The Soils of Blakeney Point : A Study of Soil Reaction and Succession in Relation to the Plant Covering.¹

BY

E. J. SALISBURY.

With Plate XV and five Figures in the Text.

I. INTRODUCTORY.

THE work connected with this investigation was in part carried out in the Field Laboratory at Blakeney Point, where the bulk of the hydrogen-ion estimations were made upon the spot.

The purpose in view was to see to what extent the phases in the development of the maritime plant associations could be related to variations in real acidity, and how far this in turn was correlated with the leaching out of carbonates and the organic content of the soil. In elucidating the answers to these questions the problem of the cause or causes of soil acidity is necessarily involved.

The striking and easily recognized phases of the maritime succession render this type of plant formation peculiarly suited to a study of the accompanying soil changes. It is highly probable that a similar edaphic succession to that here demonstrated characterizes other inland plant formations, and the results here presented form a striking confirmation, in a totally different type of habitat, of the edaphic succession already studied by the writer in woodland communities (*Journal of Ecology*, vol. ix, pp. 220-40, 1922).

But whereas the phases in woodland successions are often of a secular character and must in most cases be inferred from collateral evidence, the successions in coastal formations such as sand dunes, shingle beaches, and salt marshes are sufficiently rapid to present successive phases in one and the same area.

In this respect Blakeney Point offers exceptional advantages, though the final stages in the dune series are lacking owing to their removal by wind action.

¹ Blakeney Point Publication, No. 20.

[*Annals of Botany*, Vol. XXXVI, No. CXLIII. July, 1922.]

The writer gladly takes this opportunity of expressing his indebtedness to Professor F. W. Oliver for having asked him to undertake a soil survey of this area. Thanks are also due to Dr. P. Haas for the preparation of standard buffer solutions, to Dr. Brady for electrometrical checks, to Lieut. G. N. Oliver for the preparation of Text-fig. 1, and to the following for assistance in the collection of soil samples and in the hydrogen-ion determinations: Miss V. Anderson, Miss S. Hurwitz, Miss E. Tyler, and Mr. L. Cole.

Except where otherwise stated the samples were taken to a uniform depth of 4 in., and 10 gm. of the undried soil were stirred up with 50 c.c. of water neutral to brown-thymol blue. In practice it was found that equilibrium was attained in half an hour, after which the extract was filtered and, after discarding the first filtrate, the hydrogen-ion concentration was determined colorimetrically by the aid of standardized buffer solutions and the usual indicators.

No detectable difference in the results was obtained by using twice as much soil, by lengthening the period of extraction, or by adding the indicator to centrifugalized samples. One may therefore assume that the varying water-content of the samples did not introduce any error into the results, nor are these vitiated by filtration.

The carbonate content was determined by means of a Collins calcimeter, applying the usual corrections, and the results are expressed as calcium carbonate in 100 gm. of soil dried at 100° C.

The general topography of the area and its vegetation have already been dealt with elsewhere (cf. Oliver and Salisbury, Trans. Norfolk and Norwich Nat. Soc., vol. ix, 1913), but for convenience we shall here summarize the chief features, at the same time indicating the distribution of the soil samples taken.

The salient features of the area are shown on the map (Text-fig. 1), where the sequence of numbers and letters shows the dunes and lateral shingle beaches of successive age.

A. THE DUNE SYSTEM.

The earliest phase in dune development at Blakeney Point is usually marked by the collection of sand around a young plant of *Psamma arenaria*. As the dune thus initiated accretes sand the marram grass becomes covered and is thereby stimulated to renewed growth—in this way constituting a skeletal system which enlarges *pari passu* with the growing sand-hills and permeates the entire structure of the adult dune.

Of this skeletal system the ultimate ramifications bear the green leaves at the surface, whilst the older parts, formed when the dune was young, exhibit progressive decay till in the actual heart of a large dune only disintegrated fragments may remain.

TEXT-FIG. 1. Sketch-map of Blakeney Point on a scale of 3 inches to 1 mile (1 : 21120). The lower section (marrams—clay beach) fits at *a*, *a*, on to the right-hand end of the upper section. *Shingle beaches*, where evident, are marked in black, the laterals (or 'hooks') being numbered in their presumed developmental sequence. Thus 1 is the oldest and 20 the youngest. *Dunes* are white, successive systems being lettered; A (the Hood) being the oldest; B, remnants of the 'Long Hills'; E, the main ridge of the headland; J, the newest embryo dunes. The fringing dunes H, alphabetically out of position, represent a SE. extension of the headland series from which they are subsequent derivations, especially due to sand mobility in strong NW. winds. In *time*, though they overlap several of the other systems, they have undergone marked accretion since the G system arose. *Salt marshes* are dotted. The youngest marsh to establish (since 1910) is the detached area $\frac{1}{3}$ mile south of the Hood (A). (Adapted by E. J. S. from air survey photographs (1921) and drawn by G. N. O.).

Thus *Psamma arenaria* plays two important rôles. On the one hand it helps to stabilize the sand mass against wind action, and on the other adds colloidal material by which the water-content is increased and the necessary medium provided for bacterial activity.

In the outermost dunes on the sea face (cf. G, Text-fig. 1) *Psamma arenaria* is the only important species, but on the new spit (J, near 19 and 20) of shingle *Triticum junceum* also forms embryo dunes.

These early stages are represented by the series of samples G 01–G 029 and J 030–J 036. The very small new dunes actually form several groups on the sea face, and such also occur on the new spit (samples J 032–J 036) and close to the Lifeboat House on the shore of the estuary (samples J 030–J 031 and J 022–J 024). For convenience these, together with the rather older stages represented by the series of samples F 01–F 021, may be termed collectively the young dunes.

The next phase in the succession is represented by the samples E 1–E 31 from the main dune ridge (E, Text-fig. 1), where there is complete coalescence between the original units to form the highest ridge of the series. *Psamma arenaria*, though still the dominant species, is accompanied by *Festuca arenaria* and ephemerals such as *Myosotis collina*, *Phleum arena-rium*, *Stellaria boreana*, *Cerastium semidecandrum*, &c.; *Senecio jacobaea* is also of common occurrence.

This phase as a whole may be conveniently termed the 'main ridge' and represents an advance in stability and organic content. It furnishes the culmination of the 'yellow dune' phase with which the marram grass is particularly associated.

Still passing landwards we come to two more ridges (D and C, Text-fig. 1) parallel to the preceding system but comparatively low in height, due to the combined effects of 'settling', loss by erosion, and greatly diminished accretion. The profile no longer presents a narrow ridge, but a broad, more or less flat top, and, associated with the changed conditions, *Psamma* is much less vigorous, whilst mosses and lichens, especially *Cladonia*, mark the advent of the 'grey dune' phase and from their abundance constitute an effective protection against wind action. Here too are encountered the highly efficient sand binders *Carex arenaria* and *Convolvulus soldanella*, which, however, attain their greatest vigour where the sand has again been rendered mobile by undercutting. This type is represented by the series of samples D 1–D 45 from the Laboratory ridge, and the series C 20–C 47 from the older and more stabilized ridge on its landward side. Two still older phases are represented respectively by the Long Hills (B, Text-fig. 1, samples B 1–B 22), where alone on the area *Polypodium vulgare* occurs, and the Hood (A, Text-fig. 1, samples A 1–A 16).

Although the Hood is almost certainly the oldest dune mass on the area its comparatively small size and its isolated and exposed position

favour accretion of sand, so that, with the exception of the depression in its centre, the soil is more mobile than might be expected, whilst the character of some of the samples is scarcely commensurate with its age.

In some dune areas all transitions up to and including heath are met with, though not present on Blakeney Point. Samples from the neighbouring system of Holkham indicate, however, that the edaphic sequence which accompanies increase of age on our area are still further accentuated in the final phrases of the succession.

The carbonate content of the dune soils (cf. Table I, Appendix). Examination of the drift line reveals at once the large proportion of shell fragments which frequently accompany the vegetable remains. After removal of the loose drift, the underlying sand is found to contain a high proportion of carbonates, sometimes over four per cent. by weight (cf. Sample X. 37, Table XI). The drift line is the especial home of *Salsola kali* and *Cakile maritima*, and the following estimations show (Table II) that the sand is here well supplied both with organic material and carbonates.

TABLE II. *Drift Line.*

Sample.	Location.	Depth.	p. H.	Organic content.	Total carbonates.
		in.		%	%
Transect across D. line	a New spit with <i>S. kali</i>	0-2	7.2	0.38	0.37
	a' " "	4-8	7.2	0.44	0.65
	b Just above actual D. line	0-4	7.1	0.55	0.95
	c Just below " "	0-4	7.2	0.60	1.06
	d Sea front drift line with <i>Cakile maritima</i>	0-4	7.2-7.3	—	—
e	Sea front drift line	0-4	7.0	0.57	0.93

For the carbonate total, both here and on the dune soils generally, calcium carbonate is almost entirely responsible, and the figures given for the carbonate content have been calculated as CaCO_3 .

Various marine mollusca are the main source of supply on the sea face, whilst on the landward side *Paludetrina stagnalis* is probably the most important. This species makes up in numbers what it lacks in size, and the shells of dead individuals often accumulate along the drift line near the Hood to a depth of as much as nine inches and in a zone more than a foot broad. Since 900 shells of *P. stagnalis* occupy only 5 cubic centimetres, a square foot of such a drift line would represent some *two million shells*, which gives one a glimpse of the stupendous prolificacy of these molluscs and the vast numbers involved in their mortality. The shells as found in the drift contain over 97 per cent. of calcium carbonate, and hence constitute a most important source of supply.

The embryo dunes. Passing landwards from the drift line one comes to the small dunes which have arisen on the sea face and near the Life-

boat House during the period since this area has been under close observation, and are therefore known to vary between 3–8 years in age.

Examination of the carbonate content of these shows, like the drift line, a fairly high percentage, ranging from 0.28 per cent. to 0.61 per cent. by weight and averaging 0.425 per cent. To appreciate the significance of these figures it must be borne in mind that dune soils are much heavier, bulk for bulk, than ordinary soils. If, for instance, we wished to compare these data with those of woodland soil on clayey loam we should have to add about 60 per cent. to the figures for the embryo dunes.

In one cubic decimetre of an embryo dune the average carbonate content is very nearly 6.1 grm.

So long as any dune exhibits accretion each new layer of sand, consisting of particles brought in from the exposed sand of the sea-shore or the estuary, will contain its quota of shell fragments. So that, assuming growth to be fairly continuous, the embryo dune will exhibit, within broad limits, a certain homogeneity of carbonate content, in striking contrast to the diminishing content found in natural soils of ancient origin in which leaching has in course of time established a vertical gradient. (Cf. Salisbury, 'Stratification and Hydrogen-ion Concentration of the Soil in relation to Leaching', *Journal of Ecology*, loc. cit., 1922.)

Since sand grains and shell fragments have very different specific gravities (sand grains 1.42, shell fragments *c.* 2.7–2.9) the proportion of calcium in the layers deposited during any given wind storm will clearly vary with the velocity of the wind. On the whole very high winds will tend to deposit sand having a higher calcium content than winds of low velocity. On the other hand, however, it must be recognized that the larger fragments of shells present a larger surface for an equivalent volume than the more or less isodiametric sand grains, and may therefore be more readily wind borne despite their higher specific gravity.

TABLE III. *Carbonate Content of Wind-borne Sand deposited at c. 24 ft. above Mean Sea-level.*

<i>Sample.</i>	<i>Carbonate.</i>	<i>Sample.</i>	<i>Carbonate.</i>
	%		%
1	0.31	7	0.35
2	0.35	8	0.40
3	0.44	9	0.37
4	0.32	10	0.38
5	0.50	11	0.36
6	0.45	12	0.40

Total average, 0.385 %.

Analyses of sand which has accumulated in the loft of the Lifeboat House, about 24 ft. above mean sea-level, give a fair indication of the character of sand carried by the higher velocities of wind. It will be seen

that the carbonate content, though below the average for the smallest dunes, is higher in general than that of the main dune ridge. Incidentally these data show that any accretion which may occur on the older dune phases, i. e. those farthest from the sea, will be comparatively rich rather than deficient in calcium. So that any deficiency of carbonates in the older phases must be the outcome of leaching and not of selective wind action.

In view of the foregoing considerations it is not surprising to find considerable variation in the carbonate content as between the surface and subsurface of these embryo dunes. In two instances (cf. samples 011, 012 and 020, 021) the top four inches showed a lower content, whilst in a third locality the reverse condition obtained (cf. 015, 016). Judging by the p. H. values this is true also for the area represented by 017 and 018.

