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RECOLONISATION OF CULTIVATED LAND ALLOWED
TO REVERT TO NATURAL CONDITIONS

BY WINIFRED E. BRENCHLEY AND HELEN ADAM

(With two Figures in the Text)

I. INTRODUCTION

The ecology of British grasslands had received up to the last few years comparatively little attention. The subject presents special difficulties owing to the fact that most of the grassland in Britain is subject to manuring of various kinds and that the vegetation is profoundly influenced by the treatment which the land receives, either by the use of artificial manures or by grazing, which involves natural manuring.

Tansley¹ has classified British grasslands into chalk, limestone, siliceous and neutral, and has given their relationships to other types of vegetation. A further classification by Smith and Crampton² separates grassland into stable and migratory. The chalk and limestone grasslands of Tansley appear to belong to the former, while neutral grassland falls into the latter, as it is regarded as a phase, often artificial, derived from some other type of vegetation. Smith and Crampton also divide British grasslands into (1) turf-type, which includes many of the stable chalk and limestone grasslands; (2) meadow type; (3) tussock type, which includes in part the siliceous grasslands; (4) stooled meadow type, which occurs chiefly as a transition between a marsh belt and typical meadow land; (5) lair-grassland and camp-follower type.

Grassland presents a very complex community, and without detailed observations at different periods of the year it is difficult to decide the ecological position of any given example. Many grasses will thrive in very varied habitats, and it is usually the relative amount of the grasses present which determines the nature of the pasture. Stapledon³ emphasizes this

¹ "Types of British Vegetation."

² "British grasslands," *Journ. Agric. Sci.*, 1914, pp. 1-17.

³ "Pasture problems," *Journ. Agric. Sci.*, 1914, pp. 499-510.

fact and defines a typical grassland as a "plant community consisting of fundamental and subsidiary species," and being such that "the contribution of each fundamental species to the total flora tends to be close to an optimum figure and does not increase above a certain maximum nor decrease below a certain minimum."

Various interesting ecological problems are presented by the recolonisation of cultivated arable land when it is allowed to revert to grassland under natural conditions. Little definite information is available, as comparatively few detailed accounts go back to the early days before ecology came to the front as a definite branch of botanical science. The Rothamsted experimental fields, however, present two good instances of land which was originally under cultivation, but which has since been abandoned. In each case the resulting "wilderness" has been preserved as far as possible from interference by stock or man. In one wilderness (Geescroft) a number of rabbits occur, but hardly any are present in the other case (Broadbalk wilderness). The history of both areas for many years is known.

II. BROADBALK WILDERNESS

The piece of land now called Broadbalk wilderness was, prior to 1882, known as the "Top Butts" of Broadbalk, and carried a wheat crop every year in the same way as the rest of the field. In 1882 the wheat on this area was not harvested, but was left alone and allowed to seed itself. Four years later a search was made for all the self-sown wheat plants, and the total resulting crop is shown in Fig. 26. While the wheat had been steadily disappearing, other species of plants had been making themselves at home. As time went on the vegetation gradually reverted to a woodland type, various shrubs and trees establishing themselves to the detriment of the lower-growing herbage which at first characterised the abandoned area. When this woodland tendency became evident, all the trees and shrubs were grubbed up from half the wilderness, the other half being left untouched. At intervals the process has been repeated, so that at the present time the Broadbalk wilderness consists of two distinct halves, one covered with a dense thicket of trees and shrubs, the other with a carpet of grasses and herbs, with a few stray shrubs that will soon be removed. The thicket is really an oak-hazel wood, with which are associated various species of *Rubus* and a certain amount of herbage of various kinds. In the early part of the year, in February, *Mercurialis perennis* is the only herb that is at all conspicuous, but traces of *Brachypodium sylvaticum* occur in places. The thickness of the wooded area checks the development of the undergrowth, but *Hedera helix* occurs throughout, and in the spring *Arum maculatum*, *Sanicula europaea*, and *Viola canina* were found in the interior. Towards the outskirts *Geum urbanum*, *Brachypodium sylvaticum*, *Mercurialis perennis*,

Heracleum sphondylium, *Arrhenatherum avenaceum*, *Stachys sylvatica* and *Urtica dioica* were noted. The edge of the wood next to Broadbalk also includes species of *Rosa*, and the grassy edge running alongside is noted for a dense growth of *Lathyrus pratensis*, in addition to various species that are common to the other part of the wilderness.

The grubbed half of the wilderness was kept under constant observation from July 1913 to the present time. During the season 1913-1914, 79 species of plants (herbs, shrubs and trees) came under notice, of which 40 % are included in the three orders Graminaceae, Leguminosae and Compositae, while nearly 60 % are in these three orders together with Umbelliferae and

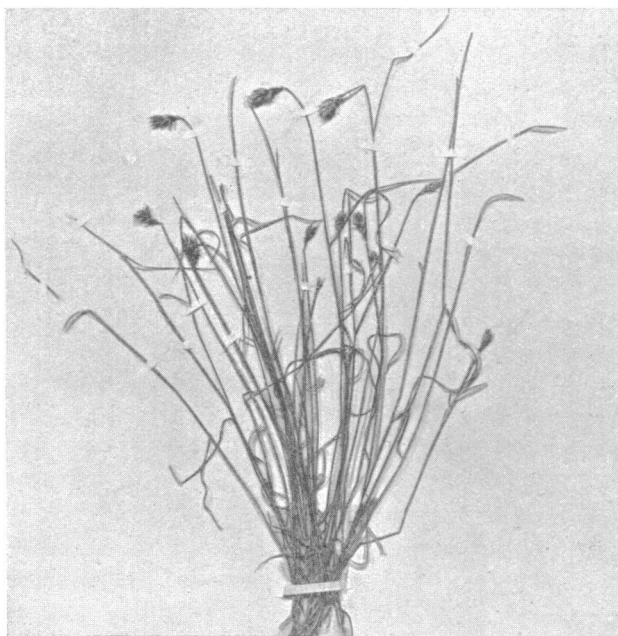


FIG. 26. Wheat collected Aug. 28, 1886, from portion of land left to seed itself and uncultivated since harvest of 1882 (Broadbalk field, Rothamsted, Experiments on Wheat).

