Spiraea Ulmaria, L., and its Bearing on the Problem of Xeromorphy in Marsh Plants.

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With Plates LXXXI-LXXXIII and eleven Figures in the Text.

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§ I. INTRODUCTION.

IN Warming's 'Pflanzengeographie', published in 1896, occurs the following passage¹: 'Das Ideal der wissenschaftlichen Behandlung der einzelnen Vereine muss der wissenschaftliche Nachweis dafür sein, wie jedes einzelne seiner Mitglieder (Lebensformen) im morphologischen, im anatomischen und im physiologischen Einklange mit den verschiedenen ökonomischen und geselligen Verhältnissen, worunter es lebt, ist.' We are as yet far from the attainment of this ideal in respect of even a single plant-

¹ Warming ('96), p. 119.

association. But in the meantime it is probable that light may be thrown on many ecological problems by the intensive study of the ecology of selected species.

The present paper, which is intended as a further contribution to our knowledge of 'swamp xerophytes',¹ is an attempt to see how far the study of a single species may help towards an explanation of xeromorphy in marsh plants. The species chosen for this purpose is the common Meadow-sweet, *Spiraea Ulmaria*, Linn., the leaves of which, as is well known, are covered beneath by a dense white felt of hairs. In this paper special attention is devoted to this characteristic pubescence, which is usually regarded as a device for depressing transpiration.

§ 2. HAIRINESS IN MARSH PLANTS.

Though aquatic phanerogams, as a class, are remarkable in being for the most part devoid of hairs, the latter are by no means uncommon on the leaves or stems of marsh plants. Indeed, I have noted the presence of a greater or less degree of hairiness in upwards of thirty of the commoner British species of marsh plants. No doubt even this list could be considerably augmented. In some cases the aerial parts are only slightly hairy, e. g. in *Angelica sylvestris*, *Hydrocotyle vulgaris*, *Valeriana sambucifolia*, *Phragmites communis*, *Molinia coerulea*, &c. In others the hairiness is more pronounced, as in *Epilobium hirsutum*, *Cnicus pratensis*, *Lysimachia vulgaris*, *Mentha aquatica*, &c. In a few cases the lower surface of the leaves is covered with a dense felt of hairs: such is the case in *Spiraea Ulmaria*, *Salix* spp., &c.

It may be remarked here that hairiness occurs most frequently in those species of marsh plants which either grow in the drier parts of marshes,² or else have their aerial parts more or less exposed to the effects of drying winds.³

§ 3. DISTRIBUTION OF CERTAIN HAIRY SPECIES OF *SPIRAEA*.

The genus *Spiraea*⁴ comprises some 127 species, which are spread over the temperate and colder regions of the northern hemisphere. Of these, the majority appear to be glabrous or nearly so, though others are hairy to a greater or less degree. A few species have dense pubescence on the under surface of their leaves; these fall naturally into two groups. In the first, which belongs to the § *Ulmaria*, are *Spiraea Ulmaria*, L., *S. palmata*, Thunb., and *S. vestita*, Wall. These are closely allied Old

¹ Cf. Yapp ('08, two papers), ('09), and ('10).

² e. g. *Spiraea Ulmaria*.

³ e. g. *Phragmites communis*, *Viburnum Opulus*, *Salix* spp., &c.

⁴ In the sense used by Linnaeus, Bentham and Hooker, and others, cf. Wenzig ('88). Other authors, probably rightly, separate the several sections of *Spiraea* as distinct genera, e. g. Focke ('94).

World forms, with pinnate leaves and exactly the same type of pubescence, i. e. their leaves are 'subtus albo-tomentosa'. The second group includes several N. American species with entire leaves, belonging to the § *Euspiraea*. Their pubescence is more or less similar to that of the first-named species,¹ e. g. *S. Douglasii*, Hook., *S. tomentosa*, L., &c.

It is interesting to note that most of these densely pubescent species have closely allied glabrous forms. Thus *S. Ulmaria* has the nearly glabrous variety *denudata*;² *S. palmata* has the varieties *tomentosa* and *glabra*; and *S. vestita* is practically indistinguishable, except in respect of

TEXT-FIG. 1. Map showing distribution of certain species of *Spiraea*.

hairiness, from the glabrous *S. Kamtschatica*, Pallas. Again, the two N. American species mentioned above are allied not only to each other, but also to the widely distributed glabrous *S. salicifolia*, L. For the general distribution of these species see Text-fig. 1.