Passing to the main ridge, the average carbonate content is slightly lower than that in the youngest phases, viz. 0.341 per cent. This represents about 4.9 gm. in a cubic decimetre, or a decrease of about 20 per cent. as compared with the 'embryo dunes'. What period of leaching this represents is not accurately known, but probably not less than 60-80 years.

The range noted varies between 0.15 per cent. and 0.65 per cent., the lower limit being thus considerably less, about half that of the youngest dunes, whilst the maximum is slightly higher.

Since these main ridge dunes are the highest of the whole series, they will only receive comparatively large fragments of shell during high winds. From the data already given, however (cf. Table III), it is clear that such accretion will consist of sand comparatively rich in calcium, and the occasional high values on the seaward face (E 24) and in the hollow represented by E 9 are perhaps the outcome of selective wind action on shell fragments of relatively large surface.

Comparison of the hydrogen-ion values for surface and subsurface for five locations show a higher value for the subsurface in three cases (E 14, E 15; E 18, E 19; E 20, E 21). In one case the same reaction was found (E 1, E 2), whilst in the fifth case (E 8, E 9) the surface was practically neutral and the subsurface slightly acid. Carbonates were only determined in one of these pairs, and this showed a higher content at the lower level. On the whole this then would appear to be the general tendency, and would indicate a preponderance of leaching action over accretion.

All the remaining series of samples represent dunes which for the most part have ceased to accrete any appreciable amount of fresh sand, though 'blow-outs', rabbit-burrows, &c., may effect a partial, if local, rejuvenescence.

The Laboratory ridge shows an average carbonate content of 0.155 per cent., and a range from 0.64 per cent. to 0.03 per cent. The average is equivalent to about 2 gm. per cubic decimetre.

Here then the source of additional calcium being almost cut off by the high main ridge on the seaward side, the leaching action of the carbonated rain-water has gone on practically unhindered, and the low content as compared with the main ridge is a measure of the time that has elapsed since the Laboratory ridge ceased to accrete actively. For equivalent volumes of soil the average carbonate content here is under 41 per cent. of that present in the main ridge, and only about 32 per cent. of the average for the embryo dunes.

The marked leaching action which these data indicate is also reflected by the strikingly different carbonate content which may obtain between the surface and subsurface (e. g. D 13, D 14), and the fact that the surface inch may be entirely devoid of carbonates (cf. samples C 20, C 40, C 41).

The Long Hills show the same phenomenon in a more advanced phase. The proximal end of these where they abut on the main beach is not cut off from the sea face by the main ridge which stops short of this junction. The actual distance from the sandy foreshore is here, moreover, only about 260 yds. It is in correspondence with this that the sea face at the proximal end exhibits a much higher carbonate content than the Long Hills generally, viz. 0.75 per cent. With this sole exception the values range from 0.5 per cent. downwards, the surface being usually entirely devoid of detectable carbonates.

The average is 0.01 per cent. by weight or 0.1344 gm. per cubic decimetre. Comparison of B 8 and B 9, and B 13 and B 14, brings out clearly the leaching effect in the vertical direction, and emphasizes the almost complete absence of carbonates from the surface layer.

The Hood, though presenting a still older system than the Long Hills, yet shows the same range and average content by weight as the latter (viz. 0.01). This we can attribute to its position, some 160 yds. from the foreshore, which facilitates a small amount of accretion. Despite this, the greater degree of leaching is brought out when we compare the weight of carbonate per unit volume, which here amounts to only 0.1281 gm. per cubic decimetre.

It is clear that for any given plant with its specific capacity for root development, the amount of carbonate in a given volume of soil is the important consideration.

The generally xerophytic character of the dune flora is so well known as to require no emphasis, but these same transpiration checks which enable the dune plants to retain their foliage during the drought conditions of summer¹ also involve a smaller intake of the soil solution during the moist conditions of spring and autumn. To appreciate fully therefore the significance

¹ During the exceptionally dry summer of 1921 the foliage of several dune and shingle species suffered considerably. Notable examples were: *Silene maritima*, *Frankenia laevis*, *Erodium neglectum*, and *Convolvulus soldanella*.

of the differences observed we must take into consideration the water-content. Data respecting the natural water-content of the different dune phases over a sufficient period are not available, but assuming that these would be more or less proportional to the maximum water-contents observed under laboratory conditions, it will be realized from a perusal of Table IV that the differences in concentration must be very pronounced.

TABLE IV.

Summary of the Carbonate Content of the various Dune Types.

Dune type.	Av. carbonate content by weight.	Av. carbonate content per cubic decimetre.	Av. concentration of carbonates at maximum water-content.
	%	gram.	%
'Yellow' dunes	Embryo dunes J and G	0.425	6.077
	Main ridge E	0.341	4.8763
'Grey' dunes	Lab. ridge D	0.155	2.139
	Long Hills B	0.010	0.1344
	Hood A	0.010	0.1281

The figures in the third column represent the average concentrations if all the carbonates present were in solution at once, so that they have little significance except in their relation to one another.

If we take the embryo dunes as unity then the relative accessibility of carbonates, on the assumption that the solubility in carbonated water is proportional to that in dilute HCl, is approximately as follows: embryo dunes, 1; main ridge, 0.8; Laboratory ridge, 0.33; Long Hills, 0.02; Hood, 0.016. As the amount of carbonate present is the limiting factor for the amount dissolved, the values realized in nature would show an even steeper gradient than these figures indicate.

The organic content of the dune soils (cf. Table I, Appendix, and Table V).

Embryo dunes. The outstanding feature of the early phases, apart from their mobility, is the low proportion of organic material, probably almost entirely derived from drift.

In the fourteen localities for which the loss on ignition of 'embryo' dunes was determined, the range was from 0.16 per cent. to 0.52 per cent., and it is significant that the highest value was obtained from a very young dune near the drift line. The average value is 0.360 per cent., or approximately 5 gram. per cubic decimetre.

The main ridge. Here, associated with the denser vegetation and greater lapse of time, the organic content ranges from 0.24 per cent. to 0.69 per cent., whilst the average value (12 loci) was found to be 0.501 per cent., or approximately 7.1 gram. per cubic decimetre.

The ridges C and D. The vegetation here has become an almost con-

tinuous carpet, and the organic range is between 0.30 per cent. and 0.96 per cent. The average for seventeen localities is 0.525 per cent., or approximately 7.2 gm. per cubic decimetre. The highest values are associated with a continuous covering of *Cladonia* (C 41, C 42) or moss (D 36 a-c, D 39, D 1). If the two estimations for ridge C may be taken as typical, then the organic content here rises to nearly 12 gm. per cubic decimetre.

Long Hills. The lowest value on these still older dunes correspond with the average for ridge D, whilst the average for the Long Hills is almost exactly double, viz. 1.154 per cent. or about 15.5 gm. per cubic decimetre. The observed range was from 0.56 per cent. to 2.69 per cent., the highest value being associated with the occurrence of *Polypodium vulgare*.

The Hood. As already indicated, this is subject to some accretion, and there are, moreover, numerous rabbits which continually disturb the normal edaphic relations by bringing to the surface the less organic sand from below. This factor operates throughout the dune area, but especially on the Long Hills and Hood. Despite these disturbing influences, the surface soil of the Hood shows a much higher organic content, ranging from 0.61 per cent. to as much as 6.34 per cent., with an average of 2.69 per cent., or nearly 34.5 gm. per cubic decimetre.

A thirty-year-old pine wood on Holkham dunes showed an average organic content of 13.2 per cent., or over 150 gm. per cubic decimetre, in the first four inches of soil.

The dunes of successively greater age thus exhibit a perfect gradation in organic content, so that when more dune systems have been examined in detail, it may be possible to determine their approximate age by this means.

If we represent the organic content of the youngest dunes by unity, the proportional values are approximately as follows: embryo dunes 1; main ridge, 1.3; Laboratory ridge, 1.4; ridge C, ? 2.3; Long Hills, 3.0; Hood, 6.7.

TABLE V. *Summary of Data respecting Organic Content of Dunes.*

Region cf. map)	J and G	E	D	C	B	A (oldest phase)
Av. %	0.360	0.501	0.525	0.86?	1.154	2.69
Weight per cubic decimetre	5.148	7.164	7.245	11.868?	15.509	34.459

The appended data (Table VI), obtained from a transect of three samples from the Southport dune system, indicate that the same type of sequence in edaphic phenomena probably characterizes dune systems in general.

TABLE VI. *Transect Southport Dunes (Samples 0-6 in.).*

	Water capacity.	p. H.	Total carbonates. %	Organic content. %	Silt + clay. %
Dune near sea face	23.5	7.4	3.5-4.85	0.30	0.34
Medium aged turf-covered dune	30.3	7.1	2.1-3.60	2.92	1.07
Old dune near fringe of cultivation	44.0	6.8	0.5-1.6	3.25	1.10

Water-content.

Since the mineral particles are fairly uniform as regards the relative proportions of the mechanical fractions in the different phases of the dune system, the variations in water-content are mainly dependent on the proportion of organic material present.

The subjoined table (Table VII), in which the maximum water-content is shown, brings out quite clearly how this increases with the increasing age of the dune system.

TABLE VII. *Maximum Water-contents.*

<i>Dune phase.</i>	<i>Water by weight.</i>	<i>Water by volume.</i>	
	%	%	
Main ridge	26.6	38.04	} Av. by weight 25.4 % " volume 36.3 %
"	26.4	37.75	
"	24.8	35.46	
"	20.3	29.0	
"	24.0	34.3	
"	25.3	36.1	
"	27.6	39.5	
"	26.0	38.0	
"	27.0	38.6	
Long Hills	28.2	38.0	} Av. by weight 29.46 % " volume 39.44 %
"	28.9	38.8	
"	28.9	38.8	
"	26.7	35.87	
"	29.0	39.88	
"	32.14	43.20	
"	30.1	40.45	
"	28.2	38.00	
"	31.2	42.00	
The Hood	43.0	55.08	} Av. by weight 35.90 % " volume 45.99 %
"	34.3	43.94	
"	34.5	44.19	
"	37.3	47.80	
"	29.8	38.20	
"	32.54	41.70	
"	33.2	42.53	
"	31.9	40.86	
"	46.59	59.68	

Comparing the average water-contents in Table VII with the average organic contents already given in Table V, we find that the Long Hills show an increased water-content over that of the main ridge of 3.06 per cent., whilst the increased water-content of the Hood as compared with the main ridge is 10.50. The respective increases in organic content are 0.653 and 2.19.

If then the increase of the water-content is due almost entirely to the increased organic material, it follows that we should be able to calculate approximately the increase of water content for the Hood from the organic increase, having regard to the figures yielded by the Long Hills. This calculated value is 10.26 instead of 10.5 as found experimentally. Put in another way the ratio $\frac{\text{increase of water-content}}{\text{increase of organic content}}$ should yield an approximate constant; the actual values obtained are 4.68 and 4.79, which are as close as could be expected.

The conclusion seems warranted, then, that the organic material is

mainly responsible for the water capacity of dune soils, and it is in conformity with this that the roots of ephemerals (cf. Text-fig. 2) tend to occupy the upper layers of the soil in which the humus is mainly present. Also it is significant that numerous rootlets are often developed around old buried rabbit droppings with which the root systems may come in contact.

TEXT-FIG. 2. Root systems of *Cerastium semidecandrum*, *Phleum arenarium*, and *Draba verna*, three dune ephemerals, showing their shallow character. ($\frac{2}{3}$ natural size.)

The subject of the nature and extent of root systems cannot be gone into here, but it may be mentioned that careful study of those of several ephemeral species shows that the volume of soil exploited is about 360 c.c. in *Cerastium semidecandrum*, 160–430 c.c. in *Phleum arenarium*, 750 c.c. in *Myosotis collina*. In most cases the average depth of the root systems of the ephemerals is about 12 cm.

In contrast to this, the larger plants have very extensive and deep

root systems on which one not infrequently notes the copious development of fine rootlets in relation to rabbit faeces, fragments of old *Psamma* rhizomes, &c. For example, the root system of a *Silene maritima* plant growing in sand occupied a volume of over eight cubic feet of sand, and the aggregate length of the main roots was over 11 ft. (For the exposure

TEXT-FIG. 3. Root systems of *Myosotis collina* and a seedling of *Senecio jacobaea*. ($\frac{2}{3}$ natural size.) of this root system I am indebted to Miss P. Hutchinson.) Here, as in other cases, the method adopted was to support the roots *in situ* by means of wire stakes and remove the sand by an air blast.

Soil Reaction and the Effect of Rabbits.

The highest p. H. values in the dunes, i. e. the most alkaline conditions, are realized in the earliest stages of the succession. The lowest p. H. value observed in the young dunes was 6.9 and the highest 7.4.

