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Autor: Tansley, A.G.
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IX.

The Vegetation of the Southern English Chalk (Obere Kreide-Formation)

By A. G. TANSLEY, Cambridge

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Introduction

The Chalk (Upper Cretaceous) Formation of southern and eastern England is a northward and westward extension of the identical or similar formation of north-eastern France. This rock forms characteristic rolling hills of smooth contour and no great height, never reaching 1,000 feet (300 meters) above sea-level, though in several places approaching that altitude. The summits of the chalk hills are rounded and the upper slopes of gentle inclination, though the escarpments and valley sides may reach an angle of as much as 38°—40° to the horizon.

The limestone of which the Chalk formation is composed is notably soft and very pure, containing over 90 per cent and sometimes over 98 p. c. of calcium carbonate. On the narrower ridges and some of the steeper slopes, where the overlying soil is very shallow (frequently only 5 to 10 cm. in depth), the vegetation is largely controlled by the immediate proximity of the limestone rock. This control is partly exercised through the relative dryness, partly through the alkalinity of the surface soil, and partly through the meagre depth available for the root systems of plants. These factors are operative most markedly during the earlier stages of succession: when vegetation has

occupied the ground for a considerable time the surface of the underlying rock becomes fissured, broken and dissolved, leaving the insoluble or only slightly soluble rock constituents as a mineral soil basis, humus is accumulated and the depth of soil available for roots is thus progressively increased. This process is however checked or at least slowed down when the grass and herb community, which is a characteristic early phase of the succession, is heavily and continuously pastured, so that the soil remains shallow, and the effect of the conditions described above is maintained.

On the grasslands of the flat chalk summits and plateaux and of very gentle slopes, such as the dipslopes, where there is little or no "run-off" of rainwater, and the whole precipitation which is not evaporated sinks into the ground, the surface layers of soil are progressively leached, with the result that they become very poor in calcium carbonate (eventually containing only about 1 per cent or less). This process, together with the accumulation of humus in the surface layer, renders the surface soil distinctly acid in reaction, and leads to its colonisation by species alien to the vegetation of the chalk soils proper, which always have a distinctly alkaline reaction owing to the presence of a considerable percentage of calcium carbonate. Thus there comes into existence on such grasslands a mixed community of plants, containing species indifferent (within limits) to soil reaction, as well as species found only or mainly on calcareous or other alkaline soils — these two categories forming the original vegetation — and finally species characteristic of somewhat acid soils (shallow-rooting or at least germinating only in the surface layer poor in calcium). Since *Calluna vulgaris* is conspicuous among those of the third class, such mixed communities of the chalk have been called "chalk-heats". They must be carefully distinguished from the genuine "heaths" developed on post-Tertiary non-calcareous deposits overlying the chalk, which in some regions cover wide areas of the extensive plateaux and dipslopes. These do not belong to the chalk succession at all. A "chalk-heath" always possesses chalk plants as well as the "heath" species.

The process of leaching and of solution and disintegration of the underlying rock of course also takes place on fairly steep slopes, whether occupied by grassland, scrub or woodland, the latter process especially where the vegetation is of luxuriant growth obstructing the surface wash of rain water down the slope; but in such situations leaching is at a minimum and is not carried far enough to bring in species inhabiting soils of acid reaction, though grassland slopes of this nature are freely colonised by plants indifferent to soil reaction (those which can inhabit soils on either side of the neutral point), and they indeed often dominate the community.

Types of Chalk vegetation

A large area of the English chalk is under the plough, and produces excellent and varied crops. The portions which are still occupied by semi-natural vegetation owe the preservation of this mainly to two factors: first the steep slope of many of the escarpments and valley sides which renders agriculture difficult or impossible, and secondly the fame of the chalk grasslands as sheep pasture, and to some extent their use also (increasingly of recent years) as cattle pasture. Over much of the chalk area the woodlands are confined to the steep slopes, and where they extend over the plateaux and gentle slopes this is due to their preservation on the large estates of landowners, and in one case (on the Chiltern Hills in Buckinghamshire) to their systematic exploitation for the chair-making industry. The rest of the slopes too steep for agriculture are occupied by pasture, which, more or less interspersed with arable land, often extends over wide areas of gentle slope and plateau also. In general, apart from the areas where the woods are preserved for game and other amenities of wealthy land owners, and where the grassland is devoted to the preservation of rabbits for shooting, there is a certain balance between arable and pasture land maintained by the farmers in accordance with their system of farming.

From the point of view of the plant-sociologist the plant communities of the chalk may be arranged as follows.

1. Vegetation of bare chalk rock.
2. Vegetation of chalk talus (pioneer stage).
3. Chalk grassland, etc.
   a) Dominated by *Festuca ovina.*
   b) Dominated by tall grasses.
   c) Chalk heath.
4. Chalk scrub (bushland).
5. Chalk woodland.
   a) Ashwood ("ash consocies").
   b) Yewwood *(Taxus* society).
   c) Beechwood ("Beech consociation").
   d) Herbland resulting from the felling of woodland.

1. Vegetation of bare chalk rock

This has been but little studied. So far as information is available the flora of the bare surface of living chalk and of detached blocks is a poor one. The principal colonists observed are an undetermined species of the green alga *Chroolepus*, the lichen *Verrucaria calciseda* with embedded thallus and perithecia occupying minute pits in the surface of the chalk, and especially the moss *Seligeria calcarea* with embedded protonema which is often abundant on the sides of quarries and on loose chalk blocks. Doubtless other species occur, as a number of species of lichen and several mosses are recorded as occurring on the surface of the older limestones, but so far as the chalk is concerned there appear to be practically no systematic English observations published. However this may be, the occurrence of such colonists on bare chalk appears to play little part in the dynamic processes leading to succession of the vegetation.

