multiplication of his flocks and herds to reduce loss as much as possible. Hence he became the enemy—if he had not already an instinctive hatred of carnivorous animals—of all such as preyed on cattle, sheep, pigs, fowls, etc. Not only did he protect his flocks from the inroads of these carnivores but he waged war, carrying it into his enemy's own country, with the result that certain of these have become extinct or nearly extinct in our island, and against those which still survive a bitter war is carried on.

More recently the rearing of birds for game has intensified the struggle and carried wider afield this warfare against all such animals as destroy or are reputed to destroy the game. The protection of these birds is left in the hands of the gamekeeper who, whatever interests are affected thereby, performs his duty only too efficiently by suppressing those animals which destroy young pheasants, etc.

Further, many carnivores are trapped for the sake of their skins, and the pursuit of this occupation tends still more to reduce their numbers. Similarly with many of our birds of prey, which are shot either for decorative purposes or because they destroy game, or at least have such charges imputed against them.

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Now the herbivorous animals and birds, whether domesticated or wild, not being molested to so great an extent by their natural enemies, multiplied in proportion and in peopling the soil eat or destroy whatever vegetation is suitable to supply their wants. In this way the increase of destructive agents may be accounted for.

The following is a list of animals which prey on mice, rabbits, birds, etc., and their names arouse at once a feeling of animosity in the popular mind, so general is the belief that they are inimical to man's welfare, or to the increase of his wealth.

Enemies of mice, rabbits, pheasants¹, etc.: Owl, Buzzard, Gull, Rook, Black Crow, Hooded Crow, Kestrel, Polecat, Stoat, Weasel, Fox, Marten, Badger, Hedgehog, Shrew.

Man, by upsetting the balance of nature, and assuming control of what directly affected his own interests, is now paying the penalty in other ways, and must, having killed or suppressed the controllers, either assume total control himself or assist in such by a judicious encouragement of those animals he once considered his inveterate foes. "Civilised man has proceeded so far in his interference with extra-human nature, has produced for himself and the living organisms associated with him such a special state of things by his rebellion against natural selection, and his defiance of Nature's pre-human dispositions, that he must either go on and acquire firmer control of the conditions or perish miserably by the vengeance certain to fall on the half-hearted meddler in great affairs²."

SUMMARY.

In the light of the foregoing what measure of success in natural regeneration may we expect to be found in the different oakwood associations?

The importance of certain animals in the economy of the woodland has been pointed out in connection with the disappearance of both the acorn and the seedling. The prevalence of certain of these animals is in large measure, of course, dependent on local circumstances, e.g. on the attitude assumed towards them by the proprietors of the various estates. Pheasants for example may to a greater or less extent be thus limited. But in the case of the rabbit, natural circumstances favour its increase on sandy soils, so that the damage done on soils of this kind is greater than on clay soils. From the data available mice do not seem to be restricted in this way, so we may assume their ravages to be fairly evenly distributed over the various types of soil.

The importance of concealment to the survival of the acorn and the value of a humus layer in this connection are pointed out. The latter occurs more abundantly in the Damp Oakwood than in either the Dry Oakwood or Oak-birch-heath associations.

The relation of germination to the type of seed bed provided is also

¹ Nisbet, Schlich, *opp. cit.*

² Lankester, *The Kingdom of Man*, p. 31, 1907.

discussed and it is pointed out that while generally no inherent difficulties are met with to prevent natural regeneration in the Damp Oakwood, seed beds of an unfavourable kind became more frequent as we pass from the Dry Oakwood to the Oak-birch-heath associations.

The efficacy of the mildew in producing fatal effects on oak seedlings is shown to be greater on sandy soils than on clay, and the bracken, by its increasing frequency in the Dry Oakwood and Oak-birch-heath associations, by greatly diminishing the supply of light and impairing the vitality of the seedlings, materially assists the fungus in producing these effects.

Summing up one can say that the chances of success decrease as we pass from the Damp Oakwood association to the Dry Oakwood and from the latter to the Oak-birch-heath—a fact to be taken into consideration by the forester when he contemplates the natural regeneration of his oakwoods.

In conclusion, to Mr Tansley, who suggested the subject to me and who helped me throughout by kindly criticism, advice and discussion, I am especially indebted. To Mr Roberts and Mr McKenzie, foresters on the Cowdray and Didlington Estates respectively, I am also indebted for the interest they showed and the assistance they gave in the carrying out of some of the experiments. Finally I acknowledge my obligation to the Carnegie Trustees for the financial assistance necessary to carry out the work.