The average for all the thirty different loci sampled was 7.17.

The sand in these early stages is therefore generally alkaline and only rarely slightly acid.

The main ridge shows a similar range, viz. p. H. 6.9–p. H. 7.3, whilst the average for twenty-six localities is slightly more acid than for the youngest phase, being 7.029.

Transferring these values from the logarithmic notation to specific alkalinities, the average value for the young dunes is represented by a specific value of 1.5, and that of the main ridge by approximately 1.

Determinations of the ridges D and C made in samples from twenty-five loci showed an average value of p. H. 6.4 for the 0–4 in. depth, or a specific acidity of approximately 3.98. The values range from p. H. 6.1–p. H. 7.3, whilst for the top inch the p. H. may be as low as 5.6.

Several series were taken at varying depths (cf. C 20–C 35; D 12–D 9; D 13–D 19; D 37–D 38). These represent nine locations, and in eight show a lower value for the surface inch. The rise in acidity from below upwards is somewhat abrupt and corresponds to the region of rapidly increasing organic content (cf. D 17, D 18).

On the Long Hills the range is from p. H. 5.9–p. H. 7.0, with p. H. 6.38 as the average value for the top four inches (fourteen locations), a slightly higher acidity than that of ridge D. Here, too, the surface layer is the most acid. B 19, B 20 offer, it is true, the reverse condition, but these are samples from the landward slope of the proximal end where limited accretion takes place.

The Hood samples show a p. H. range of from p. H. 5.5–p. H. 6.9, with an average of 6.24, corresponding to a specific acidity of about 6.3, or rather more than $1\frac{1}{2}$ times as acid as the ridges C and D.

It is then evident that the acidity of dune soils increases with their age. The presence of carbonates in appreciable amount in the early phases of dune development obviously inhibits at first the realization of an acid reaction. But, as we have already shown, the carbonates diminish owing to continued leaching action as we pass from the younger to the older dunes, so that in the latter the rising acidity develops unhindered.

If we compare only those dune soils of ridges C, B, and A, in which no detectable carbonates are present, we find that the averages still show the same increasing acidity, viz. ridge C, p. H. 6.83; B, p. H. 6.28; Hood, p. H. 6.07. Here, then, the rise is clearly not related to carbonate content, but is associated with increasing organic content accompanying increasing age.

Comparison of the samples from the Long Hills amongst themselves shows that the lowest p. H. value is associated with the highest organic content, but the lowest organic content is not associated with the highest p. H. value. That the relation is nevertheless a real one seems indicated by those

samples where both the surface and subsurface agree in having the same carbonate content or none at all. Thus samples D 17 and D 18 from the Laboratory ridge both showed 0.05 per cent. carbonates, but whilst the upper four inches, with an average organic content of 0.53 per cent., had a p. H. of 6.9, the lower level (4-8 in.), with an organic content of 0.35 per cent., had a p. H. of 7.1. The same feature is brought out by the samples B 6 and B 7, and A 1 and A 2.

In view of such results where the humus has the same source of origin, the suggestion seems warranted that such discrepancies as occur between the organic content and the p. H. value, where carbonates are absent, may be, in part at least, attributable to differences of origin of the organic material; in other words, may be influenced by the nature of the plant covering. Also the rate and state of decay are important factors.

Determinations of humus obtained from different species show considerable differences as indicated below:

<i>Psamma</i> 'leaves'	very slightly decayed	p. H. 5.4-6.0
"	" more decayed	p. H. 5.7-6.4
"	" almost completely disintegrated	p. H. 6.2-6.8
<i>Senecio jacobaea</i>	very slightly decayed	p. H. 5.6
<i>Silene maritima</i>	advanced decay	p. H. 7.3
<i>Carex arenaria</i>	partly decayed	p. H. 6.7
<i>Cladonia</i>	" "	p. H. 5.4

These estimations were based on too few examples to permit us to lay much stress on the actual values obtained, but the *Cladonia* 'humus' is clearly very acid, whilst the 'humus' formed by the pioneer species is clearly less so. Within certain limits we should expect the humus derived from a given species to have a definite reaction dependent on the degree of ionization of the substances capable of yielding hydrogen ions. Therefore on first consideration it might seem unlikely that the amount of organic matter present would influence the reaction. But the above data for *Psamma* show that the reaction varies with the stage of decay, and will therefore be influenced by the rapidity with which this proceeds. The amount of humus present is roughly a measure of the rate of decay, and hence a large organic content being associated with slow decomposition will involve a larger proportion of material in the earlier and more acid stage of decay.

Another factor that must be considered is the presence of rabbits, which are constantly feeding on such plants as *Psamma arenaria* and *Carex arenaria*, and whose faeces consist very largely of partially digested fragments of their leaves. The faeces are deposited on the dune surface of all phases, but especially the younger. Here they become buried by subsequent accretion, whilst in the older phases they are swept by the wind into the rabbit holes.

TABLE VIII.
Weight and Number of Rabbit Faeces on Dunes.

I. Number on surface.

<i>Dune type.</i>	<i>Area examined (15 counts). sq. m.</i>	<i>Total no./sq. metre.</i>	<i>Air dried. Total weight/sq. metre. gram.</i>
Main ridge slope	0.2655	1039	86.65
" "	"	773	73.60
" top	"	1042	96.70
Average for 'yellow dune' by number, 951 per sq. metre; by weight, 85.6 gram.			
Laboratory ridge	0.2655	926	59.20
" "	"	1090	92.80
Ridge P, Loose sand (<i>Soldanella</i>)	"	952	70.71
" P, <i>Cladonia</i> , moss, <i>Psamma</i>	50	332.6	19.25

Average for 'grey dune' by number, 825 per sq. metre; by weight, 60.40 gram.

II. Number and weight per unit volume to depth of 7 cm.

Area A.

<i>Condition.</i>	<i>Volume.</i>	<i>Number per sq. metre.</i>	<i>Air dried. Weight per sq. metre.</i>
	c.c.		gram.
Unenclosed	2,184 { Surface	1,600 {	Total 5,470
	2,184 { Subsurface	3,870 }	
"	2,184 { Surface	1,248 {	" 8,032
	2,184 { Subsurface	6,784 }	
"	2,184	" 3,072	" 147.2
Enclosed	2,184 { Surface	352 {	" 1,280
	2,184 { Subsurface	928 }	
"	2,184 { Surface	352 {	" 3,360
	2,184 { Subsurface	3,008 }	
"	2,184 { Surface	480 {	" 3,200
	2,184 { Subsurface	2,720 }	

Average unenclosed, 248.2 gram.

" enclosed, 100.8 gram. Difference, 147.4 gram.

Area B.

<i>Condition.</i>	<i>Volume.</i>	<i>Number per sq. metre.</i>	<i>Air dried. Weight per sq. metre.</i>
	c.c.		gram.
Unenclosed	2,184 { Surface	832 {	51.2 {
	Subsurface	1,824 }	83.2 }
		Total 2,656	Total 134.4
"	2,184 { Surface	512 {	27.2 {
	Subsurface	4,640 }	213.4 }
		" 5,152	" 240.6
"	2,184 { Surface	1,536 {	92.8 {
	Subsurface	1,568 }	51.2 }
		" 3,104	" 144.0
Enclosed	2,184 { Surface	288 {	9.6 {
	Subsurface	1,600 }	48.0 }
		" 1,888	" 57.6
"	2,184 { Surface	320 {	10.2 {
	Subsurface	864 }	20.8 }
		" 1,184	" 31.0
"	2,184 { Surface	288 {	9.6 {
	Subsurface	3,008 }	112.0 }
		" 3,296	" 121.0

Average unenclosed, 173.0 gram.

" enclosed, 69.8 gram. Difference, 103.2 gram.

" deposit per annum Areas A and B, 35.8 gram. (air dried).

" " " (dried at 100° C.) = 34 gram.

" " organic material/100 gram. soil = 0.18.

" content faeces per 100 gram. soil (unenclosed) subsurface A and B = 4.6 %.

N.B.—In the above figures only those faecal particles retained by a 0.5 mm. sieve are included. In the soil data for humus content these have almost entirely been removed by sieving.

The amount of organic material contained in these rabbit droppings is important, as also their reaction. With respect to the former point numerous counts were made of the number of rabbit droppings on a surface of unit area, and also of those present on and below the surface of a unit volume (cf. Table VIII). The figures for the surface deposit were also checked by entirely denuding an area of 50 sq. metres of all the rabbit faeces visible to the unaided eye (cf. below).

It will be realized from the data in Table VIII that rabbits play no small part in the supply of organic material to the soil.

Comparing the figures for the open dune, and those for areas of the same dune from which rabbits had been excluded for a period of $3\frac{1}{2}$ years, we arrive at the conclusion that the annual deposit (assuming the rate of decay of the old droppings to be of the same order as for old and new together in the unenclosed area) is approximately 34 grm. on an area of 312 sq. cm., or about 0.18 per cent. by weight of the soil.

A striking feature of the decay of these faeces is that their form is more or less retained throughout the process, so that one can roughly grade them according to age by the change in size, as well as by the progressively darker tint.

Estimations of the hydrogen-ion concentration show that as decay proceeds there is a similar change with age as observed for normal plant remains, the early stages being much more acid, p. H. 5.8–p. H. 6.4 (av. p. H. 6.1), than the most advanced state of decay (av. p. H. 6.9). Despite this difference, however, and the comparatively low buffer action of sand dune soils, there is only a slight difference in the reaction of the enclosed and unenclosed areas. Such difference as exists is indeed the reverse of what one might expect from the absence of recent droppings in the enclosed areas (cf. Table IX).

The clear tendency, as shown in Table VIII, 1, is for the rabbit droppings to decrease in amount from the younger to the older dunes (compare 'yellow' and 'grey' dunes, Table VIII) in correspondence with the diminishing amount of *Psamma arenaria* and other of the more favoured food plants.

TABLE IX.

Area A.

Enclosed (Sample I)	p. H. 6.85	Unenclosed (Sample I)	p. H. 6.95
" (" II)	" 6.85	" (" II)	" 6.95
" (" III)	" 6.80	" (" III)	" 7.05

Area B.

Enclosed (Sample I)	p. H. 6.9	Unenclosed (Sample I)	p. H. 7.0
" (" II)	" 6.9	" (" II)	" 6.9
" (" III)	" 6.9	" (" III)	" 6.9

Av. enclosed p. H., 6.86; av. unenclosed p. H., 6.95

As the acidity and organic content of the soil both rise with increasing age of the dune system, the influence of rabbit droppings, either as regards the amount of organic material added, or the soil reaction, is evidently of quite minor importance. Rabbit faeces are, however, of considerable significance in the water economy of the dune plants, as is shown by the frequency with which copious development of fine roots is often associated with their presence.

The Influence of the varying Soil Conditions on the Dune Vegetation.

The stages in dune succession have been shown to present a graduated series of conditions with increasing age; an edaphic succession in fact in which mobility, low organic and water contents, high calcium content, and a neutral or alkaline reaction mark the earliest phases, whilst the final phases present a stable soil, a high organic content, relatively high water-content, a total absence or negligible quantity of calcium, and an appreciable acidity. The adaptation of the pioneer species to mobile soil, the stimulated growth they exhibit when buried by further accretion, are facts so well known as to require no emphasis here. The stabilizing action of the plant covering, which enables less specialized species to become established, is also not only familiar but underlies the elaborate technique of dune maintenance and protection. The calcium content and reaction of dunes have, however, received but little attention, and it is upon the influence of the changes in these that we would lay particular stress.

The writer has elsewhere pointed out ('The Significance of the Calcicolous Habit', *Journal of Ecology*, vol. viii, pp. 202-15, 1920) that the plants normally characteristic of soils rich in calcium probably occur on such, either on account of their preference for bases or because of the dry character of these soils. The data here given show that both conditions are satisfied in the younger dune phases, and hence we might reasonably expect to find something in common between the flora of the chalk and that of the 'yellow' dune.

There is reason for suspecting that some of the pioneer species, such as *Psamma arenaria*, *Elymus arenarius*, *Agropyrum junceum*, *Euphorbia Paralias*, &c., are somewhat partial to a calcium-rich medium and may perhaps be 'oxyphobic', but their specialization to a mobile substratum precludes the expectation of their occurrence on chalk downs and, similarly, we should not expect to find representatives of the calcareous pasture on the extremely mobile soil of an embryo dune. The edaphic conditions of the later phase of the yellow dune are those where we should look for the resemblances indicated.