A certain number of flowering plants are able to settle among the finely divided chalk particles accumulated in the cracks of the joints and bedding planes exposed on the sides of chalk quarries presenting slopes at various angles. Ten species were observed on the sides of one such quarry: —

Crepis capillaris	Linaria minor
Dactylis glomerata	Senecio vulgaris
Epilobium montanum	Taraxacum erythrospermum
Koeleria gracilis	T. officinale
Leontodon hispidum	Thymus serpyllum

Doubtless observations in other localities would yield different lists of species. These plants are not of course acting as "lithophytes", but as "chomophytes". Like the lithophytes themselves they have little to do with the general dynamic processes of succession. Systematic observations on the maritime chalk cliffs, which, apart from quarrying, are the only places where bare chalk is met with, would no doubt yield interesting results.

2. Vegetation of chalk talus (pioneer stage)

As a direct result of quarrying operations, and also of the falling and disintegration of lumps of chalk detached from the sides of quarries through rainwater penetrating along the joints and bedding planes, and (accelerated by freezing) thus isolating blocks of the rock, a talus of chalk fragments of various sizes, showing a maximum slope of about 40°, frequently accumulates at the foot of vertical quarry faces. The blocks of the talus are rapidly reduced in size by solution and disintegration, and a substratum easily colonised by flowering plants is thus produced. This quarry talus consists of angular pieces of chalk of very various size. The largest may be 3 or 4 dm. across, but the majority do not exceed 5 to 10 cm. in diameter, and these are mixed with tiny fragments, among which the roots of flowering plants can penetrate, and establish themselves. In other places a talus or "spoil bank" [1] may consist of the finer fragments and particles alone. A fairly clear distinction can be drawn between the predominant colonists of the rather coarse talus (fragments above 2 cm. in diameter) and those of the fine "spoil" consisting of chalk fragments less than 1 cm. in diameter. In one locality, for instance, *Senecio jacobaea* and *Echium vulgare* were the leading species on the former, *Festuca ovina* and *Tussilago farfara* on the latter.

[1] Heap of quarried material discarded by the quarrymen.

The following occurred on the south face of a typical fine spoil heap (War Down, Hampshire) the surface of which was still about 60 p. c. bare [1].

	Abundance		Abundance
Agrostis alba	f-a = 3–4	Hieracium pilosella	f = 3
Anthoxanthum odoratum	f = 3	Leontodon hispidum	o = 2
Asperula cynanchica	o = 2	Linum catharticum	f = 3
Avena pratensis	o = 2	Lotus corniculatus	a = 4
Carex flacca	la = (4)	Sonchus oleraceus	o = 2
Carlina vulgaris	f = 3	Taraxacum erythrospermum	o = 2
Cirsium acaule	lf = (3)	Taraxacum officinale	f = 3
Cirsium palustre	o = 2	Thymus serpyllum	f = 3
Clematis vitalba	r = 1	Tussilago farfara	ld = (5)
Dactylis glomerata	o = 2	Mosses	
Echium vulgare	lf = (3)	Camptothecium lutescens	f = 3
Euphrasia nemorosa	o = 2	Hypnum chrysophyllum	o = 2
Festuca ovina	va = 5	Hypnum molluscum	f = 3
Gentiana amarella	la = (4)	Neckera complanata	o = 2

The great majority of the species here are "constant" or common "accessory" species of chalk grassland, of which this spoil bank community is clearly an early stage. Only *Clematis*, *Echium* and *Sonchus* are "chance" species occurring sporadically in that community, while *Tussilago* is a pioneer which will disappear when the community is mature. The four species of moss, on the other hand, include only one, *Camptothecium lutescens*, which is a "constant" (occurring in more than half the samples of chalk grassland taken over a wide range of country), and this is confined to those with a highly calcareous surface soil. The other three are pioneers.

No good purpose would be served by giving lists of species occurring on the floors of chalk quarries, etc., where the immigration of species is various according to the proximity of different types of vegetation, e. g. woodland, grassland and arable land, and where immigration is probably greatly aided by traffic to the quarry. One such list of no less than 60 species of flowering plants from the bare floor of a quarry in Hamp-

[1] Symbols: va = very abundant, a = abundant, f = frequent, o = occasional, r = rare, l = local, d = dominant, ld = locally dominant. In the second column the equivalents of the first five symbols are given as the numbers 5 to 1.

shire about a kilometer from the spoil bank listed above, may be mentioned. The whole of the phanerogamic plants probably occupied less than 1 p. c. of the area, while about 10 p. c. was occupied by eight species of moss. Of the 60 flowering plants, 27 might be considered grassland species, 7 woodland or wood-edge species, while most of the remaining 26 were weeds of arable or waste land. These proportions correspond roughly with the areas and proximities of adjacent types of vegetation.

3. Chalk grassland

Leaving arable land out of account, this covers by far the greatest area of the English chalk. It is almost universally pastured, and thus must be regarded as a community artificially maintained by man's flocks and herds. There can be no doubt that the vast bulk if not all of it would pass into woodland if pasturage were withdrawn. It is a very well marked community, a large number of the species showing a high degree of constancy, and it also possesses several species with a high degree of exclusiveness (Gesellschaftstreue), at least within the limits of Great Britain.

a) Dominated by *Festuca ovina.* This is the typical sheep pasture which occupies much of the southern English chalk, especially the Sussex Downs, and also other areas to the west which have not yet been thoroughly studied. The same community occurs in Cambridgeshire, and probably in all places on the chalk where sheep pasturage has been long established. Moderate rabbit attack accentuates the characters of this community. Herbage 2 to 10 cm. high. pH of surface 5 cm. soil mostly 7.2 to 7.6.

b) Dominated by taller grasses, especially *Avena pratensis* or *Bromus erectus.* This may occur where sheep pasturage is less severe and continuous, and on steep north slopes where desiccation is less, so that the taller grasses have better opportunities for growth. Several of them occur in a) but much less abundantly. The abundance of taller grasses reduces the abundance and often the number of the lower growing species present in a). *Festuca ovina* rarely disappears alto-

gether though its dominance is destroyed and its frequency reduced. Herbage 15—30 cm. high. pH of surface 5 cm. of soil mostly 7.2—7.6.

c) C h a l k h e a t h. This occurs, as explained in the Introduction, on plateaux and gentle slopes where the surface layers of soil have been extensively leached of calcium carbonate, so that the surface soil reaction is more or less acid (surface 5 cm. pH 6 to 7) and a number of species alien to the typical chalk soil have entered the community, without however completely replacing the chalk grassland species.