Rosaceae. The herbage is fairly mixed, as a good number of the plants are well represented, but the dominant species during the early summer months is *Arrhenatherum avenaceum*, whereas later on in the summer *Centaurea nigra* is the most conspicuous and dominant plant. Nine species of leguminous plants occur, but no one is so abundant as to be much in evidence. A considerable portion of the area is now occupied by a very dense carpet of ivy, which has practically excluded every other species, though a few isolated plants of *Centaurea nigra* and *Senecio erucifolius* penetrate it here and there. A second zone surrounds the dense centre, in

which the ivy and other vegetation are apparently struggling for the mastery. Close inspection reveals the presence of more or less ivy over the whole of the area; this plant has obtained a very firm footing and the indications are

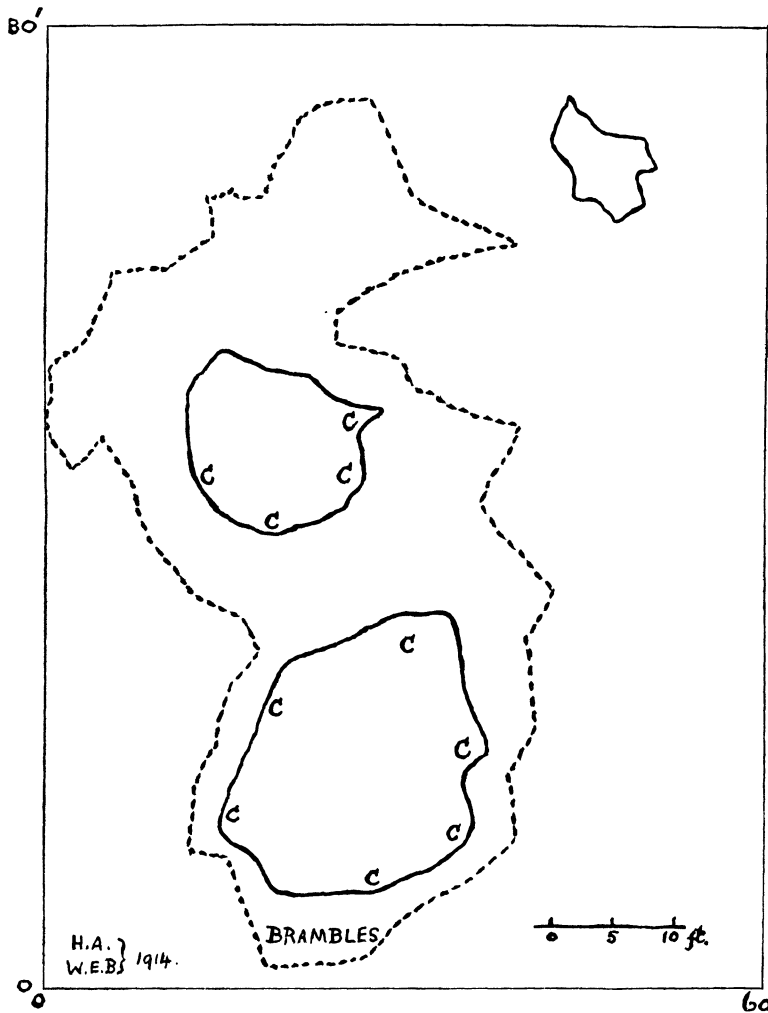


FIG. 27. Map of part of Broadbalk wilderness, showing the outlines of the main clumps of ivy (*Hedera helix*). The areas outlined with a continuous line are pure ivy, with a few isolated plants of *Centaurea nigra* and *Senecio erucifolius* round the outer edge (position indicated by C). The broken line delineates the second zone in which the ivy and other vegetation are in close competition.

that if it is not disturbed it will eventually dominate the whole situation to the detriment of other plants. A map of the main clump of ivy has been made, in order that the spread of the plant may be followed up in years to come (Fig. 27).

A comparison of the wilderness flora with the past and present weed flora of Broadbalk yields most interesting results. Of the 79 species occurring on the wilderness, 18 species are found as weeds among the wheat crop at the present time, a variety of types being represented, both of plants which are very common as weeds and those which are relatively scarce. These species are

<i>Agrostis alba</i>	<i>Heracleum sphondylium</i>	<i>Sonchus arvensis</i>
<i>Poa trivialis</i>	<i>Galium aparine</i>	<i>Tussilago farfara</i>
<i>Lathyrus pratensis</i>	<i>Valerianella dentata</i>	<i>Myosotis arvensis</i>
<i>Medicago lupulina</i>	<i>Scabiosa arvensis</i>	<i>Convolvulus arvensis</i>
<i>Vicia hirsuta</i>	<i>Cirsium arvense</i>	<i>Bartsia odontites</i>
„ <i>sativa</i>	<i>Matricaria inodora</i>	<i>Rumex crispus</i>

Besides these, nine species are still found on the wilderness which were present as weeds on Broadbalk in 1867, but which have now apparently disappeared from the cultivated area :

<i>Dactylis glomerata</i>	<i>Potentilla reptans</i>	<i>Leontodon hispidus</i>
<i>Trifolium pratense</i>	<i>Epilobium montanum</i>	<i>Sonchus asper</i>
„ <i>repens</i>	<i>Cirsium lanceolatum</i>	<i>Plantago lanceolata</i>

Several other plants which now occur on the wilderness are such as might be expected to come in as hedge plants or with the woodland type of flora.

Periodical examinations of the wilderness have been made since its establishment in 1882, and detailed notes of the flora are available for the years 1886, 1895, 1903, and 1913. It must, however, be remembered that each of the earlier lists was made upon one or two days only, so that probably some species were overlooked which would have been noticed had the investigation been carried out as systematically and regularly as during 1913 to 1915.

Nevertheless, a comparison of the data given in Table I indicates clearly the changes that have taken place in the vegetation, two main features being prominent.