Actually no species especially characteristic of the chalk flora are met with on the Blakeney Point dune system, but elsewhere in this country and in other parts of Europe the calcicole element in the dune flora is

a marked feature. Robert Smith describing the fixed dunes near Edinburgh mentions the occurrence of *Thalictrum minus*, *Anthyllis Vulneraria*, *Astragalus danicus*, *A. Glycyphyllos*, and *Gentiana Amarella* (Scottish Geog. Mag., vol. xvi, pp. 385-416, 1900). The list given by W. G. Smith for the dunes on the coast of Fife includes *Astragalus danicus*, *Ononis repens*, *Linum catharticum*, *Trifolium procumbens*, *Medicago lupulina*, *Galium verum*, *Gentiana campestris*, *G. Amarella*, *Thymus serpyllum* and *Koeleria cristata* (Scottish Geog. Mag., vol. xxi, pp. 70-1, 1905). Moss, describing the dunes of Somerset (Journ. Roy. Geog. Soc., pp. 8-17, 1907), enumerates several dune species which attain their greatest abundance on chalky soils, of which *Iris foetidissima*, *Carlina vulgaris*, *Anthyllis Vulneraria*, and *Inula Conyza* are perhaps the most noteworthy. In 'Types of British Vegetation' *Anthyllis Vulneraria*, *Chlora perfoliata*, *Gentiana campestris*, *G. baltica*, *Epipactis latifolia*, and *Orchis pyramidalis* are mentioned as occurring on the Lancashire dunes.

In Ireland the same feature holds. Colgan and Scully in the 'Cybele Hibernica' (2nd ed., 1898) cite many species as calcicolous in that country, of which nine are mentioned as occurring on sand dunes. These are *Arabis hirsuta*, *Viola hirsuta*, *Orchis pyramidalis*, *Ophrys apifera*, *Asperula cynanchica*, *Carlina vulgaris*, *Leontodon hirtus*, *Gentiana verna*, and *Clematis Vitalba*.

As might be expected this feature extends also to the Cryptogamic flora, and Watson (Journal of Ecology, pp. 126-42) cites *Barbula tophacea*, *Trichostomum crispulum*, *Camptothecium lutescens*, *Pellia fabbroniana*, *Preis-sia quadrata*, *Lophozia badensis*, and *Scapania aspera*, as species whose occurrence on dunes is determined by the presence of comminuted shells.

On the Continent the same feature is strikingly exhibited. Massart ('Essai de Géographie botanique,' pp. 390-1, 1907) cites no less than twenty species which in Belgium are practically confined to dunes and calcareous soils. Of the total of 117 flowering plants cited by Abromeit ('Handbuch des deutschen Dünenbaues', Berlin, 1900) as present on German dunes some 19 specimens are more or less marked calcicoles. The same feature in another field is exemplified by the occurrence of the calcicole snail, *Cyclostoma elegans*, on sand dunes (cf. A. E. Boycott, Proc. Malac. Soc., vol. xiv, p. 128, 1921).

At the other extreme the oldest dunes present, as we have seen, an almost entire absence of carbonates, and it is associated with this condition and a high acidity that *Polypodium vulgare* is met with in our area on the Long Hills, whilst *Pteris* and *Athyrium* occur on the Hood.

On other systems these oldest phases of leached dune soils are marked by the presence of *Calluna vulgaris* and other ericaceous plants. Any factor tending to accelerate leaching will naturally favour the colonization of 'calcifuge' plants. As the writer has pointed out, in relation, particu-

larly, to other types of vegetation (cf. *Journal of Ecology*, vol. ix, pp. 220–40, 1922), leaching being most rapid at the crest of a hill or the upper part of a valley slope, the flora tends as a rule to become more calcifuge in character as we ascend. It is in conformity with this generalization that, as pointed out by W. G. Smith for the dunes of Fife, *Calluna vulgaris* and *Erica cinerea* occur more particularly towards the crest of the dune ridges (loc. cit., p. 71).

Even in these old dunes, with their low proportion of plant food, the hollows support a type of vegetation which bears much the same relation to the calcifuge flora of the ridges as the path and valley-bottom vegetation bears to that of the general woodland vegetation in an acid oak wood (cf. *Salisbury, Journal of Ecology*, vols. iv and vi, 'The *Quercus-Carpinus* Woods of Hertfordshire').

The extreme calcifuge character of ancient dunes is sufficiently emphasized by the fact that such species as *Corallorrhiza innata*, *Vaccinium myrtillus*, *V. Vitis-idaea*, and *Pyrola rotundifolia* have been recorded from old dune systems in this country. That other dune systems show the same feature as those of Blakeney is illustrated by the data given on p. 400 for a series of samples from the Southport dunes.

The dune soils exhibit the usual humus gradient (cf. *Salisbury, Journal of Ecology*, vol. ix, p. 221), which is well illustrated by the appended data from two areas on the Long Hills, one covered by vegetation and the other bare, as well as by the estimations already furnished.

<i>Depth.</i>	<i>No vegetation.</i>	<i>Vegetation.</i>
in.		
0–6	4.78	3.96
6–12	1.38	1.14
12–18	0.68	0.93

It is this increase in humus in the surface layer that is probably mainly responsible for the colonization of the younger 'fixed' dunes by *Tortula ruraliformis* and other mosses. Although relatively dry in summer the surface soil, from its comparatively high organic content (cf. D 36–D 48, D 43, &c.), ensures considerable moisture during the winter months.

In the Blakeney system *Triticum junceum*, *Arenaria peploides*, *Festuca arenaria*, and *Eryngium maritimum* are more or less restricted to the earlier 'yellow' dune phases. In the more stabilized condition *Psamma* decreases in amount and the individuals exhibit diminished vigour.

On the ridge D mosses, particularly *T. ruraliformis*, *Carex arenaria*, *Erodium*, &c., make their appearance.

THE LATERAL SHINGLE BEACHES.

From the point of view of edaphic succession it must be borne in mind that the main shingle bank throughout its entire extent is more or less subject to (*a*) addition of new material, (*b*) removal of material from the sea-face landwards, (*c*) submergence by excessively high tides bringing with them new supplies of organic material and carbonates in the form of shells. These conditions maintain the main beach in a more or less juvenile state, so that the natural changes which might be anticipated with the lapse of time tend to be masked.

The instability of the shingle is considerably diminished by the presence of *Suaeda* bushes, and where these are most numerous, viz. opposite the marrams, the largest number of species and the most extensive carpet of vegetation anywhere upon the main shingle bank are met with. The importance of this lack of mobility is further emphasized by the location of certain species, e. g. *Convolvulus soldanella* in the neighbourhood of the *Suaeda* bushes, with every indication of having spread from these latter as their centres of origin (cf. F. W. Oliver, 'The Shingle Beach as a Plant Habitat', New. Phyt., vol. ii, pp. 73-99, 1912, and Oliver and Salisbury, 'Vegetation and Mobile Ground', Journal of Ecology, vol. i, pp. 249-72, 1913).

The lateral hooks still further emphasize the great importance of the degree of mobility. These are for the most part extremely stable and present in their older phases a continuity of vegetation which is never attained on the main bank itself.

Each lateral bank represents a landward deflexion of an original termination of the main bank, which latter subsequently continues its growth in a sympodial manner.

The interval between two successive laterals is thus an indication of the time interval between the violent storms during which the laterals are formed. The latter, owing to the continued growth of the main beach, are relatively sheltered, and this protection is increased with the formation of each new lateral (cf. Oliver, 'The Shingle Beach as a Plant Habitat').

Mechanical Analysis and Mobility.

Perusal of the data in Table X respecting the mechanical analysis of the successive shingle laterals into coarse and fine particles shows that the proportion below 0.5 mm. in diameter increases with the increasing age of the shingle bank, the lowest values being obtained in samples from the main beach. The oldest laterals have indeed nearly seven times the proportion of fine particles present in the shingle of the main beach.

It will be noted that both the observed range and average for the oldest lateral but two (Bank III) is higher than for the oldest lateral itself.

This, taken in conjunction with the higher carbonate content and lower acidity of the latter, is indicative of an edaphic condition not strictly in conformity with its position in the series.

The increasing proportion of fine material on the older banks naturally tends to cement together the larger stones more firmly, thus effectively contributing to the augmenting stability. In addition, it further reacts on the power of water retention, so that plants less tolerant of both drought conditions and mobility are able to colonize the shingle. (For a discussion of the water relations of shingle beaches, cf. Hill and Hanley, *Journal of Ecology*, vol. ii, pp. 21–35, 1914.)

TABLE X.

Mechanical Analysis of Shingle.

Percentage of fine particles below 0.5 mm. in diameter.

<i>Main shingle bank.</i>	<i>Range observed.</i>	<i>Average.</i>
	%	%
(a) Bare shingle	2.7–10.6	6.7
(b) Under <i>Suaeda</i> bush	2.8–8.6	5
(c) Fine shingle with grasses	0.4	—
(d) Fine shingle bare	0.19	—
<i>Lateral banks.</i>		
Bank XVII	18–19	18.7
„ XII ('Yankee')	11–30	19
„ VIII ('Watchhouse')	28–31	29
„ VII	27–32	30
„ IV	20–35	26
„ III	35–60	47
„ I (oldest)	33–56	45

The two chief pioneers, *Arenaria peploides* and *Silene maritima*, are both 'mat' formers which react freely to burial under shingle and are stimulated to more vigorous growth thereby. Both freely develop adventitious roots, and *Silene maritima* not infrequently adventitious buds, from the deep-seated and extensive root system.

Any attempt to dig up either of these species will convince the most sceptical of the extent of root and shoot systems and their efficacy as shingle binders.

When NW. gales combine with high tides the main shingle bank may at very infrequent and irregular intervals become awash, and in these conditions the soil fractions become to some extent elutriated. The finest particles are probably carried down to the landward side or on to the marshes, the heaviest pebbles may be moved only slightly, whilst the fine shingle bestrews the floor of the percolation gully. Therefore such shingle patches, as will be seen from Table X (c) and (d), contain an extremely low proportion of particles under 0.5 mm., and only about 27 to 31 per cent. over 6.5 mm., as compared with 35–61 per cent. elsewhere. This water-sifted shingle is the especial home of *Poa loliacea*, *Lepturus filiformis*, and *Sedum acre*, whilst the most stable shingle of the main beach supports the

densest growth of *Silene maritima* and *A. peploides*, with the addition in particular of *Sonchus arvensis* v. *angustifolius*, *Festuca rubra*, three isolated patches of *Convolvulus soldanella* and two of *Tussilago Farfara*. The latter is often regarded as characteristic of stiff clayey soils, but its absence from many lighter types is very probably an outcome of their poverty in mineral salts and acid tendency. Unless it be the conditions associated with a more or less neutral reaction that determine the occurrence of *T. Farfara* its presence here demands explanation.

Organic Content, Carbonates, and p. H.

In order to appreciate the significance of the data regarding the organic content, carbonate content, and hydrogen-ion concentration, it is necessary to appreciate that, just as the main dune ridge, which marks the oldest range with marked accretion, is the highest, so too the shingle laterals develop to a maximum, after which they undergo a flattening process partly perhaps the outcome of wave action, but largely the natural process of 'settling' which manifests itself chiefly in the replacement of the convex crest by a flat one. The highest level reached by laterals is at their L-shaped distal end, which forms a high elbow here, although only reached by the highest tides during exceptional storms; the same flattening of the profile is to be noted.

As a consequence of this lowering of the level with age, the oldest lateral banks share in common with the younger the fact that they are more frequently tide-covered than those of intermediate age; it is to this that we must attribute the attainment of the most extreme conditions associated with increasing age on the Watchhouse bank and high elbows.

The Carbonate Content.

The data in Table XI, Appendix, and the appended summary Table XII, show that the total carbonates are highest in the youngest lateral XX and fall to their minimum in laterals IV to VIII, again rising slightly in I and III.

TABLE XII.

Summary of Data for Crest of Laterals.

	(Averages of all estimations.)								
	Youngest bank = XX; oldest = I.								
	XX.	XVII.	XVI.	XII.	VIII.	VII.	IV.	III.	I.
Av. loss on ignition %	0.486	0.32	—	7.12	22.45	5.52	2.39	2.64	3.19
„ total carbonates %	0.813	0.16	—	0.103	0.03	0.03	0.00	0.006	0.015
„ p. H.	7.59	7.22	7.0	6.72	6.38	6.59	6.96	6.86	6.90

Here then, too, as on the older dunes, we see the effect of leaching clearly marked. In the case of Bank VIII the two spots on the high elbow

(X.46 and X.46a) show a lower carbonate content than the main bank, but the single sample from the high elbow of VII shows a slightly higher

TEXT-FIG. 4. Graph showing the relation between organic content and carbonates in dunes of varying ages as indicated by the letters A to J (cf. map, Text-fig. 1).

content than the other parts of the bank. Taking all the banks into consideration, however, there is a general tendency for the lowest values to be found towards the higher levels at the distal end, which supports the view that leaching is the main factor involved.