In the following table [1] a) and b) are taken together and treated as one community though their physiognomy is distinctly different, and the "abundance" and "constancy" coefficients of various species would be different if they were treated separately. The region covered by the table is representative and fairly extensive. The individual areas from which the sample lists (Aufnahmen) were taken were of no definite size. They ranged from about one eighth to about one half a hectare, but were always limited to a sample of homogeneous physiognomy.

Table I. Analysis of 40 samples of chalk grassland (2 in Hampshire and 38 in Sussex), excluding those in which *Calluna vulgaris* occurs, but including those dominated by *Festuca ovina* and those dominated by tall grasses. The region extends over a distance of 90 km. in a direct line from W. to E. about 10° S of E, and mainly follows the escarpment of the Lower Chalk, which, except in one place, follows this line pretty closely.

In the above table the first column after the name of the species gives the number of areas, out of the total of 40, in which the species occurred, the second column the corresponding percentage. The third column gives the abundance, the symbols commonly used in England being replaced by the numbers 1—5 in accordance with the recommendation of Braun-Blanquet and Pavillard.[1] Thus *va* (very abundant) = 5, *a* (abundant) = 4, *f* (frequent) = 3, *o* (occasional) = 2,

[1] The data from which this table is made will appear in fuller detail in a forthcoming paper — Tansley A. G. and Adamson R. S., "A Preliminary Survey of the Chalk Grasslands of the Sussex Downs". J o u r n. E c o l. **13**, 1925.

Life form	Species	Occurrences		Abundance	Constancy	Exclusiveness (Treue)	Sociability	Dynamic behaviour
		Number	Per cent.					
	38 Species occurring in half or more than half the areas.							
H	Achillea millefolium	29	72	2-4	4	2		
H	Agrostis alba	20	50	2-4	3	2		
H	Anthoxanthum odoratum	26	65	2-4	4	2		
H	Asperula cynanchica	27	67	2-3	4	4		
H	Avena pratensis	36	90	4	5	3	2-5	maintaining
H	Avena pubescens	25	62	3	4	3	1-3	
H	Bellis perennis	25	62	2	4	2		
H	Briza media	38	95	3	5	3		
H	Bromus erectus	24	60	1-5	3	4	2-5	maintaining
H	Campanula rotundifolia	24	60	2-3	3	2		
G	Carex flacca (glauca)	39	97	4	5	2	1-3	
H	Centaurea nigra	25	62	1-4	4	2		
H	Cirsium acaule	38	95	2-5	5	4	1-2	destructive
H	Dactylis glomerata	28	70	1-5	4	2		
Th	Euphrasia nemorosa	23	57	2-3	3	2		
H	Festuca ovina	38	95	4-5	5	3	5	constructive, maintaining and consolidating
H	Galium verum	25	62	2-4	4	3	1-3	
H	Hieracium pilosella	30	75	2-4	4	3	2	
H	Koeleria gracilis	31	77	3	4	3		
H	Leontodon hispidum	31	77	2-4	4	2		
Th	Linum catharticum	37	92	3	5	3		
H	Lotus corniculatus	36	90	2-4	5	2		
H	Phyteuma orbiculare	28	70	1-3	4	5		
H	Pimpinella saxifraga	33	82	3	5	3		
H	Plantagō lanceolata	40	100	3	5	2		
H	Plantago media	28	70	2	4	3		
H	Polygala vulgaris	22	55	2	3	2		
H	Poterium sanguisorba	38	95	4-5	5	3	1-3	
H	Primula veris	23	57	2	3	2	2	
H	Prunella vulgaris	25	62	2-3	4	2		
H	Ranunculus bulbosus	27	67	2	4	2		
H	Scabiosa columbaria	36	90	3	5	4		
Ch	Thymus serpyllum	38	95	2-4	5	3		
H	Trifolium pratense	34	85	2	5	2		
H	Trisetum flavescens	25	62	3	4	3		

Life form	Species	Occurrences		Abundance	Constancy	Exclusiveness (Treue)	Sociability	Dynamic behaviour
		Number	Per cent.					
	Brachythecium purum	31	77	4	4	2	3-4	
	Hylocomium squarrosum	24	60	2-4	3	2	2-3	
	Hylocomium triquetrum	23	57	3-5	3	2	2-4	
	28 Species occurring in less than one half and at least one quarter of the areas.							
H	Anthyllis vulneraria	10	25	2-3	2	4		
H	Carex caryophyllea	18	45	2	3	2		
H	Carlina vulgaris	19	48	2	3	3		
Ch	Cerastium vulgatum	14	35	1-3	2	2		
G	*Cirsium arvense*	*11*	*27*	*1-2*	*2*	*1*	2	
H	Cynosurus cristatus	15	37	2-3	2	2		
H	Daucus carota	13	32	2	2	3		
H	Deschampsia caespitosa	13	32	2	2	2		
H	Filipendula hexapetala	11	27	3	2	4		
H	Galium erectum	18	45	2	3	3	2	
Th	Gentiana amarella	16	40	2	2	2		
H	Hippocrepis comosa	13	32	3-5	2	4	2-3	
H	Holcus lanatus	18	45	2	3	2	2	
H	Leontodon autumnale	12	30	2	2	2		
Th	Medicago lupulina	19	48	2	3	2		
H	Phleum pratense	12	30	2	2	2		
G	Poa pratensis	11	27	2	2	2		
H	Rumex acetosa	17	42	2	3	2		
H	Succisa pratensis	13	32	2	2	2		
H	Senecio jacobaea	13	32	1-2	2	2		
H	Trifolium repens	14	35	2	2	2		
Ch	Veronica chamaedrys	17	42	2	3	2		
H	Viola hirta	17	42	2	3	3		
H	Viola riviniana	10	25	2	2	2		
	Camptothecium lutescens	17	42	2-5	3	3	1-3	
	Dicranum scoparium	16	40	3-4	2	2	2	
	Hylocomium splendens	15	37	3-5	2	2	2	
	Hypnum cuspidatum	13	32	2-3	2	1		
	52 Species occurring in less than one quarter of the areas, excluding casuals.							
G	Aceras anthropophora	1	2	1	1	5		
H	Agrimonia eupatoria	4	10	2	1	2		