(a) The dominant species varies from time to time. In 1886 dominance was shared by *Agrostis vulgaris* and *Medicago lupulina*, and this was still the case in 1895, though at this time *Lathyrus pratensis* was also abundant. By 1903 the two dominants had entirely lost their position, being replaced by *Dactylis glomerata*, which formed 35 % of the herbage in that year, *Lathyrus pratensis* coming a good second with 18 %. In 1913 both of these dominants had retired in their turn, their place being taken by *Arrhenatherum avenaceum* and *Centaurea nigra*. It is a noteworthy fact that *Arrhenatherum* is not mentioned at all till after 1895, so that it has reached its present position in less than eighteen years.

(b) The relative abundance of some species has undergone considerable

TABLE I

*Table of plants (herbs) occurring on Broadbalk wilderness, showing their relative prevalence in the years 1886, 1895, 1903 and 1913. Species marked * are not found on Geescroft wilderness. Dates on which the lists were made:—1886, July 27; 1895, uncertain; 1903, April 3 and July 3; 1913, several dates*

Contractions:—exc. a., exceedingly abundant; v. a., very abundant; a., abundant; mod., moderately abundant; pl., plentiful; f., frequent; o., occasional; sc., scarce; r., rare.

		1886	1895	1903	1913	
Graminaceae	<i>Agrostis vulgaris</i>	exc. a.	exc. a.	pl.	mod.	
	<i>Alopecurus agrestis</i>	pl.	pl.			
	„ <i>pratensis</i>		o.	sc.		
	<i>Arrhenatherum avenaceum</i>			mod.	exc. a.	
	<i>Avena flavescens</i>			sc.	o.	
	<i>Brachypodium sylvaticum</i>				o.	
	<i>Bromus asper</i>			sc.		
	<i>Cynosurus cristatus</i>	sc.	sc.			
	<i>Dactylis glomerata</i>	sc.	mod.	exc. a.	mod.	
	<i>Festuca ovina</i>			sc.	mod.	
	<i>Holcus lanatus</i>	o.	o.	sc.	o.	
	* <i>Lolium perenne</i>			mod.	o.	
	<i>Phleum pratense</i>	o.	o.	mod.	o.	
	<i>Poa pratensis</i>		o.	sc.		
	„ <i>trivialis</i>	mod.	mod.	mod.	sc.	
	Leguminosae	<i>Lathyrus pratensis</i>	f.	a.	v. a.	mod.
		<i>Lotus corniculatus</i>		r.		o.
* <i>Medicago lupulina</i>		v. a.	v. a.	mod.	mod.	
<i>Trifolium pratense</i>		r.	r.	sc.	o.	
„ <i>repens</i>		f.	f.	mod.	o.	
* <i>Vicia angustifolia</i>					sc.	
„ <i>hirsuta</i>		r.	o.	sc.	o.	
„ <i>sativa</i>					sc.	
„ <i>sepium</i>				sc.		
„ <i>tetrasperma</i>					sc.	
Ranunculaceae	<i>Ranunculus repens</i>	o.	o.	sc.		
Papaveraceae	<i>Papaver rhoeas</i>		r.			
Violaceae	<i>Viola canina</i>				o.	
	„ <i>tricolor</i>	sc.	sc.	sc.		
Caryophyllaceae	<i>Cerastium vulgatum</i>	f.	o.	sc.		
	<i>Lychnis flos-cuculi</i>			sc.		
	* <i>Stellaria graminea</i>			sc.	mod.	
	„ <i>holostea</i>			sc.	o.	
Rosaceae	„ <i>media</i>		o.			
	<i>Agrimonia eupatoria</i>			sc.	sc.	
	<i>Geum urbanum</i>			sc.	sc.	
Onagraceae	* <i>Potentilla reptans</i>			sc.	o.	
	* <i>Epilobium angustifolium</i>			sc.		
Umbelliferae	„ <i>montanum</i>				o.	
	<i>Aethusa cynapium</i>	f.	o.	sc.		
	<i>Anthriscus sylvestris</i>			sc.	o.	
	<i>Caucalis arvensis</i>	f.	o.			
	* <i>Chaerophyllum temulum</i>				o.	
	<i>Heracleum sphondylium</i>	o.	o.	mod.	mod.	
	* <i>Pimpinella major</i>				sc.	
Rubiaceae	„ <i>saxifraga</i>			sc.	o.	
	<i>Galium aparine</i>		sc.	sc.	o.	
	* „ <i>mollugo</i>				o.	
	„ <i>tricorne</i>	o.	sc.			
Valerianaceae	„ <i>verum</i>			sc.		
	<i>Valerianella dentata</i>				sc.	

TABLE I (continued)

		1886	1895	1903	1913
Dipsaceae	* <i>Scabiosa arvensis</i>	o.	o.	mod.	mod.
Compositae	<i>Achillea millefolium</i>			sc.	mod.
	<i>Anthemis cotula</i>	o.	sc.		
	<i>Bellis perennis</i>	r.	r.	sc.	sc.
	<i>Centaurea nigra</i>	r.	o.	mod.	a.
	<i>Chrysanthemum leucanthemum</i>				sc.
	<i>Cirsium arvensis</i>	f.	f.	sc.	mod.
	<i>lanceolatum</i>				o.
	<i>Gnaphalium uliginosum</i>	o.	sc.		
	<i>Hypochaeris radicata</i>			sc.	o.
	<i>Lapsana communis</i>	pl.	mod.	sc.	
	<i>Leontodon autumnalis</i>			sc.	
	<i>hispidus</i>				sc.
	<i>Matricaria inodora</i>				o.
	* <i>Senecio erucifolius</i>				o.
	<i>jacobaea</i>		o.	sc.	
	<i>Sonchus arvensis</i>	o.	mod.		o.
	<i>oleraceus</i>	sc	sc.		o.
	<i>Taraxacum vulgare</i>	f.	f.	sc.	
	<i>Tussilago farfara</i>	pl.	pl.	sc.	o.
Primulaceae	<i>Anagallis arvensis</i>	o.	sc.		
Boraginaceae	<i>Myosotis arvensis</i>	f.	o.		sc.
Convolvulaceae	<i>Convolvulus arvensis</i>	pl.	o.	sc.	o.
Scrophulariaceae	<i>Bartsia odontites</i>	f.	sc.	sc.	sc.
	<i>Veronica agrestis</i>	sc.	sc.		
	<i>chamaedrys</i>				o.
	<i>Lamium purpureum</i>			sc.	
Lamiaceae	* <i>Nepeta album</i>			sc.	
	<i>hederacea</i>			sc.	mod.
	<i>Prunella vulgaris</i>	sc.	sc.	sc.	o.
	* <i>Satureia calamintha</i>			sc.	o.
	* <i>vulgaris</i>				mod.
	<i>Stachys officinalis</i>				o.
	<i>sylvatica</i>	r.	r.	sc.	mod.
Plantaginaceae	<i>Plantago lanceolata</i>	r.	o.	mod.	mod.
	<i>media</i>			sc.	
Chenopodiaceae	<i>Atriplex patula</i>		sc.		
Polygonaceae	<i>Rumex acetosa</i>				o.
	<i>crispus</i>				o.
Euphorbiaceae	<i>Euphorbia exigua</i>	f.	o.		
	<i>Mercurialis perennis</i>			sc.	mod.
Urticaceae	<i>Urtica dioica</i>		sc.		mod.
Orchidaceae	<i>Orchis maculata</i>				sc.
Juncaceae	<i>Luzula campestris</i>			sc.	
Araceae	* <i>Arum maculatum</i>				sc.
Equisetaceae	<i>Equisetum arvense</i>	pl.	mod.		