The Organic Content.

The youngest bank has a very low organic content, under a half per cent., whilst again the eighth lateral shows the extreme condition with an average of over 22 per cent., and there is falling off in the older laterals.

Here, then, it is quite evident that the increasing organic content accompanying increasing age is a feature of the lateral shingle banks as well as of the dunes. That the diminished organic content of the oldest

TEXT-FIG. 5. Graph showing relation between percentage carbonate content of the soil of the crest of shingle laterals and their age as indicated by their positions in the shingle system.

laterals is correlated with their lower level is borne out by the exceptionally high organic content shown by the soils of the 'high elbows' of both laterals VIII and VII. In the former the organic content may be nearly 29 per cent., and in the latter nearly 15 per cent. as compared with about 12 per cent. and 4 per cent. as the respective observed maxima for the lower parts of the crest.

The Hydrogen-ion Concentration (cf. Tables XI and XIII, Appendix).

As is to be expected from the foregoing considerations, the reaction of the soil of these laterals exhibits an increasing acidity with age, which attains its maximum on the high elbow of Bank VIII with a p. H. of 5.9. The

averages show a perfect gradation from XX to VIII, with a subsequent decrease in acidity (rise of p. H.) in the oldest laterals.

It is evident that the inundation of these latter, infrequent though it be, is sufficient to restrain the development of a high acidity, and hence by favouring the oxidation of the organic material precludes the accumulation of a high proportion of humus.

The crest of the lateral banks, therefore, presents us with a definite edaphic sequence of the same general type as that shown by sand dunes or by woodlands, but whereas in these cases the increasing acidity would appear to be more or less continuous till the curve flattens out, here a topographical change intervenes to cause retrogression.

Vegetation (cf. Appendix, Table XIV).

The high elbows of VII and VIII exhibiting as they do the maximum of *both* height and age, we not unnaturally find here the greatest departure from the maritime condition. The less specialized habitat, consequent upon the increased proportions of organic material and finer soil particles, and the still greater freedom from tidal inundation, associated as these are with increased stability and the operation of the time factor, brings with it an augmented flora. It is interesting in this connexion to note that, as shown in the accompanying lists (Appendix, Table XIV) for laterals of varying age, the maximum number of species, viz. fifty-one, is recorded for Bank VIII, whilst the smallest number, viz. six, is present on the newly-formed lateral. That the time factor alone is not responsible is shown, however, by the diminution in number on the oldest laterals as shown below.

Number of Species present on Crest of Laterals of Increasing Age.

	Youngest ← ————— → Oldest								
	XX.	XVII.	XII.	VIII.	VII.	VI.	IV.	III.	I.
No. of species	6	6	34	51	36	25	21	24	16

On the youngest phases several species are present whose occurrence may be attributed to their proximity to dunes. This especially applies to Bank XII, where alone we find *Phleum arenarium* and *Stellaria boreana* occupying a shingle crest. Other species which are characteristic of the earlier phases and absent from the oldest are *Senecio jacobaea*, *Rumex crispus* v. *trigranulatus*, *Glaucium luteum*, and *Arenaria peploides*.

Silene maritima, although common on the oldest banks, is yet not so abundant as on those of medium age, nor are the individuals so vigorous.

Amongst the species confined to the 'high elbow' are *Galium verum*, *Trifolium procumbens*, and *Vicia angustifolia*. These, together with *Aira praecox*, *Festuca ovina*, *Plantago Coronopus*, *Trifolium arvense*, *T. striatum*,

Rumex Acetosella, and *Senecio sylvaticus*, and several others, are frequent and characteristic species of some of the gravelly heaths inland. *Rumex Acetosella* in particular, and the abundant *Cladonia* on all the older banks, serve to illustrate the tendency on the older banks to develop an acid-tolerant type of vegetation.

The Flanks.

Occupying the slopes of the laterals on either side there are several zones, of which the most conspicuous is the *Suaeda fruticosa* zone clothing the lower edge, and more or less corresponding in position to the normal zone of drift deposition. Above the *Suaeda* zone is a zone of rather open vegetation with numerous bare pebbles, and characterized by the presence of *Statice binervosa* and *Frankenia laevis*. Locally, at the upper limit of this zone where it passes into the crest, sometimes at the upper limit of the *Suaeda* zone, but probably always where drift tends to be deposited by the highest tides and during storms, we find a zone in which *Triticum pungens* is a marked feature, sometimes accompanied by *Atriplex littoralis*.

Within the upper portion of the *Suaeda fruticosa* zone, particularly on the basisopic side of the banks where there is more shelter and the slope is gentler, *Festuca rubra* may form an interrupted zone, whilst on this side also *Artemisia maritima* frequently occupies the lower margin of the *Suaeda* zone.

As might be expected, both the *Suaeda* and the *Triticum* zones show a high organic content, three localities in the former yielding a range from 4.9 per cent. to 15.7 per cent. (cf. also marsh vegetation, p. 418), whilst a similar number for the *Triticum* zone showed a range of from 6.38 per cent. to 41.5 per cent. The corresponding hydrogen-ion estimations ranged from 7.2–7.4 for the *Suaeda* zone and 7.0–7.6 for the *Triticum* zone. From the marrams area only one carbonate determination was made for the *Suaeda* zone, viz. 2.55 per cent., though elsewhere on the area *Suaeda fruticosa* occurs in soil with as low a value as 0.26 per cent. In the *Triticum* zone the total carbonates range from 0.04 to 4.2 per cent.

On the whole, then, the *Suaeda* and *Triticum* zones, that is, the zones of drift deposit, show a high organic content and an appreciable or often considerable proportion of carbonates.

In contrast to these, the *Binervosa* zone has a low carbonate content, varying from 0.01 to 0.07 per cent. (av. 0.028 per cent.), whilst the highest organic content observed was 4.91 per cent. and the lowest 0.47 per cent. (av. 2.63 per cent.). Appendix, Table XVI, shows also that the chloride content is subject to considerable variation in one and the same bank. These facts, combined with the slope of the surface, tend to render the habitat a decidedly xerophytic one, and it is significant that not only are the dominant species pronounced xerophytes, but that *S. binervosa* here

assumes a very dwarf habit in comparison with that of plants growing on the crest, whilst *Plantago Coronopus*, which is found in the normal state on the crest, here assumes the *forma pygmaea* (that this is only a habitat form and not a variety has been experimentally demonstrated by the writer).

The Main Beach.

The data regarding the main beach (Appendix, Table XIII) serve to show its close resemblance as a whole to the younger phases of the laterals. There is, however, a marked difference between the bare shingle and that covered with vegetation. Whereas the average carbonate content of the former is 0.53, that of the latter is 1.39 per cent., whilst the average organic content under vegetation is 2.53 per cent. as compared with 0.99 as the average for bare shingle. Since drift is often carried high up on to the main beach, this naturally tends to collect around the *Suaeda* bushes and on the mats of vegetation, so that the organic material supplied by the plants themselves is augmented by supplies of drift, which also brings with it carbonates in the form of shell fragments. Thus the influence of the plants themselves on the stability and character of the shingle soil tends to be cumulative in its action.

Chloride Determinations.

A few determinations of chlorides for various parts of the area given in Table XVI (Appendix), though insufficient to warrant any detailed consideration, are sufficient to show that the percentage of chlorides is low both for the dunes and the crests of the older shingle banks. The main shingle bank exhibits considerable variation, and indeed these data seem to indicate that the percentage of chlorides, except perhaps in the salt marsh itself, is chiefly significant in relation to the vegetation, as an index of the incidence of tidal inundation.

THE MARSH VEGETATION.

Consideration of the data in Table XV (Appendix) would seem to indicate that the differences in p. H. value have little, if any, significance in relation to the zones of marsh vegetation.

These latter are three in number: the *Suaeda fruticosa* zone, occupying the upper edge flanking the shingle; the *Salicornietum*, occupying the floor of the marsh; and the *Obione* zone, situated on the slight slope between.

Both the averages for all the data and for the transects alone show the same relation to hold with respect to the carbonates and organic matter present; namely maximum values for the *Salicornietum* (organic 9.19 per cent., carb. 2.55 per cent.) and minimum values for the *Suaeda fruticosa* zone (organic 1.36 per cent., carb. 0.676 per cent.), those for the *Obione* zone

being more or less intermediate (organic 2.74 per cent., carb. 0.92 per cent.). The chloride estimations show that the percentage of these may become very high (6.34 per cent.) in the *Salicornietum*, doubtless, as also in the case of the 3.5 per cent. recorded for the large how on the Long Hills, an outcome of evaporation.

The estimations for the *Suaeda* zone on the lateral beaches show that it flourishes in soil with as high an organic content and with a carbonate content as high as the average for the *Salicornietum*. Similarly, the appended values for an old *Obione* marsh on the marrams area obtained by Mr. Hanley indicate that the proportion of organic material is not the determining factor for this species.

	in.		%		%
Old <i>Obione</i> marsh marram	0-4	Organic matter	12.64	Chlorides	0.684
" " "	4-10	" "	7.59	"	0.576
" " "	10-14	" "	3.20	"	0.342

The observed gradient, then, with respect to carbonates and organic material, when we pass from the *Salicornietum* to the *Suaeda* zone on the *Pelvetia* marsh would appear to be important as an indication of the varying conditions rather than of significance in itself.

The differences observed are indications of the change in level and the consequent change in frequency and degree of their tidal inundation. That neither *Obione portulacoides* nor *Suaeda fruticosa* is tolerant of very high salinities is shown by their normal method of occurrence and growth behaviour. The former on old saltings is especially characteristic of the high banks of the creeks and hummocks, whilst the latter not only attains its maximum luxuriance in the upper part of the *Suaeda* zone, but, by the high development of anthocyanin pigmentation which it frequently exhibits in the low-lying areas of its distribution, betrays the existence of conditions which, whilst favourable to the formation of assimilates, are unfavourable to growth—conditions, that is, of physiological drought.

As noted by Professor Oliver at Erquy in Brittany, halophytes are very susceptible to the influence of rainfall (New Phyt., vol. v, p. 190, 1906), so much so, that the extent of growth made would appear to be largely conditioned by whether the precipitation for any given season falls mainly in the periods of the 'neap' tides or the 'springs'. This would seem to show that growth remains more or less in abeyance except during the periods following rain when the soil solution is relatively dilute. The appended data obtained at Erquy not only illustrate the rapid effect of rain in leaching out the chlorides, but also how much this is accentuated by the slightly higher level in the region occupied by the *Glyceria* sward, and still more by the higher level of the raised bank occupied by *Obione*. (During the period of observation none of these zones were reached by the

tide.) Presumably, therefore, the effect is even greater in the *Suaeda* zone. In addition to the enhanced leaching effect which the higher level brings about, the less frequent and shorter duration of inundation increases the probability of the rainfall being efficacious. The views here expressed fully accord with those of R. H. Yapp and D. and O. T. Jones, whose study of the Dovey marshes led them to state that 'the vertical distribution of salt marsh plants . . . depends largely on the frequency and duration of the periods of submergence and emergence respectively' (Journ. Ecology, vol. v, p. 100, 1917).

	Chlorides.		Decrease.	
	Before rain	%	After rain	%
<i>Salicornietum</i>		5.7		
<i>Glyceria-Salicornia-Suaeda maritima</i>	"	3.79-3.27	"	4.19-4.36
<i>Obione portulacoides</i>	"	2.96-3.14	"	2.50-2.08
				0.37
				25
				35
				87

Both the species in question occur high up on the shingle laterals where inundation is a rare phenomenon. As compared with plants similarly situated on the main beach, however, they are low in stature, and not infrequently of unhealthy appearance. Probably the low proportion of mineral salts and the acid reaction are here the limiting factors.

Miss Halket found (Ann. Bot., vol. cxiii, 1915, pp. 143-54) that *Glyceria maritima* grew best when the water contained no Tidman's sea-salt, *S. ramosissima* and *Suaeda maritima* grew best in a 1 per cent. solution, whilst *S. Oliveri* grown in varying concentrations of NaCl showed maximum growth in 2 per cent. solution. Since, in the last instance, sodium chloride was employed instead of the balanced solution furnished by sea-salt, it seems probable that maximum growth would have been exhibited in an even higher concentration of the latter. In any case it is significant that *Salicornia Oliveri* occupied the lowest zone at the Bouche d'Erquy, *S. ramosissima* an intermediate zone, and *Glyceria* the highest parts.