Life form	Species	Occurrences		Abundance	Constancy	Exclusiveness (Treue)	Sociability	Dynamic behaviour
		Number	Per cent.					
H	Agrostis tenuis	4	10	2-4	1	1		
H	Arabis hirsuta	4	10	2	1	2		
Th	Arenaria serpyllifolia	2	5	2	1	2		
H	Arrhenatherum elatius	8	20	1-4	1	2	2	
Th	Blackstonia perfoliata	1	2	2	1	2		
Th	Bartsia odontites	2	5	1	1	1		
H	Brachypodium pinnatum [1]	7	18	1-5	1	4	2-5	↓ destructive
H	Brachypodium silvaticum	5	12	1	1	1		
H	Campanula glomerata	5	12	2	1	4		
H	Centaurea scabiosa	2	5	2	1	3		
H	Cirsium lanceolatum	7	18	1-2	1	2		
H	Cirsium palustre	2	5	2	1	2		
Th	Crepis capillaris	3	8	1-3	1	2		
Th	Erythraea centaurium	2	5	1	1	2		
H	Festuca elatior	4	10	2-5	1	1		
H	Festuca rubra	8	20	2-5	1	2		
G	Gymnadenia conopea	3	7	2	1	3		
G	Habenaria viridis	1	2	1	1	2		
Ch	Helianthemum vulgare	5	12	2-4	1	4	2-3	
H	Hypericum perforatum	3	7	1-2	1	1		
H	Knautia arvensis	5	12	1-3	1	2		
H	Leucanthemum vulgare	7	18	2	1	2		
Th	Linum angustifolium	1	2	1-2	1	3		
G	Listera ovata	2	5	1	1	2		
H	Luzula campestris	6	15	2	1	2		
Th	Myosotis arvensis	6	15	2	1	2		
H	Ononis repens	5	12	2-3	1	2		
G	Ophrys apifera	6	15	1-2	1	4		
G	Orchis maculata	3	7	2	1	3		
G	Orchis pyramidalis	2	5	1-2	1	4		
H	Origanum vulgare	6	15	2	1	3		
Th	Rhinanthus cristagalli	4	10	1-2	1	2		
H	Senecio campestris	5	12	2-4	1	5		

[1] *Brachypodium pinnatum* occurs in this region only on the eastern Downs, where it is rapidly spreading and becoming locally dominant. Its growth tends to exclude other species, and it is sometimes burned off by the local shepherds.

Life form	Species	Occurrences		Abundance	Constancy	Exclusiveness (Treue)	Sociability	Dynamic behaviour
		Number	Per cent.					
H	Sieglingia decumbens	3	7	1-2	1	1		
H	Spiranthes spiralis	2	5	2	1	3		
H	Taraxacum erythrospermum	4	10	2	1	3		
H	Taraxacum officinale	7	18	1-2	1	1		
G	Thesium linophyllum	3	7	2	1	5		
H	Tragopogon minus	5	12	1-2	1	2		
Ch	Veronica officinalis	5	12	2	1	1		
	Fissidens taxifolius	9	22	2	2	2		
	Hypnum chrysophyllum	1	2	2	1	3		
	Hypnum cupressiforme var. elatum	6	15	2-3	1	3		
	Hypnum molluscum	6	15	2-3	1	3		
	Neckera crispa	5	12	2-5	1	3		
	Rhacomitrium lanuginosum	1	2	2	1	1		
	Thuidium abietinum	2	5	3	1	3		
	Thuidium tamariscinum	2	5	2	1	2		
	Frullania tamarisci	3	7	2-3	1	1		
	Scapania nemorosa	2	5	2-3	1	1		
	Cladonia spp.	6	15	3-4	1	2		

r (rare) = 1. A difficulty has been found in assigning the correct number because the abundance of a species often differs a great deal in the different areas recorded. Where most of the records belong to one category the corresponding number has alone been recorded. Where the categories are various and more evenly balanced the r a n g e has been indicated, as averaging the figures seems unsatisfactory and would often not result in a whole number.

The fourth column gives the constancy [1] on the scale 1—5, (1 = 1—20 p. c. of the areas, 2 = 21—40 p. c., 3 = 41—60 p. c., 4 = 61—80 p. c., 5 = 81—100 p. c.). The fifth gives the e x c l u s i v e n e s s (Treue, fidélité), understood as referring only to Great Britain. The figures in this column are derived partly

[1] V o c a b u l a i r e d e S o c i o l o g i e V é g é t a l e, 1922.

from personal experience, partly by comparison of records in various floras; and their absolute accuracy cannot be guaranteed. To give accurate "exclusiveness" figures would require a precise and encyclopaedic knowledge of the distribution of species in different communities which does not yet exist.

It will be remarked that the community is a well-characterized "association" according to BRAUN-BLANQUET's standard. Of the 38 "constants" (occurring in more than half the samples) 13 have the highest constancy figure (5) and 16 the next figure (4). Of the whole list of 118 species only 4 are absolutely "exclusive" or "faithful" to the community in Great Britain, so far as is known, but 12 are thought to deserve the figure 4, though there has often been doubt in deciding between 4 and 3, where the real distribution and abundance of the species in other communities, which have not been at all carefully studied, are not accurately known. Similarly there has been doubt as between 3 and 2, especially in regard to species common on dry soils, but with no special "preference" for limestone. *Festuca ovina* itself and *Bromus erectus*, for instance, are in that sense "indifferent", but they are characteristic dominants of the chalk grassland, which is the most important and extensive "dry soil" grassland community in southern and eastern England. *Festuca ovina* however (often in company with *Agrostis tenuis)* is so abundant and widespread also on dry siliceous soils of the west and north, as well as on many of the less acid "heaths" that it cannot, as a member of the chalk grassland, be assigned an exclusiveness coefficient of more than 3 at the most, while *Bromus erectus* is given 4, probably with justice. Again it is a question whether *Thymus serpyllum* and *Galium verum* should have 2 or 3. They are certainly what we in England would call "characteristic of" chalk grassland, but they are equally abundant on many "grass heaths" and other "siliceous" grasslands.