fluctuation, and that of others has remained comparatively constant. *Alopecurus agrestis*, *Cerastium vulgatum*, *Caucalis arvensis*, *Euphorbia exigua* and *Equisetum arvense* were all originally present in some quantity, but entirely died out within twenty years; *Taraxacum vulgare* and *Lapsana communis* were also plentiful but have now disappeared. Several other species are apparently on the down-grade and look like being eliminated within the next few years; such are *Agrostis vulgaris*, *Medicago lupulina*, *Trifolium repens*, *Cirsium arvense*, *Tussilago farfara*, *Myosotis arvensis*, *Convolvulus arvensis* and *Bartsia odontites*. On the other hand a few species show very considerable increase—*Arrhenatherum avenaceum*, *Centaurea nigra*, *Heracleum*

sphondylium have made their appearance, with a number of other plants which are not yet present in any great abundance. The number of species of Gramineae and Leguminosae has not varied very considerably or constantly from the beginning, but the increase in miscellaneous species has been more marked, especially during the last ten years¹.

TABLE II

Species occurring on Broadbalk Wilderness (exclusive of shrubs and trees)

	1883	1895	1903	1913
Gramineae	7	9	12	10
Leguminosae	5	6	6	9
Miscellaneous	28	34	39	46
Total	40	49	57	65

The leguminous plants are apparently dying out gradually. In 1895 *Medicago lupulina* and *Lathyrus pratensis* were very abundant and were increasing rapidly in quantity. In 1903 the *Lathyrus* was so plentiful that it formed 18 % of the entire herbage, while *Medicago* accounted for another 3 %, the leguminous plants of all species forming 25 % of the herbage. At the present time the Leguminosae on the whole are relatively insignificant in amount.

A careful examination of the table of compared floras indicates that the vegetation of Broadbalk wilderness is in a state of flux. This condition will probably continue, but in view of the new factor introduced by the competition of the ivy it may be that the trend of events will somewhat alter, but it is impossible to forecast the direction that the change will follow.

III. GEESCROFT WILDERNESS

The soil on this area is a heavy loam, tending to be damp and cold, and difficult to cultivate satisfactorily. It was originally included in a larger experimental field, but while the greater part of this was thrown into the adjoining park and turned into grassland in 1885, the wilderness corner was simply abandoned. The piece of land was for several years under an experimental bean crop, being divided up into plots, each of which was manured in some specific manner. From 1847 to 1858 inclusive, beans were grown every year, and the land became very foul. From 1859 to 1881 beans were grown as often as possible and attempts were made to clean the land by fallowing and by applying fresh burnt lime, a wheat crop being taken in one year. In 1881 this experiment was discontinued, and after one or two

¹ It is possible, however, that a few plants of the incoming species may have occurred in 1903, but in such small numbers that no specimen was present in the sample which was separated out to give the species and percentage composition.

attempts to establish grass and clover the area was finally abandoned and allowed to recolonise itself, remaining untouched until the present time.

The general aspect of the wilderness at most seasons of the year is that of a desolate area densely covered with tufts of the very coarse grass *Aira caespitosa*, studded with a few small trees and shrubs of various kinds. Closer investigation shows that at one end the *Aira* dominates the situation almost to the exclusion of other plants, whereas at the other end many species have a firm footing in spite of the domination of the grass.

Altogether at the present time eighty-eight species (herbs, shrubs and trees) are to be recognised, of which nearly half are included in three orders (Graminaceae, Compositae, Leguminosae), while 60% of the species are accounted for by the three orders with the addition of Rosaceae and Umbelliferae.

The soil of Geescroft wilderness is very wet and boggy, so much so that in wet weather the water stands in pools on the surface in some parts. This fact is reflected in the flora, several damp-loving species being present and flourishing well. The chief of these is *Aira caespitosa*, which grows so luxuriantly that in the summer months it is very difficult to move about amongst it. A most unexpected plant is *Phalaris arundinacea*, of which at least two large clumps occur. The usual habitats for this species are on the banks of streams or in marshes, so that its presence in a field is an eloquent testimony to the wetness of the ground. It is difficult to understand how it was first introduced; the nearest rivers are $1\frac{1}{2}$ and $2\frac{1}{2}$ miles away, and in each case a hill intervenes between the river and the wilderness—unconscious human agency provides a possible explanation. *Rumex conglomeratus*, *Ophioglossum vulgatum*, *Cirsium palustre*, *Epilobium tetragonum* and several species of mosses and liverworts owe their presence to the same characteristic. The bryophytic flora is rich and plentiful in winter, an hour's search disclosing the following species¹:

Thuidium tamariscinum B. et S.	Hylocomium squarrosus B. et S.
Eurhynchium praelongum Schimp.	Plagiothecium sylvaticum B. et S.
Catharina undulata Web. et Mohr.	Brachythecium purum Dixon
Mnium cuspidatum Hedw.	Hypnum cuspidatum L.
„ cf. affine Bland (very young)	Lophocolea bidentata Dum.
Fissidens taxifolius Hedw.	