The *Statice*s, which are so well represented at Blakeney, present a series of species which, like the *Salicornias*, occupy successively higher zones of the marsh. Of these *Statice humilis* occupies the most frequently inundated marshes, and it may be for this reason is the only British species which fails to grow vigorously in ordinary garden soil. *Suaeda fruticosa* and *Statice binervosa* will, on the other hand, grow in garden soil with extreme luxuriance.

Of the *Salicornietum* samples, those from the middle region of the *Pelvetia* marsh represent an old condition, whilst those from the Samphire marsh represent a very recent one. It will be noted that the proportion of organic material is greater in the older marsh. Similarly, whilst the relatively recent *Obione* zone of the *Pelvetia* marsh occupies a soil with from 1.01 to 5.21 per cent. organic material, that of the old *Obione* marshes

ranges from 12.64 to 21.69 per cent. There is evidently then a tendency for the organic content to increase with the lapse of time.

SUMMARY.

An account is given of the soils of Blakeney Point as they affect the vegetation, based on the examination of a large number of samples from phases of very diverse age, of which, however, the sequence is known with a high degree of certainty.

These show that the dune systems as they grow older exhibit a diminution of carbonates and an increase of the organic content. Accompanying these changes, which are the result of leaching and the augmented plant covering, there is a change from an appreciably alkaline condition exhibited by the embryo dunes to a marked acidity in the oldest phases. With these edaphic changes are correlated the accompanying succession in the vegetation.

The part played by rabbit droppings in influencing the organic content and the reaction is considered, and quantitative data are furnished.

The hydrogen-ion concentration is shown to vary, not only with the degree of leaching and organic content, but also according to the source of origin of the organic material and the phase of its decomposition.

The relation between the organic content and the water-content of dune soils is shown to be a close one.

The shingle banks are found to show a similar sequence alike in respect to reaction, organic content, and water-content, as also in stability. This is brought out by a study of shingle laterals of successive age, of which also tabulated floristic lists are given.

The salt-marsh phases likewise show indications of increasing organic content, but here the important edaphic factor would appear to be the duration and frequency of tidal inundation.

APPENDIX.

TABLE I. *Dune Soils.*

Sample No.	Young Dunes J. and G. Series.	p. H.	Loss on ignition. %	Total carbonates. %
J. 030	Embryo <i>Psamma</i> dune E. of Lifeboat House	7.2	0.37	0.34
J. 031	" " W. " "	7.3	0.35	0.39
J. 022	" " " " "	7.1	—	—
J. 023	" " " " "	7.1	—	—
J. 024	Rather larger than 022-023 same system	7.0	—	—
J. 032	Very young <i>Psamma</i> dune on New Spit	7.4	0.16	0.44
J. 033	" <i>Triticum</i> " "	7.3	0.43	0.46
J. 036	" " " "	7.4	0.34	0.32
G. 01	" dune on sea-face	7.4	0.52	0.35
G. 001	" " "	7.4	—	0.39
G. 014	" dune 4 in. high	7.2	—	—
G. 013	" dune 12 in. high near 014	7.1	—	—
G. 015	Young dune near 013, 30 in. high (0-4)	7.0	0.30	0.61
G. 016	Same as 015 (4-10)	6.9	—	0.41
G. 025	Very young outer dune	7.2	0.39	0.36

TABLE I (continued).

Sample No.	Young Dunes J. and G. Series.	p. H.	Loss on ignition. %	Total carbonates. %
G. 026	Very young outer dune	7.4	—	0.58
G. 09	" " 30 yds. seawards of 010	7.1	—	—
G. 010	Young dune larger than 09 on sea-face	7.0	—	0.58
G. 017	Near but larger than 016, 0-4 in.	7.05	—	—
G. 018	As 017, but 4-10 in.	6.9	—	—
G. 07	Young dune 50 yds. SW. of 010	7.1	0.33	0.32
G. 071	" " " "	7.1	—	0.39
G. 05	50 yds. SW. of 07	7.2	—	—
G. 06	13 yds. landward of 05	7.2	—	—
G. 08	13 yds. " 07	7.1	—	—
G. 027	Very young dune near 'Glaux' low	7.1	0.23	0.38
G. 028	" " "	—	0.35	0.35
G. 029	" " "	—	—	0.28
F. 019	Hollow between young dunes	7.0	—	—
F. 02	Young dune, <i>Psamma</i> flowering freely	7.3	—	—
F. 03	" 75 yds. NE. of 01	7.3	0.46	0.60
F. 04	Larger dunes of outer system 17 yds. N. of 03	7.1	—	—
F. 011	Outermost dunes with <i>Psamma</i> and <i>Arenaria</i> <i>peploides</i> 0-4 in.	7.1	0.36	0.34
F. 012	As 011 but 4-10 in.	7.1	—	0.57
F. 020	Older dune 0-4 in.	7.0	0.42	0.36
F. 021	As 020 but 4-10 in.	7.1	0.42	0.41

p. H. range, 6.9-7.4; av. 7.1. Loss on ignition, 0.23-0.52 %; av. 0.36 %. Carbonates, 0.28-0.61 %; av. 0.425.

Main Ridge. Series E.

E. 1	Seaward slope near 'Glaux' low 0-4 in.	6.9	—	—
E. 2	" " " 4-8 in.	6.9	—	—
E. 3	Landward slope 13 yds. from E. 1	7.0	—	—
E. 4	Near big 'blow-out'	7.0	—	—
E. 5	5 yds. S. of Notice Board	6.9	—	—
E. 8	20 yds. SW. of E. 7 in hollow 0-4 in.	7.1	—	—
E. 9	Same as E. 8 in hollow 4-8 in.	6.9	—	0.65
E. 12	Burnt patch of <i>Psamma</i> seaward slope	6.9	—	0.47
E. 13	" " landward slope	7.0	—	—
E. 16	8 yds. down seaward slope near E. 14	7.0	0.34	0.43
E. 17	8 yds. " landward " "	6.9	—	—
E. 20	Hollow 25 yds. S. of E. 18 0-4 in.	6.9	0.33	0.21
E. 21	" " " 4-8 in.	7.1	—	0.23
E. 22	Southern edge of main ridge	7.0	—	—
E. 24	Seaward slope	7.3	—	0.65
E. 25	Slope	—	0.29	0.21
E. 32	"	—	—	0.20
E. 33	"	—	1.60	0.15
E. 6	Crest of ridge near E. 8	7.1	0.38	0.23
E. 7	" " E. 6	7.0	0.51	0.50
E. 10	" " "	7.0	—	—
E. 11	" " "	6.9	0.39	0.41
E. 14	0-4 in.	7.0	—	—
E. 15	4-10 in.	7.1	—	—
E. 18	Crest extreme outer end of ridge 0-4 in.	6.9	—	—
E. 19	" " " 4-10 in.	7.0	—	—
E. 23	Crest of main ridge	7.1	0.40	0.32
E. 26	" "	7.2	0.51	0.49
E. 27	" "	7.2	0.69	0.20
E. 28	" "	7.1	0.64	0.27
E. 29	" "	7.2	0.40	0.26
E. 30	" "	7.1	0.38	0.20
E. 31	" "	7.2	0.24	0.40

p. H., 6.9-7.3; av. 7.03. Loss on ignition, 0.24-1.60 %; av. 0.501 %. Carbonates, 0.2-0.65 %; av. 0.341.

TABLE I (continued).

Laboratory. Ridge D.

Sample No.	Young Dunes J. and G. Series.	p. H.	Loss on ignition. %	Total carbonates. %
D. 1	<i>Tortula ruraliformis</i> and <i>Cladonia</i>	6.9	0.56	0.05
D. 2	Highest part of	6.9	—	—
D. 3	" "	6.9	—	—
D. 4	" "	6.8	—	—
D. 5	" "	6.9	—	—
D. 6	" "	6.8	—	—
D. 7	122 yds. along ridge D	6.95	0.46	0.15
D. 8	<i>Psamma</i> dom.	6.80	0.39	0.64
D. 12	Side of 'blow-out', <i>Psamma</i> dom. 0-4 in.	6.8	0.30	0.34
D. 11	" " " 12 in.	6.9	—	—
D. 10	" " " 24 in.	6.95	—	—
D. 9	" " " 36 in.	6.9	—	—
D. 13	Ridge D. near Lifeboat House 0-4 in.	6.9	0.40	0.09
D. 14	" " " 4-8 in.	7.0	—	0.12
D. 15	<i>Tortula-Psamma</i> near Lab. 0-4 in.	6.9	—	—
D. 16	" " " 4-8 in.	6.9	—	—
D. 17	" " another locality 0-4 in.	6.9	0.53	0.05
D. 18	" " " 4-8 in.	7.1	0.35	0.05
D. 19	Crest, 0-4 in.	6.9	—	—
D. 39	<i>Tortula</i> dom., <i>Cladonia</i>	—	0.58	0.03
D. 40	<i>Brachythecium albicans</i>	7.0	0.44	0.11
D. 36	<i>Tortula ruraliformis</i>	7.3	0.67	—
D. 37	" "	7.0	0.69	0.16
D. 38	" "	7.0	0.70	—
D. 44	Dense <i>Cladonia</i> and <i>Hypnum</i> 0-1 in.	5.6	—	—
D. 45	" " " 1-6 in.	6.7	—	—
D. 43	<i>Brachythecium albicans</i> dom.	—	0.76	0.07

p. H., 5.6-7.1; av., 6.908. Loss on ignition, 0.3-0.76 %; av., 0.525 %. Carbonates, 0.3-0.64 %; av., 0.155 %.

Ridge C.

C. 20	<i>Cladonia</i> dom. 0-1 in.	6.8	—	0.00
C. 21	" " 3 in.	6.9	—	—
C. 22	" " 6 in.	7.0	—	—
C. 23	" " 9 in.	7.0	—	—
C. 24	" near C. 20 0-1 in.	6.0	—	—
C. 25	" dom. 3 in.	6.9	—	—
C. 26	" " 6 in.	6.9	—	—
C. 27	" " 9 in.	6.9	—	—
C. 28	" " 0-1 in.	6.4	—	—
C. 29	" " 3 in.	6.9	—	—
C. 30	" " 6 in.	6.9	—	—
C. 31	" " 9 in.	6.9	—	—
C. 32	" " 0-1 in.	6.9	—	—
C. 33	" " 3 in.	7.1	—	—
C. 34	" " 6 in.	7.1	—	—
C. 35	" " 9 in.	7.1	—	—
C. 40	" " 0-4 in.	6.8	—	0.00
C. 41	" " 0-4 in.	—	0.82	0.05
C. 42	" " 0-4 in.	—	0.90	0.07
C. 46	<i>Soldanella</i> dune with freshly-blown sand	7.1	—	0.33
C. 47	" " " "	7.1	—	0.37

p. H., 6.0-7.1; av. 6.89; av organic, 0.86 %. Carbonates, 0.00-0.37 %; av. carbonates (4 samples excluding C. 46 and C. 47 where accretion occurs), 0.03 %.

TABLE I (continued).

Long Hills. Series B.

Sample No.	Young Dunes J. and G. Series.	p. H.	Loss on ignition. %	Total carbonates. %
B. 1	Seaward slope near main beach, some accretion	7.0	0.56	0.75
B. 2	Middle of dune in line with B. 1 and B. 3	6.0	1.10	0.00
B. 3	Landward slope	6.5	1.32	0.05
B. 4	Crest between B. 2 and B. 5	6.0	—	—
B. 5	<i>Silene maritima</i> dom.	6.7	0.69	0.00
B. 6	<i>Polypodium vulgare</i> patch 0-4 in.	5.9	2.69	0.00
B. 7	" " 4-8 in.	6.0	0.66	0.00
B. 8	8 yds. S. of B. 16 " 0-4 in.	6.0	0.64	0.00
B. 9	" " 4-8 in.	6.0	—	0.05
B. 10	25 yds. E. of bow of 'Yankee'	6.1	—	0.00
B. 11	Landward slope, middle 0-4 in.	6.1	—	—
B. 12	" " 4-8 in.	6.7	—	—
B. 13	Crest near B. 11 " 0-4 in.	6.5	1.03	0.00
B. 14	" " 4-8 in.	6.8	—	0.02
B. 15	Seaward slope near B. 11 0-4 in.	6.9	—	—
B. 16	" " 4-8 in.	6.9	—	—
B. 17	Seaward slope 0-4 in.	6.9	1.50	0.00
B. 18	Crest 0-4 in.	6.0	—	0.01
B. 19	Landward slope near B. 18 0-4 in.	6.8	—	—
B. 20	" " 4-8 in.	6.7	—	—
B. 21	Crest 0-4 in.	—	1.30	—
B. 22	" 0-4 in.	—	1.21	—

p. H., 5.9-7.0; av., 6.38. Loss on ignition, 0.56-2.69 %; av., 1.154 %. Carbonates, 0.00-0.75 %; av. carbonates (exclusive of B. 1) = 0.01 %.