A complete list of English chalk grassland species (cf. the one given in Types of British Vegetation, 1911, pp. 176—178, which however, requires a certain amount of revision) would include several more species confined to this community and therefore possessing an exclusiveness coefficient of 5. Most

of these are rare plants confined to the chalk of the east or south-east of England. The Sussex list corresponds remarkably closely with the list of species from Fleam Dyke in Cambridgeshire, about 150 km. north of the Sussex Downs (see Types, pp. 179—181), only a few species, apart from casuals, being found in one and not in the other, e. g. *Thalictrum minus* and *Astragalus danicus* in Cambridgeshire, *Phyteuma orbiculare* in Sussex.

In the sixth column the "sociability", and in the seventh the "dynamic behaviour" of a few species, in which these characters are conspicuous, have been indicated. Not enough study has yet been given to make it possible to do more than indicate a few of the more obvious characterisations under these heads. The great majority of the species are probably "neutral" in "dynamic behaviour".

Of the "constant" herbs and grasses approximately 90 p. c. are hemicryptophytes, a very high percentage even for a climate which markedly favours this type of life form. Of the whole list 72 p. c. are hemicryptophytes, 12 p. c. therophytes, 11 p. c. geophytes and 5 p. c. chamaephytes.

c) Chalk Heath. Detailed analysis of this community would scarcely repay the space devoted to it. It may be stated generally that it is marked by the appearance or increase in abundance of one or all of the following species: *Calluna vulgaris*, *Agrostis tenuis*, *Sieglingia decumbens*, *Potentilla erecta* (*Erica cinerea* and other heath species do not typically occur except on genuine heaths on deep non-calcareous soil in which the members of the chalk grassland association are no longer met with). The chalk grassland plants of the chalk heath are unaffected, except a few species which no longer appear, e. g. *Phyteuma orbiculare* and the chalk orchids; and to some extent the smaller plants of the community, e. g. *Asperula cynanchica*, tend to decrease, as the result perhaps of heightened competition.

4. Chalk Scrub (Bushland)

No detailed studies of this community have been made, and the list given in Types of British Vegetation (pp. 171—2), to

which should be added *Tamus communis* (f—a), is substantially accurate. A few general notes may however be added here.

In moderately pastured chalk grassland isolated shrubs often occur, mostly of spinose species. Of these the most characteristic are *Juniperus communis* (la), *Rosa rubiginosa* (f) and *R. micrantha* (f), *R. agrestis* (r), with *R. canina* and *R. arvensis* (f), *Prunus spinosa* (f—la) and *Crataegus monogyna* (ubiquitous). These are all pioneers, colonising the open Chalk grassland as isolated bushes. In their shelter non-spinous species frequently settle, such as *Cornus sanguinea*, *Viburnum lantana*, *Euonymus europaeus*, etc. and sometimes trees, such as *Fraxinus*, *Quercus robur*, *Sorbus aria* and *Taxus baccata*, thus forming nuclei for the formation of the early stages of woodland. This general colonisation by isolated (mostly spinous) bushes and clumps is to be distinguished from the colonisation by a fringe of shrubs advancing on to grassland from the sheltered edge of forest.

The author has described [1] the results of excluding pasturage and rabbit attack from a small area of chalk grassland on the edge of a wood for a period of 12 years, distinguishing "edge colonisation" (in this case by *Rubus leucostachys* and *Prunus spinosa)* from general colonisation (by *Rosa* spp. and *Crataegus).*

WATT has described [2] in general terms the development of chalk scrub on chalk grassland as preceding the appearance of woodland when pasturage is diminished or withdrawn. These accounts refer to different areas in West Sussex, both within the region from which the chalk grassland data given earlier in the paper were taken.

The following lists of the woody plants of the scrub communities described by WATT are taken from his data, the "ab-

[1] TANSLEY A. G., "Early stages in the redevelopment of woody vegetation on chalk grassland". Journ. Ecol. **10**, 1922, p. 168.

[2] WATT A. S., "On the ecology of British beechwoods, with special reference to their regeneration, Part II. The development and structure of beech communities on the Sussex Downs". Journ. Ecol. **12**, 1924, pp. 154—160.

undance coefficients" being translated from his "frequency letters" as in Table I.

Table II.

Abundance of constituent species of chalk scrub described by WATT in the Goodwood region of West Sussex.

Exclusiveness		Abundance		Exclusiveness		Abundance	
		Exposed situations	Sheltered situations			Exposed situations	Sheltered situations
2	Crataegus monogyna	2-3	2-5	2	Acer campestre		2
3	Cornus sanguinea	2-4	2-4	2	Ilex aquifolium	1-2	2
3	Juniperus communis	2-4	2-3	?5	Atropa belladonna	1	1
2	Rubus fruticosus	2-4	2-4				
3	Sambucus nigra	2-4	2-4		Climbers		
2	Prunus spinosa	2-4	2-4	4	Clematis vitalba	1-2	2-4
3	Sorbus aria	2-4	2-3	3	Tamus communis	1	2
3	Taxus baccata	2-4	1-3	2	Lonicera periclymenum	2	2
3	Ligustrum vulgare	1-4	2	2			
2	Rosa arvensis	2-3	2	2	Solanum dulcamara		1
5	Rosa eglanteria		3	2	Hedera helix		1
4	Rosa micrantha	2	1-3				
2	Rosa sarmentacea	2	2		Wood-Forming trees		
3	Viburnum lantana	2	1-2	3	Fagus silvatica	2-5	2-3
2	Acer campestre		2	2	Fraxinus excelsior	1-2	2-4
2	Corylus avellana	1-2	1-2		Pinus silvestris		
3	Euonymus europaeus	2	2	1	(subsp.)	2	1
4	Rhamnus catharticus	1-2	1-2	2	Quercus robur	1-2	1-4

The exclusiveness coefficients are not WATT's but are added by the author, and are subject to the same reservations as those made for the grassland species.