The mosses are not only to be found on the ground between the plants, but they also form banks round the base of the clumps of *Aira*, which afford them support.

In 1867 a survey was made of the weed flora of the bean plots in Geescroft, 46 species of plants being present. Practically all the species were those

¹ We are indebted to Mr C. H. Wright, of Kew, for the identification of these bryophytes.

normally occurring on arable land, comparing very closely with those found on the other experimental fields, both as regards the number and identity of the species. Of the original weed species 18 still survive. It is noticeable that the majority of these plants are such as are fairly general in their distribution, being as often found in waste places and hedges as on cultivated ground. On the other hand, those species which are more particularly associated with arable land have completely disappeared. An interesting survival is *Solanum dulcamara*, an unusual weed among a crop, which is still present in small amount, even though it was only very occasional nearly fifty years ago. Tansley¹ records this species from the alder willow association and from the aquatic vegetation of East Norfolk, so that it is evidently encouraged by the wetness of the soil.

The following is the complete list of survivals from 1867 to 1913 :

<i>Agrostis vulgaris</i>	<i>Geranium dissectum</i>	<i>Plantago lanceolata</i>
<i>Dactylis glomerata</i>	<i>Galium aparine</i>	<i>Solanum dulcamara</i>
<i>Poa trivialis</i>	<i>Cirsium arvense</i>	<i>Stachys sylvatica</i>
<i>Ranunculus repens</i>	<i>Taraxacum vulgare</i>	<i>Rumex crispus</i>
„ <i>acris</i>	<i>Myosotis arvensis</i>	<i>Urtica dioica</i>
<i>Cerastium vulgatum</i>	<i>Convolvulus arvensis</i>	<i>Equisetum arvense</i>

The following plants have now been crowded out :

<i>Lolium italicum</i>	<i>Leontodon autumnalis</i>	<i>Veronica arvensis</i>
<i>Poa annua</i>	<i>Matricaria inodora</i>	„ <i>tournefortii</i>
<i>Papaver rhoeas</i>	<i>Senecio vulgaris</i>	<i>Lamium purpureum</i>
<i>Capsella bursa-pastoris</i>	<i>Sonchus asper</i>	<i>Plantago major</i>
<i>Viola arvensis</i>	„ <i>oleraceus</i>	<i>Atriplex patula</i>
<i>Stellaria media</i>	<i>Anagallis arvensis</i>	<i>Polygonum aviculare</i>
<i>Aethusa cynapium</i>	<i>Linaria elatine</i>	„ <i>convolvulus</i>
<i>Anthemis arvensis</i>	„ <i>minor</i>	„ <i>persicaria</i>
<i>Filago germanica</i>	<i>Veronica agrestis</i>	<i>Euphorbia exigua</i>
<i>Lapsana communis</i>		

A comparison (Table III) between the surveys made in 1867, 1903 and 1913 shows that the native flora of Geescroft wilderness has undergone radical alteration. At the earliest date, 1867, the composition of the flora was greatly influenced by the previous cultivation of the land for arable crops, so that the plants were in the main typical “weeds of arable land.” When the land was allowed to revert to natural conditions *Aira caespitosa* gained a foothold, and found such specially advantageous conditions that in 1903 it dominated the situation, forming 86 % of the herbage. This excessive competition reduced the total number of species to 25, of which no less than ten were grasses, forming altogether 95 % of the herbage; evidently the broad leaved plants found life almost impossible under the circumstances. By 1913 a further change had occurred. The two ends of the wilderness

¹ “Types of British Vegetation,” p. 76.

TABLE III

*Table of plants (herbs) occurring on Geescroft wilderness, showing their relative prevalence in the years 1867, 1903 and 1913. Species marked * are not found on Broadbalk wilderness. Dates on which the lists were made:—1867, Sept. 18; 1903, July 3; 1913, several dates*

Contractions:—pr., present; others as in Table I.

	1867	1903	1913 ¹	
Graminaceae	Agrostis vulgaris	pr.	o.	
	*Aira caespitosa		exc. a.	
	Alopecurus pratensis		mod.	
	Anthoxanthum odoratum		f.	
	Arrhenatherum avenaceum		mod.	
	Avena flavescens		o.	
	Brachypodium sylvaticum		o.	
	*Briza media		o.	
	*Cynosurus cristatus		mod.	
	Dactylis glomerata	pr.	mod.	
	Festuca elatior		sc.	
	" ovina		sc.	
	* " pratensis		o.	
	* " rubra		a.	
	Holcus lanatus		r.	
	Lolium italicum	pr.		
	" perenne		r.	
	*Phalaris arundinacea			in patches
	Phleum pratense		sc.	f.
	Poa annua	pr.		
" pratensis		sc.	sc.	
" trivialis	pr.		f.	
Leguminosae	Lathyrus pratensis		o.	
	Lotus corniculatus		o.	
	Trifolium minus		o.	
	" pratense		o.	
	" repens		sc.	
	Vicia sativa		o.	
	" sepium		sc.	
	" hirsuta		o.	
" tetrasperma		sc.		
Ranunculaceae	Ranunculus acris	pr.	mod.	
	" repens	pr.	sc.	
Papaveraceae	Papaver rhoeas	pr.		
Cruciferae	Capsella bursa-pastoris	pr.		
Violaceae	Viola arvensis	pr.		
Caryophyllaceae	Cerastium vulgatum	pr.	sc.	
	Stellaria holostea		o.	
" media	pr.			
Hypericaceae	Hypericum hirsutum		o.	
Malvaceae	*Malva moschata	sc.	(?)	
Geraniaceae	Geranium dissectum	pr.	sc.	
Rosaceae	Agrimonia eupatoria		o.	
	Geum urbanum		o.	
Onagraceae	Epilobium montanum		o.	
	" tetragonum		sc.	
Umbelliferae	Aethusa cynapium	pr.		
	Anthriscus sylvestris		sc.	
	Caucalis anthriscus		sc.	
	Conopodium denudatum		sc.	
	Heracleum sphondylium		mod.	
	Pimpinella saxifraga		o.	
			sc.	