The Hood. Series A.

A. 1	Hollow with sparse <i>Psamma</i> and <i>Carex arenaria</i> c. 0-2 in.	6.1	10.10	0.00
A. 2	Hollow with sparse <i>Psamma</i> and <i>Carex arenaria</i> c. 2-4 in.	6.2	1.04	0.00
A. 3	<i>Corynephorus canescens</i> dom. (seaward face)	6.6	3.20	0.02
A. 4	Sparse <i>Psamma</i> mosses and lichens	6.7	—	0.05
A. 5	" " " "	—	1.90	—
A. 6	Crest W. side, some new-blown sand	6.9	0.61	0.03
A. 7	Centre of hollow, mosses about	6.3	3.00	0.00
A. 8	Dense vegetation	6.0	6.34	0.01
A. 9	W. of summit	6.3	1.34	0.00
A. 10	E. " "	6.1	2.76	0.01
A. 11	Outlying dune near Hood	6.3	1.41	0.02
A. 12	N. side of crest, <i>Carex arenaria</i> dom.	6.1	1.93	0.00
A. 13	NE. corner	5.5	3.51	0.00
A. 14	Dense vegetation	—	2.57	—
A. 15	Crest	—	1.85	—
A. 16	" "	—	1.60	—

p. H., 5.5-6.9; av., 6.24. Loss on ignition (0-4 in.), 0.61-6.34 %; av., 2.69 %. Carbonates, 0.00 to 0.05 %; av., 0.01 %.

TABLE XI.

Lateral Shingle Hooks.

[illegible]

TABLE XI (continued).

Sample No.	Bank No.	Location on lateral.	Vegetation.	p. H.	Loss on ignition. %	Total carbonates. %
X. 47	VII	Crest	Turfy, proximal end	7.0	3.28	0.02
X. 48	"	"	" middle	6.9	2.64	0.03
X. 48 ^a	"	"	Middle	—	2.71	—
X. 49	"	"	Distal end	6.6	4.31	0.03
X. 1	"	"	High elbow, <i>Aira praecox</i> , &c.	6.0	14.68	0.04
X. 61	"	"	" "	—	7.01	—
X. 2	"	"	" <i>Cladonia</i> , <i>Armeria</i> , <i>Silene</i>	6.0	—	—
X. 62	"	"	<i>Cladonia</i> , &c.	—	4.04	—
X. 5	"	" 0-2 in.	<i>Festuca</i> , <i>Triticum</i> , <i>Cladonia</i>	6.7	—	—
X. 6	"	" 2-4 "	" "	6.9	—	—
X. 4	"	<i>Binervosa</i> zone	<i>Statice binervosa</i> and <i>Franke-</i> <i>nia</i> , W. side	7.3	—	—
X. 7	"	" "	<i>Statice binervosa</i> and <i>Franke-</i> <i>nia</i> , E. side	7.5	3.28	0.04
X. 59	"	" "	<i>Statice binervosa</i> and <i>Franke-</i> <i>nia</i> , E. side	—	2.43	—
X. 8	"	<i>Suaeda</i> zone	<i>Suaeda fruticosa</i> , W. side	7.4	15.70	2.55
X. 60	"	" "	" "	—	15.50	—
X. 3	"	" "	<i>Suaeda</i> , <i>Artemisia</i> , <i>Festuca</i> , E. side	7.2	4.9	—

p. H., 6-7.5; av. crest, 6.59. Organic (crest), 2.64-14.68 %; av., 5.52 %. Carbonates (crest), 0.02-0.04 %; av., 0.03 %.

X. 50	IV	Crest	Proximal end	6.95	2.12	0.00
X. 51	"	"	Middle of bank	6.9	2.52	0.01
X. 51 ^a	"	"	" "	7.05	—	—
X. 52	"	"	Distal end	6.9	2.55	0.00
X. 52 ^a	"	"	" "	7.0	—	—

Av. p. H., 6.96. Av. organic, 2.39 %. Carbonates av., 0.00 %.

X. 53	III	Crest	Proximal end	6.9	3.23	0.01
X. 54	"	"	Middle	6.85	1.82	0.01
X. 55	"	"	Distal end	6.85	2.89	0.00

Av. p. H., 6.86. Av. organic, 2.64 %. Carbonates av., 0.006 %.

X. 56	I	Crest	Proximal end	7.1	3.82	0.03
X. 57	"	"	Middle, <i>Cladonia</i> , <i>Silene</i>	7.1	3.78	0.03
X. 57 ^a	"	"	" " "	7.1	2.18	—
X. 58	"	"	Distal end	6.8	2.90	0.00
X. 15	"	"	<i>Silene maritima</i> , <i>Cladonia</i>	6.9	—	—
X. 9	"	"	<i>Agrostis maritima</i> , <i>Cladonia</i> , 30 yds. from high elbow	6.9	3.31	0.00
X. 13	"	"	<i>Silene</i> , <i>Festuca</i> , <i>Aira</i> , mosses	6.5	—	—
X. 14	"	"	" " " " "	6.8	—	—
			10 yds. E. of X. 13			
X. 10	"	<i>Binervosa</i> zone	<i>Statice binervosa</i> , <i>Frankenia</i>	7.1	4.91	0.01
X. 10 ^a	"	" "	" "	7.1	—	0.03
X. 11	"	Drift zone	<i>Triticum</i> , <i>Festuca</i> , <i>Atriplex</i> , 0-2 in.	7.0	—	—
X. 12	"	" "	<i>Triticum</i> , <i>Festuca</i> , <i>Atriplex</i> , 2-4 in.	7.3	6.38	0.04

Crest, p. H., 6.5-7.1; av., 6.90. Crest, organic, 2.18-3.82 %; av., 3.19 %. Carbonates, 0.00-0.03 %.

TABLE XIII.

Main Beach.

Sample No.	Location on lateral.	Vegetation.	p. H.	Loss on ignition. %	Total carbonates. %
S. 1	Crest	<i>Arenaria peploides</i> , sparse	7.0	—	—
S. 2	"	" " dense	7.3	0.40	0.39
S. 15	"	" " " under mat	7.2	—	—
S. 16	"	" " " "	7.3	—	—
S. 8	"	Shingle with <i>Silene maritima</i>	7.1	—	—
S. 13	"	Beneath mat of <i>S. maritima</i>	7.2	—	—
S. 14	"	" " " "	7.3	5.08	1.20
S. 11	"	" rosette of <i>Rumex trigranulatus</i>	6.9	—	2.10
S. 12	"	Beneath rosette of <i>Rumex trigranulatus</i>	6.7	—	1.90
S. 10	"	Beneath bush of <i>Suaeda fruticosa</i> just below crest	7.0	—	—
S. 9	"	Beneath bush of <i>Suaeda fruticosa</i> just on crest	6.9	6.49	1.36
S. 30	"	Beneath bush of <i>Suaeda fruticosa</i>	—	2.00	—
S. 31	"	" " " "	—	3.30	—
S. 32	"	" " " "	—	2.1	—
S. 33	"	" " " "	—	1.4	—
S. 34	"	" " " "	—	2.0	—
S. 35	"	Fine shingle, shallow-rooted grasses, <i>Lepturus</i> , &c.	—	0.0	—
S. 6	"	Fine shingle with <i>S. binervosa</i> and <i>Sclerochloa loliacea</i>	7.1	—	—
S. 36	"	Bare fine shingle	—	0.0	—
S. 3	"	Fine shingle, bare of vegetation	7.1	0.39	0.83
S. 4	"	" " " " near embryo dunes	7.25	—	—
S. 7	"	Bare shingle, landward side of dunes	7.2	0.69	0.23
S. 36	"	Bare shingle	—	1.0	—
S. 37	"	" close to <i>Suaeda</i> bush	—	1.6	—
S. 38	"	" " " "	—	1.5	—
S. 39	"	" " " "	—	1.1	—
S. 40	"	" " " "	—	1.3	—
S. 41	"	Bare shingle	—	1.1	—
S. 42	"	"	—	1.3	—
S. 43	"	"	—	0.9	—

Main beach, p. H., 6.7-7.3; av., 7.11. Organic, 0.0-6.49 %; av., 1.68 %. Carbonates, 0.23-2.1 %; av., 1.14 %.

Shingle 'Lows'.

	Vegetation.	p. H.	Loss on ignition. %
1	0-4 in. 'long' low. <i>Plantago coronopus</i> , f. <i>pygmaea</i>	6.9	0.79
2	" " " "	6.9	—
3	" " " "	6.9	—
4	" " " "	7.0	—
5	4-8 in. " " " "	6.9	—
6	" " " "	6.9	—
7	" " " "	6.9	—
8	'Glaux' low	—	0.52
9	Low near Lifeboat House, <i>S. reticulata</i> decreasing	—	0.81
10	Low at Hood, <i>P. coronopus</i> , f. <i>pygmaea</i> , dead <i>Suaeda</i>	—	1.31
11	Terminal low, 'Long Hills'	—	1.75
12	Small low, centre of 'Long Hills'	—	1.22
13	Large " " "	—	3.3

TABLE XIV. *Vegetation of Lateral Banks.*

(For numbering see map, Text-fig. 1.)

<i>Species.</i>	Youngest ← → Oldest								
	XX.	XVII.	XII.	VIII.	VII.	VI.	IV.	III.	I.
<i>Agrostis maritima</i>	—	—	—	c.	c.	c.	c.	c.	c.
<i>Aira praecox</i>	—	—	f.	f.	l.c. (high elbow)	r.	—	—	—
<i>Anagallis arvensis</i>	—	—	o.-f.	—	—	—	—	—	—
<i>Arenaria peploides</i>	o.	c.	c.	l.	l.	—	—	—	—
„ <i>serpyllifolia</i>	—	—	—	c.	c.	c.	c.	c.	—
<i>Armeria maritima</i>	—	—	v.c.	v.c.	v.c.	c.	c.	f.c.	c.
<i>Arrhenatherum elatius</i>	—	—	—	v.r.	—	—	—	—	—
<i>Artemisia maritima</i>	—	o.	f.	c.	c.	c.	c.	c.	c.
<i>Atriplex babingtonii</i>	—	—	f.	f.	—	—	—	—	—
„ <i>littoralis</i>	—	—	o.	l.f.	—	—	—	—	—
<i>Bellis perennis</i>	—	—	—	r.	—	—	—	—	—
<i>Bromus mollis</i>	—	—	v.r.	f.	l.f. (high elbow)	—	—	r.	—
<i>Cakile maritima</i>	f.	—	—	—	—	—	—	—	—
<i>Cerastium semidecandrum</i>	—	—	—	f.	f.c.	—	—	—	—
„ <i>tetrandrum</i>	—	—	f.c.	o.	r.	r.	f.	f.	—
<i>Cirsium lanceolatum</i>	—	—	—	r.r.	—	—	—	—	—
<i>Cochlearia danica</i>	—	—	r.	l.f.	l.f.	r.	—	r.r.	—
„ <i>officinalis</i>	—	—	l.f.	l.f.	—	—	—	—	—
<i>Crepis capillaris</i>	—	—	—	v.r.	—	—	—	—	—
<i>Erodium neglectum</i>	—	—	o.	r.	—	—	—	—	—
<i>Festuca myurus</i>	—	—	—	v.r.	—	—	—	—	—
„ <i>ovina</i>	—	—	—	l.	—	v.r.	—	—	—
„ <i>rubra</i>	—	—	—	f.	c.	c.	c.	c.	f.
<i>Filago minima</i>	—	—	r.	—	—	—	—	—	—
<i>Frankenia laevis</i>	—	—	l.c.	c.	c.	c.	c.	f.	—
<i>Galium verum</i>	—	—	—	f. (high elbow)	r. (high elbow)	—	—	—	—
<i>Geranium molle</i>	—	—	v.r.	v.r.	—	—	—	—	—
<i>Glaucium luteum</i>	v.r.	v.r.	—	—	—	—	—	—	—
<i>Glyceria maritima</i>	—	—	—	c.	c.	c.	c.	c.	c.
<i>Hordeum murinum</i>	—	—	—	r. (high elbow)	—	—	—	—	—
<i>Hypochoeris glabra</i>	—	—	r.	—	—	—	—	—	—
<i>Koeleria cristata</i>	—	—	—	r.	—	—	—	—	—
<i>Lepturus filiformis</i>	—	—	r.	l.	r.r.	l.f.	l.f.	f.	r.
<i>Lotus corniculatus</i>	—	—	f.	f.c.	f.c.	l.	—	—	f.
<i>Myosotis collina</i>	—	—	v.r.	—	f.	—	—	—	—
<i>Obione portulacoides</i>	—	—	o.	f.	l.f.	l.f.	f.	f.	f.
<i>Phleum arenarium</i>	—	—	v.r.	—	—	—	—	—	—
<i>Plantago coronopus</i>	—	o.	f.c.	f.c.	o.-l.f.	l.f.	f.	f.c.	c.
„ <i>lanceolata</i>	—	—	—	f.	l.f. (high elbow)	—	—	—	—
<i>Poa annua</i>	—	—	f.	o.	—	—	—	—	—
„ <i>loliacea</i>	—	—	o.	—	r.r.	—	l.f.	l.f.	—
„ <i>pratensis</i>	—	—	—	f.c.	f.	l.f.	r.	r.r.	o.
<i>Psamma arenaria</i>	o.	—	r.	—	—	—	—	—	—
<i>Rumex acetosella</i>	—	—	f.	f.c.	f.	—	l.f.	f.	—
„ <i>crispus</i> v. <i>trigranulatus</i>	—	—	f.	o.	r.r.	v.r.	—	—	—
<i>Sagina maritima</i>	—	—	o.	o.	r.r.	r.	—	l.f.	—
<i>Salsola kali</i>	f.	—	—	—	—	—	—	—	—
<i>Sedum acre</i>	—	—	f.	f.	f.c.	f.	f.	f.	o.
„ <i>anglicum</i>	—	—	—	o. (high elbow)	r. (high elbow)	—	—	—	—
<i>Senecio jacobaea</i>	—	—	f.	v.r.	v.r.	—	—	—	—
„ <i>sylvaticus</i>	—	—	—	r.	—	—	—	—	—
<i>Silene maritima</i>	—	ab.	ab.	v.c.	c.	c.	c.	f.c.	f.
<i>Spergularia salina</i>	—	—	—	v.r.	—	—	—	—	—
<i>Statice binervosa</i>	—	—	c.	c.	c.	c.	c.	c.	f.
<i>Stellaria boreana</i>	—	—	v.r.	—	—	—	—	—	—