No detailed studies have been made of the herbaceous flora of the chalk scrub. In general it may be stated that, as would be expected, it possesses a mixed flora of "wood margin" and "shade" species.

5. Chalk woodland (forest)

The characteristic woodland of the chalk of southern England (except the south west) is beech forest composed of nearly pure *Fagus silvatica*. The status of this species in Great Britain

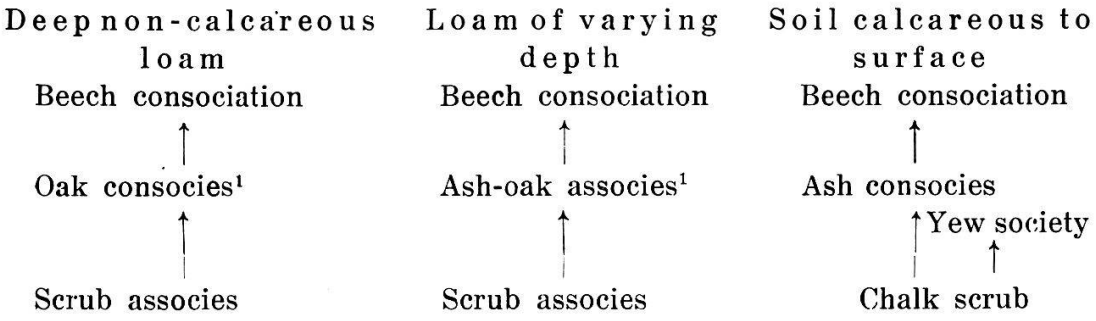
is still open to doubt, though it is generally regarded as indigenous. The principal reason for doubting its nativity is CAESAR's statement that he saw no woods of *Fagus* such as existed in Gaul, and he certainly traversed the country where they now exist. But whether the tree entered Great Britain naturally or was introduced by human agency it has now all the appearance and behaviour of a native tree in south-eastern and south-central England, spreading naturally, when it gets the chance, on certain habitats.

The great majority of the English woods are of course kept in an artificial condition. They are sharply limited by enclosure or by pasturage and show little or no natural regeneration. But WATT has demonstrated quite conclusively [1] that certain of the beechwoods and related tree communities of the West Sussex Downs are now in a substantially natural condition and show, over an area of many square kilometers, typical phenomena of forest development and succession, though they are, at least partly, developed on land which was once arable. The beechwoods thoroughly studied by WATT are mostly situated, not on the shallow chalk soil which bears the typical chalk grassland described in an earlier section, but on loam of varying depth which covers the plateau and dipslope of the chalk. The shallowest (highly calcareous) soils in which the proximity of the chalk rock has the greatest effect upon the vegetation are met with, it will be remembered, mainly on steep slopes and narrow ridges. The type of beechwood met with on these — the "beech hangers" as they are called locally — is recognised by WATT as an extreme type. They are not sufficiently extensive in the region he worked in to permit of a thorough developmental study, but on the basis of a comparison of his results with observations in other areas he was able to infer the existence of an "ash consocies"[2] following "chalk scrub" in succession and itself succeeded by the climax "beech consociation" [2] of extreme type, i. e. with a soil highly calcareous to the surface. In simplified form WATT's developmental scheme of the

[1] A. S. WATT, op. cit.

[2] CLEMENTS' terms.

woody vegetation developed on soils overlying the chalk is as follows.



It will be understood that only the woody vegetation in the righthand column is considered in this paper.

a) Ash consocies

No detailed data are available for the vegetation of the ash consocies, whose existence as a definite member of this successional series has rather been inferred (though on very good comparative grounds) than observed. The ashwoods of the Chalk Downs in the Isle of Wight, etc. (referred to in Types of British Vegetation, p. 162) are presumably examples of this community, just outside the limits of the region to which the beech has penetrated. The comparative rarity of well-developed ash communities of any considerable extent on the dry chalk soils is probably related to the fact that on the South Downs the moisture conditions are often minimal for the good growth of this species.

b) Yew woods

Taxus baccata is a very prominent tree on the South Downs, frequently occurring in chalk scrub, sometimes forming small pure woods, and often met with also in the beechwoods themselves. Watt, who has given the yew woods considerable attention, is of opinion that this tree belongs to the scrub stage of the succession, and that the pure woods which it sometimes forms are to be regarded as a lingering on, owing to the long life of this tree, and the very deep shade which it casts, of a special phase of the scrub stage, which is normally succeeded by the

[1] Clements' terms.

beech community. He therefore regards the yew as forming a society (CLEMENTS' term for a climax unit of lower grade than a consociation). WATT gives (op. cit. p. 168) the following list of species associated with the *Taxus* society.

Table III

Woody plants	Abundance	Herbs	Abundance
Taxus baccata	5	Sanicula europea	3[1]
Fraxinus excelsior	4	Viola silvatica	3[1]
Sorbus aria	3	Fragaria vesca	2
Crataegus monogyna	3[1]	Prunella vulgaris	2
Cornus sanguinea	3[1]	Urtica dioica	2
Ligustrum vulgare	3[1]	Veronica officinalis	2
Lonicera periclymenum	3[1]	Viola hirta	2
Fagus silvatica	2	Potentilla erecta	2
Quercus robur	2	Galium mollugo	1
		Mosses	
Thuidium tamariscinum	4[1]	E. striatum	2
Brachythecium rutabulum	3	Fissidens taxifolius	2
Catharinea undulata	3[1]	Hylocomium loreum	2
Mnium undulatum	3[1]	H. splendens	2[1]
Brachythecium purum	2	H. triquetrum	2
Eurhynchium praelongum	2	Hypnum cupressiforme	2

The figures are those of abundance, translated, as before, from the English "frequency letters". The list is taken from the *Taxus* society of a soil which possesses a shallow loam, but this is usually calcareous and the species list (with the possible exceptions of *Lonicera periclymenum* and *Potentilla erecta)* would not differ much from that of a yew wood on the shallowest chalk soil.

c) Beech wood

As already mentioned, WATT has not directly studied the development of beechwood on the shallowest and most highly calcareous chalk soils. ADAMSON however gives extensive lists [2] of the flora of five examples of the beech consociation belonging to this series ("beechwoods on chalk"). These lists are too

[1] Local.