¹ The nomenclature for 1913 in this table was adapted to correspond with that used in 1903 by other observers—hence the difference in this respect from Table V.

TABLE III (*continued*)

		1867	1903	1913 ¹	
Rubiaceae	Galium aparine	pr		o.	
Compositae	Achillea millefolium		r.	o.	
	Anthemis arvensis	pr.			
	Bellis perennis			o.	
	Centaurea nigra			f.	
	" scabiosa			sc.	
	Chrysanthemum leucanthemum		r.	o.	
	Cirsium arvense	pr.	sc.	o.	
	" lanceolatum			o.	
	* " palustre		sc.	o.	
	Crepis virens			sc.	
	Filago germanica	pr.			
	Hypochaeris radicata			sc.	
	Lapsana communis	pr.			
	Leontodon autumnalis	pr.			
	Matricaria inodora	pr.			
	Senecio vulgaris	pr.			
	" jacobaea			o.	
	Sonchus arvensis			sc.	
	" asper	pr.			
	" oleraceus	pr.			
Taraxacum vulgare	pr.	sc.	sc.		
Primulaceae	Anagallis arvensis	pr.			
Boraginaceae	Myosotis arvensis	pr.		mod	
Convolvulaceae	Convolvulus arvensis	pr.		o	
Solanaceae	*Solanum elaeagnifolium	pr.		sc.	
Scrophulariaceae	Linaria elatine	pr.			
	" minor	pr.			
	Veronica agrestis	pr.			
	" arvensis	pr.			
	" tournefortii	pr.			
	" chamaedrys			mod.	
Lamiaceae	Lamium purpureum	pr.			
	Nepeta hederacea			o.	
	Prunella vulgaris		sc.	o.	
Plantaginaceae	Stachys sylvatica			o.	
	Plantago lanceolata	pr.	sc.	f.	
Chenopodiaceae	" major	pr.			
	Atriplex patula	pr.			
Polygonaceae	Polygonum aviculare	pr.			
	" convolvulus	pr.			
	" persecaria	pr.			
	Rumex acetosa	pr.		o.	
	" conglomeratus			sc.	
	" crispus	pr.		sc.	
	" obtusifolius		o		
	* " sanguineus			sc.	
	Euphorbiaceae	Euphorbia exigua	pr		
	Mercurialis perennis			sc.	
Urticaceae	Urtica dioica	pr.		sc.	
Juncaceae	*Luzula campestris		r.	o.	
	" sylvatica			sc.	
Cyperaceae	*Carex sylvatica		sc.	o.	
Equisetaceae	*Equisetum arvense	pr.		sc.	
Filicineae	*Aspidium filix-mas			sc.	
	*Ophioglossum vulgatum			sc.	
	*Pteris aquilina			sc.	

¹ The nomenclature for 1913 in this table was adapted to correspond with that used in 1903 by other observers—hence the difference in this respect from Table V.

are now distinct in character. At the south-west end the *Aira* is still so thick that very few other plants can grow at all, and it is possible that that part of Geescroft is fairly representative of the conditions obtaining ten years ago. At the north-east end the *Aira* has failed to maintain such absolute supremacy, so that whereas it is still the dominant plant in the summer months, yet in the autumn *Centaurea nigra* (which did not occur at all in 1903) almost shares its dominance, and many other species have obtained a more or less secure footing. As shown in Table IV, the number of grasses has now increased to 18, but the rise in miscellaneous species is far more marked, from 13 in 1903 to 50 in 1913.

TABLE IV

Species occurring on Geescroft Wilderness (exclusive of shrubs and trees)

	1867	1903	1913
Graminaceae	5	10	18
Leguminosae	0	2	9
Miscellaneous	41	13	50
Total	46	25 ¹	77

For many years it was a Rothamsted tradition that no leguminous plants occurred in Geescroft wilderness, and this was probably true till shortly before 1903. The analysis of a sample taken about July 3 in that year showed the presence of 0.4 %, made up of *Trifolium repens* and *Vicia sepium*. At the present time, at the one end of the wilderness, at least ten species of the order are now established, some of them in appreciable quantity. *Trifolium pratense*, *T. repens* and *Lotus corniculatus* occur in patches, while *Lathyrus pratensis*, *Ulex europaeus*, *Trifolium minus* and several species of *Vicia* are also present in greater or less amount. The south-west end at which the *Aira* is thickest is still to a large extent free from the incursion of this order, possibly on account of the extra wetness of the ground which excludes so many plants. The one exception to this is *Lathyrus pratensis*, which is largely found within the tufts of *Aira*, where it appears to flourish very luxuriantly. *Lathyrus* appears to be very tolerant in regard to the water content of the soil; it is noted by Stapledon² to be a good drought resister and to be able to increase during drought. An example of this was noted in Broadbalk where tufts of *Lathyrus* had invaded patches of young shoots of *Hedera helix* which had apparently been killed by heat.

¹ This figure is probably very low, as it was obtained from analytical figures only and not from field observations.

² "Drought resistance," *Journ. Agric. Sci.*, 1913, pp. 129-151

The following trees and shrubs were present in 1914:

<i>Ulex europaeus</i>	<i>Sambucus nigra</i>	<i>Rubus</i> sp.
<i>Corylus avellana</i>	<i>Ulmus sativa</i>	<i>Prunus</i> sp.
<i>Quercus robur</i>	<i>Fraxinus elatior</i>	<i>Rosa</i> , various spp.
<i>Acer campestre</i>	<i>Crataegus oxyacantha</i>	

IV. SEQUENCE OF EVENTS THROUGHOUT THE YEAR.

Broadbalk Wilderness. As described above the wilderness consists of two areas, meadow and thicket. The meadow belongs to Tansley's neutral grassland and to the "meadow" type of Smith and Crampton. The species and distribution have been already given. In January the wilderness presents a very different appearance from that of typical meadow land, as the dried stalks and flower heads which would be removed by cutting and grazing are still standing. *Centaurea nigra* and *Arrhenatherum avenaceum* are undoubtedly the dominant plants, and the leaves of many perennials can still be recognised. In spring (April and May) the wilderness has the appearance of a typical meadow; *Arrhenatherum*, *Dactylis* and *Agrostis* are very abundant, and, using the nomenclature of Stapledon (5) these grasses would represent the "fundamental" species. With regard to plants other than grasses *Mercurialis*, *Plantago lanceolata*, *Stellaria holostea*, *Veronica chamaedrys*, *Bellis perennis* and *Primula veris* are at this time in flower.