TABLE XIV (continued).

Species.	Youngest ← —————→ Oldest.								
	XX.	XVII.	XII.	VIII.	VII.	VI.	IV.	III.	I.
<i>Suaeda fruticosa</i>	—	c.	c.	c.	c.	c.	c.	c.	v.c.
<i>Trifolium arvense</i>	—	—	—	f.	l.f.	r.	r.	f.	r.
„ <i>procumbens</i>	—	—	—	r. (high elbow)	v.r. (high elbow)	—	—	—	—
„ <i>striatum</i>	—	—	—	l.f.	—	—	—	—	—
<i>Triticum junceum</i>	o.	—	—	f.	c.	l.	l.c.	l.c.	—
„ <i>pungens</i>	—	—	—	l.c.	l.c.	c.	c.	c.	c.
<i>Vicia angustifolia</i>	—	—	—	f. (high elbow)	v.r. (high elbow)	—	—	—	—
Totals	6	6	34	51	36	25	21	24	16

ab. = abundant; c. = common; f. = frequent; o. = occasional; l. = local; r. = rare, &c.

TABLE XV.

Sample No.	Marsh soils.	p. H.	Loss on ignition.	Carbonates.
			%	%
K. 7	<i>Salicornietum</i> (<i>S. herbacea</i>)	7.3	—	—
K. 8	„ „ „ <i>Pelvetia</i>	7.6	—	—
K. 9	Bare area near K. 8	7.3	1.08	1.72
K. 15	<i>S. herbacea</i> , <i>Pelvetia</i> , <i>Obione</i> sparse	7.3	—	—
K. 16	„ „ „	7.6	—	—
K. 17	„ „ and <i>Aster tripolium</i>	7.6	—	—
K. 29	Same transect as K. 27 and K. 28	7.5	—	—
K. 32	„ „ K. 30 „ K. 31	7.5	9.26	2.26
K. 35	„ „ K. 33 „ K. 34	7.4	—	—
K. 38	„ „ K. 36 „ K. 37	7.5	—	—
K. 40	<i>S. herbacea</i> , <i>Pelvetia</i> , <i>Pelvetia</i> marsh	—	—	0.14
K. 46	Same transect as K. 47 and K. 41 (near edge)	7.6	5.33	2.18
K. 44	Same transect as K. 43 and K. 48 (near edge)	7.5	4.78	1.75
K. 45	Same transect as K. 42 and K. 49 (near edge)	7.5	4.71	2.70
K. 55	<i>Pelvetia</i> marsh E. (middle)	8.0	14.63	2.02
K. 56	„ „ centre „	8.0	14.41	2.04
K. 57	„ „ west „	8.2	12.18	3.50
K. 52	Samphire marsh E.	7.9	12.20	5.10
K. 53	„ „ middle	8.0	11.13	4.55
K. 54	„ „ west	7.8	11.36	2.95

p. H. (7.3–8.2); av., 7.63. Loss on ignition, 1.08–14.63 %; av., 9.19 %. Carbonates, 0.14–5.10 %; av., 2.55 %.

K. 5	Centre of <i>Obione</i> zone	7.3	1.01	0.62
K. 4	Upper edge „	7.3	—	—
K. 6	Lower edge „	7.1	—	—
K. 13	Another transect, centre of <i>Obione</i> zone	7.3	—	0.20
K. 12	Upper edge „ „	7.25	—	—
K. 14	Lower edge (with <i>S. radicans</i>)	7.2	—	—
K. 28	Centre of <i>Obione</i> zone (cf. K. 27 and K. 29)	7.6	—	—
K. 31	„ „ (cf. K. 30 and K. 32)	7.6	3.21	1.83
K. 34	„ „ (cf. K. 33 and K. 35)	7.4	—	—
K. 37	„ „ (cf. K. 36 and K. 38)	7.4	—	—
K. 21	„ 0–2 in.	7.5	—	—
K. 22	„ 8–10 in.	7.15	—	—
K. 23	„ 15–18 in.	7.2	—	—
K. 39	„ of <i>Obione</i> zone	—	—	1.00
K. 41	<i>Obione</i> zone	7.4	5.21	1.55
K. 48	„	7.45	2.46	0.55
K. 49	„	7.4	1.84	0.70
K. 50	Old <i>Obione</i> salting	—	2.40	—

p. H., 7.1–7.6; av., 7.34. Loss on ignition, 1.01–21.40 %; av. (exclusive of K. 50), 2.74 %. Carbonates, 0.55–1.83 %; av., 0.92 %.

TABLE XV (continued).

Suaeda Zone.

Sample No.	Marsh soils.	p. H.	Loss on ignition. %	Carbonates. %
K. 1	Centre of <i>Suaeda fruticosa</i> zone	7.3	1.77	0.71
K. 2	Upper edge	7.1	—	—
K. 3	Lower „	7.2	—	—
K. 10	<i>Suaeda</i> zone on sand	7.6	—	—
K. 11	Slightly higher than K. 11	7.3	—	—
K. 27	Centre of zone (cf. K. 28 and K. 29)	7.3	—	—
K. 30	„ „ (cf. K. 31 and K. 32)	7.6	1.70	1.49
K. 33	„ „ (cf. K. 34 and K. 35)	7.6	—	—
K. 36	„ „ (cf. K. 37 and K. 38)	7.4	—	—
K. 18	0-2 in.	7.35	—	—
K. 19	8-12 in. (maximum root zone)	7.2	—	—
K. 20	18-20 in.	7.3	—	—
K. 42	Centre of zone, same transect as K. 45 and K. 49	7.5	0.59	0.26
K. 43	Centre of zone, same transect as K. 44 and K. 48	7.4	1.33	0.57
K. 47	Centre of zone, same transect as K. 41 and K. 46	7.5	1.41	0.35

p. H., 7.1-7.6 (av., 7.37). Loss on ignition, 0.59-1.77 %; av., 1.36 %. Carbonates, 0.26-1.49 %; av., 0.676 %.

TABLE XVI.

Percentage Chlorides taken from the Unpublished Observations of Blakeney Point (Estimations by Miss A. C. Halket and Dr. H. B. Hutchinson),

Soil type.	Vegetation.	Chlorides. %
Sand dune, main ridge	<i>Psamma</i> , <i>Arenaria</i>	0.0042-0.0046
Dune, Long Hills	0-6 in. <i>Psamma</i> , &c.	0.010
„	6-12 in. „	0.014
„	12-18 in. „	0.005
„	0-6 in. bare sand	0.000
„	6-12 in. „	0.01
„	12-18 in. „	0.198
Main shingle bank	Sparse <i>Arenaria</i> and <i>Silene</i>	0.0017
„	Bare shingle	0.25
„	„	1.17
„	„	0.86
„	„	0.33
„	„	0.26
„	„	0.98
„	„	0.92
„	„	0.44
„	Under <i>Suaeda fruticosa</i>	1.72
„	„ „	3.08
„	„ „	1.30
„	„ „	0.85
„	„ „	2.10
Gully on main bank (fine shingle)	<i>Desmazeria loliacea</i> and <i>Lepturus filiformis</i>	0.12
Side of gully	Bare	0.26

Range 0.25-1.17
Av. 0.65

0.85-3.08
Av. 1.81

TABLE XVI (continued).

Soil type.	Chlorides. %	
<i>Lateral shingle bank—</i>		
High elbow, bank 7	0.29	
Crest, bank 7	0.17	
" " 8	0.072	
<i>Statice binervosa</i> zone, bank 7	0.90	
" " " 7	0.005	
<i>Triticum</i> zone, bank 8	0.158	
<i>Festuca</i> zone, bank 7	1.60	
<i>Suaeda fruticosa</i> zone, bank 7	3.05	
" " " 8	0.197	
" " " 7	0.4633	
" " " 7	0.3941	
" main beach (0-9)	0.232	
" " (0-9)	0.3536	
" " (9-18)	0.3378	
" " (18-24)	0.2802	
 <i>Locality.</i>	 <i>Vegetation.</i>	
	<i>Chlorides.</i> %	
<i>Shingle lows—</i>		
End of Long Hills	<i>Statice reticulata</i> , <i>Frankenia laevis</i> , <i>Plantago coronopus</i>	0.36
Large low middle Long Hills	<i>Statice reticulata</i> , <i>Frankenia laevis</i> , <i>Plantago coronopus</i>	3.50
Small " "	<i>Statice reticulata</i> , <i>Frankenia laevis</i> , <i>Plantago coronopus</i>	0.30
Low W. Lifeboat House	<i>S. reticulata</i> , dying out	1.04
Low on Hood	Dead <i>Suaeda</i> bushes	1.39
'Glaux' Lagoon	<i>Glaux maritima</i>	1.70
<i>Salt marsh—</i>		
<i>Obione</i> zone	<i>Obione</i> , <i>Salicornia</i>	0.55
" "	" "	1.17
<i>Salicornia radicans</i> zone	<i>S. radicans</i> , <i>Obione</i> , and <i>S. herbacea</i>	0.95
<i>Salicornia annua</i> zone	<i>S. annua</i> , <i>Pelvetia</i>	1.35
" "	" "	1.88
" "	" "	1.908
" "	" "	0.95
" "	" "	6.342
" "	" "	3.060
" "	" "	1.19
Aster Society, edge	Bare patch	0.97
" " centre	<i>A. tripolium</i>	1.33
" "	" "	

It has been possible to print the data *in extenso* through a grant from the Blakeney Point Publication Fund established through the generosity of East Anglians interested in the work carried on at Blakeney. The cost of the plate has also been defrayed from this fund.

DESCRIPTION OF PLATE XV.

The headland as seen from the air. The various dune systems can be recognized by reference to Text-fig. 1. Note in particular the gradual coalescence and greater continuity of the plant covering as one passes from the youngest to the oldest dune systems.

For description see p. 431 and Text-fig 1, p. 393

Salisbury, E. J. 1922. "The soils of Blakeney point: a study of soil reaction and succession in relation to the plant covering." *Annals of botany* 36, 391–431.
<https://doi.org/10.1093/oxfordjournals.aob.a089814>.

View This Item Online: <https://www.biodiversitylibrary.org/item/234428>

DOI: <https://doi.org/10.1093/oxfordjournals.aob.a089814>

Permalink: <https://www.biodiversitylibrary.org/partpdf/319051>

Holding Institution

Smithsonian Libraries

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: Not in copyright. The BHL knows of no copyright restrictions on this item.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.