[2] ADAMSON R. S., "The Woodland of Ditcham Park, Hampshire". Journ. Ecol. 9, 1921, pp. 122—125.

long to reproduce here, and the following plan has been adopted. In the first place only those species are given which occur in at least 3 out of the 5 woods, and to these are added a few species which occur in fewer than these, but are known to be characteristic of beech wood, though not of abundant occurrence. The figures in the first column give the range of abundance, following ADAMSON's frequency letters, in the second column the number of woods (3, 4 or 5) in which the species occurs. This gives a very rough measure of constancy, though the number of areas listed is of course very small. The third column gives the exclusiveness coefficient, with the same reserve as before.

Table IV

Trees and Shrubs

		Abundance	Constancy	Exclusiveness			Abundance	Constancy	Exclusiveness
MM	Fagus silvatica	5	5	4	M	Taxus baccata	1-4	5	3
MM	Fraxinus excelsior	2-3	5	3	M	Corylus avellana	2	5	2
M[1]	Acer campestre	2-3	5	2	M	Euonymus europaeus	2	5	3
N or M	Cornus sanguinea	2-3	5	3	N	Rosa arvensis	1-2	5	2
M	Crataegus monogyna	2-3	5	2	H	Rubus leucostachys	2-3	3	2
H	Rubus caesius	2-3	5	2	M	Viburnum lantana	2	3	3
M	Ilex aquifolium	2-3	5	2	N	Rosa lutetiana	1-2	3	2
M	Sambucus nigra	2-3	5	3	MM	Quercus robur	1-2	4[2]	1
MM	Sorbus aria	1-3	5	3					

Fraxinus and *Cornus* occur in quantity only in openings, and are killed out as the beeches close in. Most of the other shrubs are present only where the beech canopy is thin. *Sorbus aria* sometimes reaches the height of the canopy.

The bryophytes occur very largely on and around the bases of the trees, though also scattered on the soil where this is not

[1] Practically always as a shrub.

[2] In two of the woods only seedlings which would not survive. Adult trees are exceedingly rare.

		Abundance	Constancy	Exclusiveness			Abundance	Constancy	Exclusiveness
	Ground Vegetation.								
Ch	Hedera helix[1]	3-5	5	2	H	Hypericum hirsutum	1-2	4	3
M	Clematis vitalba[2]	2-4	5	4	G	Monotropa hypopitys	1-2	4	5
H	Mercurialis perennis	2-5	5	3	H	Senecio jacobaea[3]	1-2	4	1
H	Viola silvestris	2-4	5	3	H	Ficaria verna	3-4	3	2
Ch	Lamium galeobdolon	2-4	5	2	G	Anemone nemorosa	2-4	3	2
H	Ajuga reptans	2-4	5	2	H	Bromus ramosus	1-3	3	2
H	Fragaria vesca	2-3	5	2	G	Melica uniflora	2-3	3	2
Ch	Veronica chamaedrys	2-3	5	2	H	Dryopteris filix-mas	2-3	3	2
H	Arctium minus	2	5	2	H	Poa nemoralis	1-2	3	2
G	Cephalanthera grandiflora	2	5	4	G	Neottia nidus-avis	1-2	3	4
G	Tamus communis	1-2	5	3	H	Geranium robertianum	1-2	2	2
H	Sanicula europaea	2-5	4	2	H	Taraxacum officinale[4]	1	3	1
G	Asperula odorata	3-4	4	3	H	Scrophularia nodosa	2-3	2	2
G	Circaea lutetiana	3-4	4	2	H	Viola hirta	2	2	3
H	Epilobium angustifolium[3]	4-5	4	2	G	Polygonatum multiflorum	2-3	2	3
H	Carex silvatica	1-4	4	2	H	Helleborus viridis	1	2	3
H	Urtica dioica[4]	2-4	4	1	H	Brachypodium silvaticum	1-2	2	2
H	Lactuca muralis	1-4	4	3	H	Festuca gigantea	2	2	3
G	Epipactis latifolia	2-3	4	2	H	Aquilegia vulgaris	1	1	3
H	Euphorbia amygdaloides	1-3	4	2					
	Bryophytes.								
	Hypnum cupressiforme	4-5	5			Orthotrichum affine	2	5	
	Hypnum molluscum	4-5	5			Lophocolea bidentata	2-3	5	
	Neckera complanata	3-4	5			Seligeria calcarea	2-4	4	
	Brachythecium rutabulum	3-4	5			Porotrichum alopecurum	2-4	4	
	Metzgeria furcata	3-4	5			Eurhynchium confertum	2-3	4	
	Frullania dilatata	3-4	5			Brachythecium velutinum	3	3	
	Fissidens taxifolius	2-4	5			Eurhynchium striatum	3	3	
	Madotheca platyphylla	2-3	5			Barbula rubella	1-2	3	
	Anomodon viticulosus	2-3	5						
	Camptothecium sericeum	2-3	5						

[1] The ivy is one of the most prominent and abundant members of the ground flora (Ch), but it only occurs on trees (M) occasionally, partly because the foresters cut it down.

[2] Only in fairly well-lighted spots.

[3] Very local, confined to openings.

[4] Weeds, introduced by traffic, or otherwise.

covered throughout the year with a continuous litter of dead beech leaves. In places where this permanent litter occurs, the ground is free of vegetation, except occasionally for trailing shoots of ivy, rooted some distance away, and for an occasional plant of one of the two characteristic saprophytes, *Monotropa* and *Neottia*, whose rootstocks are buried in the humus below, and whose aerial parts push up through the dead leaves.