In June the true meadow types of plants are fully in flower, e.g. *Arrhenatherum*, *Dactylis*, *Lolium* and *Agrostis*. The leguminous plants begin to be prominent; *Medicago lupulina* and *Lathyrus pratensis* are plentiful, and *Lotus corniculatus* and *Trifolium repens* occur in less quantity. These plants seem to reach their maximum development in July, so that the date at which an analysis of any grassland is carried out is of great importance in estimating results. In autumn (September and October) the grasses have finished flowering, except a little *Arrhenatherum* and *Agrostis* are still in flower. *Satureia clinopodium*, *Centaurea nigra*, *Cirsium arvense*, *Pimpinella saxifraga*, *Stachys betonica* and *Senecio jacobaea* are plentiful. This autumn phase is unusual in meadows as it is prevented by the haying. The most abundant plants appear to be more characteristic of permanent grassland (e.g. chalk grassland of Tansley) than of the true meadow type. Possibly these late flowering plants are killed out on cultivated pastures.

The thicket is of the nature of the "damp oak wood" or "oak-hazel wood" of Tansley¹, and the relationship between this type of wood and neutral grassland is clearly demonstrated.

Geescroft Wilderness. The sequence of events is very similar in this case. The early part of the year is marked by the dried stems of the grasses; about May, *Festuca ovina* and *F. rubra*, *Anthoxanthum*, *Veronica*

¹ "Types of British Vegetation," p. 76.

chamaedrys, *Bellis perennis* and *Nepeta hederacea* are in flower. In June the grasses are in full flower and the leguminous plants are prominent, e.g. *Lotus corniculatus*, *Lathyrus pratensis*, *Vicia hirsuta* and some *Trifolium pratense*; *Chrysanthemum*, *Heracleum*, *Prunella*, *Agrimonia* and *Geum* are abundant; *Chrysanthemum* seems to be increasing in quantity very rapidly. The autumnal phase is marked by an abundance of *Centaurea*, *Prunella*, *Senecio jacobaea* and *Stachys sylvatica*.

This wilderness, like Broadbalk, belongs to the neutral grassland but should probably be placed in the "stooled meadow type" of Smith and Crampton, as the great predominance of the tufted *Aira caespitosa* removes it from the typical meadow type.

V. COMPARISON BETWEEN BROADBALK AND GEESCROFT WILDERNESSES

Floristic Differences. At the present time the great majority of species are common to both wildernesses, but certain species are peculiar to each—these are starred in the lists of species (Tables I and III). One noticeable point is the abundance of *Holcus lanatus* and *Anthoxanthum odoratum* on Geescroft and their scarcity on Broadbalk.

The plants peculiar to Geescroft are those characteristic of damp land. Some of them, e.g. *Phalaris* and *Aira*, are characteristic of Marsh or Fen associations.

The case of *Holcus*, *Anthoxanthum* and *Cynosurus* is probably different. These grasses are found in very varied situations, especially on poor land. Possibly they are unable to compete successfully with other plants in favourable situations, but are very persistent, so that when conditions are unfavourable to many other species they are freed from competition and can grow successfully. They are all three noted by Stapledon¹ as bad drought resisters, and as flourishing well on damp land. This is especially the case with *Holcus*, which seems very sensitive to water content and is frequently very abundant on carr and fen land. This may be due either to an absence of competition or to a marked preference for a high amount of available water in the soil. The presence of these grasses in fairly large quantities in Geescroft is probably due to a combination of these factors.

The plants peculiar to Broadbalk are those characteristic of dry meadows. *Hedera helix* has probably spread from the thicket. *Brachypodium sylvaticum*, which is fairly abundant in the meadow, is also a woodland grass. The most abundant grasses, *Arrhenatherum* and *Dactylis*, are recorded as abundant in the undergrowth of the "damp oak wood" types, as are many of the other plants in the meadow portion, e.g. *Veronica chamaedrys*, *Nepeta hederacea*, *Stachys betonica*.

¹ "Drought resistance," *Journ. Agric. Sci.*, 1913, pp. 129-151.

General comparison. The wildernesses provide instances of two pieces of land of very similar history which have been left to colonise themselves for the same period of time, since 1882. Both areas had been under arable cultivation for some length of time, though the crops differed. The nature of the soils was much the same, being a heavy loam inclined to be sticky in wet weather. Geescroft soil contains only 0·005 % calcium carbonate and is slightly acid, whereas Broadbalk soil contains about 3 % calcium carbonate and is alkaline in reaction. This causes considerable difference in water content, and much of the later differentiation of vegetation must be attributed to the variation in the relative wetness of the soil. This relationship has been variously discussed in terms of the so-called "Coefficient of Humidity" of the soil¹, and the "Relative Saturation" of the soil², it being claimed that for each plant, as well as for each association, there is a maximum, optimum and minimum value.