The soil is shallow, the uppermost layer consisting of very dark humus to a depth of about 10 cm. and often containing minute chalk particles. Below this is either a very chalky pale soil with numerous chalk fragments but little humus, of a depth of as little as 5 or as much as 35 cm. to the rock surface, or a more humous brown soil 7 to 15 cm. in depth and containing very numerous chalk fragments, underlain by broken chalk with soil between. The total depth from the upper surface of the humus to the rock surface only varies between 10 and 45 cm. The soils are all alkaline with pH values of 7.5 to 8, or even higher where the chalk shows on the surface. Only in exceptionally thick humus have distinctly acid reactions (pH 6.5) been recorded. On the shallowest soils all but the woody roots are confined to the surface 10 cm. (humus layer). In the deeper soils they may penetrate 12 to 20 cm. The tree roots extend to the chalk surface, often running horizontally over it, while branch roots penetrate into the cracks of the rock (ADAMSON, op. cit.).

The sparseness of the ground flora in many places is determined for the summer plants (shade phase of the wood) partly by the low light intensity, which in July and August may be as low as 1 p. c. of full sunlight in the open, allowing only a very sparse flora, or *Hedera* alone, to exist. In April however, before the beech leaves are expanded, values varying from 17.5 to 63 p. c. of full sunlight were recorded, with an average of 39 p. c. All the plants (with the exception of *Hedera*, which does not flower at all, and the saprophytes) occurring in the darkest parts of the woods flower during the early "light phase" or at least before the full leaf canopy is established in June. Below a summer value of 1 p. c. of full sunlight no vegetation

occurs, but bare areas exist with as high a value as 4·7 p. c. These were all places with a deep surface layer of leaf litter.

The slopes of these woods vary from 18° to 34° where there is anything like a continuous cover of ground vegetation. Slopes having a steeper angle than this present great difficulties to colonisation, the surface soil being continually washed down the slope.

In regard to the life forms of the more constant herbaceous flora of the beechwoods compared with that of chalk grassland, the hemicryptophytes (66 p. c.) are still high, but there is a total absence of therophytes and a marked increase of geophytes (26 p. c.).

d) Herbland resulting from the felling of woodland

When an area of beechwood is felled, and the ground abandoned for a time, it is occupied by a mixed vegetation consisting (1) of woodland plants whose growth has been stimulated by access of light and by the vigorous nitrification following exposure to partial desiccation of the humus, (2) weeds which have invaded the area. If the area is in the proximity of chalk grassland it is also invaded by (3) grassland species. Later on (4) wood edge species come in. On the other hand many of the shade species of woodland completely disappear at once. All these changes are independent of, and take place before, woodland regeneration.

An area of beechwood on a steep northern exposure was clear felled in 1917. In 1920 it was examined [1] and found to be mainly occupied by a tall growth of herbs, 1 to 1.5 m. in height, and composed principally of *Atropa belladonna*, *Epilobium angustifolium*, *E. parviflorum*, *Senecio jacobaea*, *Urtica dioica*, all of exceptionally vigorous growth and forming dense thickets. The true woodland plants whose growth was stimulated by the clearance of trees were (besides *Urtica dioica)* *Arctium minus*, *Hypericum hirsutum*, *Polygonatum multiflorum* and *Viola hirta*. *Monotropa*, *Neottia*, *Listera*, *Cephalanthera* and *Epipactis* had apparently completely disappeared, while other shade plants

[1] Adamson, op. cit. pp. 138—140.

had greatly decreased in abundance. None of the trees or shrubs of beechwood, except locally *Sambucus nigra*, showed any signs of colonising the area, though it was only about 200 m. square and surrounded on three sides by untouched woodland.

Other areas which originally bore woodland but have been felled at an earlier date show quite a different appearance. In place of the first vigorous growth of particular species almost completely occupying the ground, the flora consists of a mixture of woodedge and grassland species and weeds, of which the last named tend to decrease and the two former to increase, the one or the other according to the proximity of their parent vegetation.

No studies of regeneration of woodland on such felled areas have been made. In the areas investigated it is very slow, local, and uncertain owing to a variety of factors.

Conclusion

In this paper some endeavour has been made to give the reader an analysis of the vegetation, based on quantitative data so far as these are available, of a representative region of the Southern English chalk, where this rock exercises the maximum influence on the vegetation. It is obvious enough that our knowledge is still very far from complete, both in regard to the vegetation itself and in regard to the factors determining it. But the recent publication of several detailed investigations (ADAMSON, WATT, TANSLEY, opera citata) enable a much closer and clearer picture to be formed than was possible when the first tentative account (TANSLEY and RANKIN in Types of British Vegetation, pp. 161—181) was written in 1911. In this paper considerations of time and space have necessitated a rigid selection among the available data. The object has been to present those which give the clearest picture of essentials.

The method of presentation has followed the lines of the development or succession of vegetation which can be traced on this habitat. Without recapitulating the facts it is sufficiently clear that the vegetation cannot be understood, or the communities rightly placed and assigned to their proper status, unless they

are investigated from the developmental standpoint, as well as in relation to certain essential habitat factors. At the same time the introduction of the numerical characterisation of the different features of the various communities which we owe to the Zürich school and to PAVILLARD, undoubtedly gives a clearer view of the nature of the different communities and of the status of their constituent members.

This combination of different methods of approach to a phytosociological and synecological problem is specially appropriate in a publication devoted to the honour of the distinguished and beloved founder of the Zürich school, who has contributed so much by example and personality to international understanding and co-operation.

Dritter Teil

Phyto-Plankton

I.

Aperçu sociologique sur le Phytoplankton marin

Par J. PAVILLARD, Montpellier

Eingegangen 19. Januar 1925

«Die Schwebeflora unserer Seen», donnée par C. SCHRÖTER au Nouvel An de 1897, avait été l'éloquente réplique d'un limnologue très qualifié à l'étude mémorable de FR. SCHÜTT: «Pflanzenleben der Hochsee».

L'Essai didactique de 1902 (Vorschläge für eine Nomenklatur der Formationslehre), élaboré, comme on sait, par C. SCHRÖTER à l'occasion d'une monographie du lac de Constance, fut la contribution méthodologique d'un maître parvenu à l'apogée de la puissance intellectuelle et capable d'affronter les plus hautes responsabilités.