During the summer months from June to September the water content of the wildernesses is very similar, varying from 12–17 %. From October to May, Broadbalk is never waterlogged, the water content fluctuating between 18 % and 21 %, whereas Geescroft is waterlogged nearly all the time, the water content ranging from 20 % to 24 % at least. Broadbalk soil, though heavy, is comparatively well drained, and so the wilderness does not tend to get excessively wet even in bad weather. Geescroft soil drains very badly, probably on account of the deficiency of calcium carbonate, with the result that the land is always more or less waterlogged, keeping its boggy character even in dry weather. This excessive water supply has profoundly influenced the character of the vegetation. Comparatively few plants are able to withstand successfully a perpetual condition of waterlogging at the roots, with its attendant factor of deficient aeration, so that many species which might otherwise have flourished were automatically ruled out at the outset. This in itself greatly reduced competition, and therefore when the damp-loving *Aira caespitosa* made its appearance everything favoured its extensive spread, as it found the soil conditions that suited it together with a lack of competition from other species. It is evident that at the present time the north-east end of Geescroft is becoming somewhat less wet and boggy than heretofore; probably the level of this end is slightly higher than that of the south-west, as the adjoining road is very much on the slope. This fact of gradual drying is marked by the ingress of a considerable number of other species which are gradually wresting from *Aira caespitosa* its marked supremacy (Table V). A certain number of trees and shrubs are present on the area, but these do not show any tendency to increase to

¹ Crump, W. B., "The coefficient of humidity," *New Phyt.*, 1913.

² Brown, George, "Note on relative saturation," this JOURNAL, 3, 1915.

TABLE V

List of plants (herbs) occurring on the North-eastern and South-western halves of Geescroft wilderness, 1914-1915

Contractions: a., abundant; d., dominant; o., occasional; r., scarce or rare.

N.E. half		S.W. half	
Aira caespitosa	a.	Aira caespitosa	d.
Agrostis vulgaris	a.		
Arrhenatherum avenaceum	a.		
Alopecurus pratensis	o.	Alopecurus pratensis	o.
Anthoxanthum odoratum	a.		
Avena flavescens	o.		
Brachypodium sylvaticum	r.		
Briza media	o.		
Cynosurus cristatus	o.		
Dactylis glomerata	a.	Dactylis glomerata	a.
Festuca ovina, F. rubra	a.	Festuca ovina	o.
Holcus lanatus	o.	Holcus lanatus	a.
Phleum pratense	o.		
Poa nemoralis	o.	Poa nemoralis	o.
		„ pratensis	o.
Poa trivialis	o.		
		Phalaris arundinacea	o.
Lathyrus pratensis	a.	Lathyrus pratensis	a.
Lotus corniculatus	a.		
Trifolium pratense	o.		
„ repens	o.		
„ minus	r.		
Vicia hirsuta	o.	Vicia hirsuta	o.
„ sativa	o.		
„ tetrasperma	o.	Vicia tetrasperma	o.
Ranunculus repens	o.		
„ acris	o.		
Cardamine pratensis	r.		
Cerastium vulgatum	o.		
Stellaria holostea	o.		
Hypericum hirsutum	o.	Hypericum hirsutum	o.
		„ perforatum	r.
Malva moschata	r.		
Agrimonia eupatoria	o.	Agrimonia eupatoria	o.
Geum urbanum	o.	Geum urbanum	o.
Epilobium montanum	r.	Epilobium montanum	o.
		„ tetragonum	r.
Caucalis anthriscus	r.		
Heracleum sphondylium	o.	Heracleum sphondylium	a.
Pimpinella saxifraga	r.		
Achillea millefolium	a.		
Bellis perennis	o.		
Centaurea nigra	a.	Centaurea nigra	a.
Chrysanthemum leucanthemum	a.		
Cirsium arvense	o.		
„ lanceolatum	o.	Cirsium lanceolatum	o.
		„ palustre	o.
Hypochaeris radicata	o.		
Leontodon autumnalis	r.		
Taraxacum vulgare	r.		
Senecio jacobaea	o.		
Myosotis arvensis	o.	Myosotis arvensis	a.
Convolvulus arvensis	o.		
Veronica chamaedrys	a.	Veronica chamaedrys	o.
Ajuga reptans	o.	Ajuga reptans	o.
Nepeta hederacea	o.	Nepeta hederacea	o.
Prunella vulgaris	a.		
Stachys sylvatica	r.	Stachys sylvatica	o.
Plantago lanceolata	a.	Plantago lanceolata	o.

TABLE V (*continued*)

N.E. half		S.W. half	
Rumex acetosa	o.	Rumex acetosa	a
„ crispus	r.		
„ conglomeratus	r.	Rumex sanguineus	a
Mercurialis perennis	r.		
Urtica dioica	r.	Urtica dioica	o.
Luzula campestris	r.	Luzula campestris	o.
		Carex sylvatica	r.
Pteris aquilina	r.		
Aspidium filix-mas	r.	Ophioglossum vulgatum	r.
		Equisetum arvense	r.

any extent, so that while considerable changes may be expected to occur in the ground vegetation, it is improbable that any reversion to woodland will occur, unless radical changes in the drainage should take place. At present the vegetation is grassland studded with a few trees and shrubs, but it is probable that the water content is nearly at its limiting value for the meadow type, so that if this increases a transformation to the marsh type may be expected. On Broadbalk wilderness the soil does not get waterlogged to any appreciable extent, and therefore the damp-loving species so characteristic of Geescroft are conspicuous by their absence. One or two species are always strongly dominant, but this dominance is less exclusive than in Geescroft and also the master species are not always the same, but vary from time to time, such different plants as *Agrostis*, *Medicago*, *Dactylis*, *Lathyrus*, *Arrhenatherum* and *Centaurea* having all had their turn at supremacy, either singly or together. The vegetation on the grubbed half is always struggling to revert to woodland, so that the herbage is under slightly artificial conditions induced by the removal of the shrubs and trees. The true comparison with Geescroft is with the thicket on Broadbalk, rather than with the grubbed half with its dense ground vegetation.

Though the essential difference in the recolonisation of the wildernesses has been attributed chiefly to the waterlogged condition of Geescroft soil, it must not be forgotten that this simple ecological factor brings other differences in its train, and that a waterlogged soil does not only supply an excess of moisture, but is associated with deficient aeration, lowering of soil temperature and other possible factors which all act and react on one another and play their part in determining the flora borne by the soil. As the two areas considered are so similar in such respects as the nature and treatment of the soil, climatic conditions, etc., they provide an excellent illustration of the far-reaching effects induced by one initial ecological factor unfavourable to the majority of species.

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