§ 4. HABIT AND HABITATS OF *SPIRAEA ULMARIA*.

S. Ulmaria (= *Filipendula Ulmaria*, Max.) is a perennial herb with a sympodial rhizome which creeps on or just below the surface of the soil (Text-fig. 2). The aerial parts die back in autumn, leaving the persistent

¹ Densely downy leaves, similar to those of the species mentioned above, are apparently not very common in the Rosaceae, though they are met with in various genera, e. g. *Rubus*, *Prunus*, *Couepia*, &c.

² In Rouy et Camus ('00), p. 151, var. γ , *S. unicolor*, Nob. (= *S. denudata*, Presl.), is stated to be glabrous, except for pubescence on the veins below; while var. δ , *glaberrima*, Nob., is entirely glabrous.

rhizome with its winter buds. The plant thus belongs to Raunkiaer's class of 'hemicryptophytes'.¹ The winter buds begin to unfold during March, and each produces several radical leaves. In a vigorous adult plant such a bud may subsequently form an erect flowering shoot, with cauline leaves. In young plants, or buds of less vigour, however, the shoot does not elongate, but remains prostrate. In the latter case it continues to form radical leaves till September. These two kinds of shoot will be referred to in this paper as the *erect flowering shoots* and the *non-flowering shoots* respectively.

Text-fig. 1 shows that *S. Ulmaria* is widely spread over the north temperate and colder regions of the Old World. In Great Britain it is a com-

TEXT-FIG. 2. Sympodial rhizome of *Spiraea Ulmaria*, showing four years' growth. The winter bud has unfolded (April), but has not yet formed the erect flowering shoot. Leaves are numbered in order of age. About $\frac{1}{3}$ natural size.

mon plant, being found in the whole of Watson's 112 counties,² whilst its altitudinal range is from the coast to some 2,700 feet above sea-level.³

Itself a characteristic plant of the drier parts of marshes and fens,⁴ the habitat of *Spiraea Ulmaria* is usually where the water content of the soil is considerable rather than excessive. It prefers soils with a high water capacity, such as peat or clay. Provided that its needs in respect to soil moisture are satisfied, it will grow almost anywhere: at the edges of marshes and rivers; in the damper parts of meadows; in roadside ditches; on the sea-coast;⁵ in damp hollows between sand-dunes;⁶ and even in woods, if

¹ Raunkiaer ('07), p. 49.

³ Watson ('47), p. 334.

⁵ In 1910 my friend Professor Weiss sent me some specimens collected close by the sea, growing practically in brackish water.

² London Catalogue ('08).

⁴ Yapp ('08, second paper), pp. 70 and 72.

⁶ Moss ('07), p. 16.

the shade is not too dense.¹ It readily colonizes moist ground which has been recently disturbed; and hence frequently establishes itself at the foot of railway embankments, &c.²

§ 5. THE DISTRIBUTION OF PUBESCENCE ON THE LEAVES.

The various British Floras state that the type form of *Spiraea Ulmaria* has pinnate leaves covered with white down beneath. Consequently, in September of 1906 I was surprised to find that the *Spiraeas* at Wicken Fen varied markedly in this respect. Some leaves were completely hairy on the lower surface; others were glabrous, while all possible transitions were to be found (see Pl. LXXXII). The reasons for this extreme variability were by no means obvious, so a large number of specimens were grown for some years. It was hoped that if any explanation for such a marked phenomenon were forthcoming, it might throw light on the general problem of xeromorphy in marsh plants.

The experiments (confirmed by many field observations) revealed the existence of a regular periodicity in the production of hairs. The rules governing hair formation may now be stated. It should be borne in mind that all the following descriptions refer to the hairy type form of *S. Ulmaria*, and not to its glabrous variety, *denudata*.

(a) *Seedlings*. In all cases the seedlings are glabrous. This applies to every leaf formed during the first year. The plant, if small and weak, may remain in this juvenile glabrous condition for two or more years; though if under favourable conditions, it may form normal hairy shoots in the second year.

(b) *Erect flowering shoots of adult plants*. When a winter bud opens early in the year (about March), the first leaves unfolded are juvenile in type, i.e. they are small and glabrous. After a variable number (usually from 3 to 5³) of these glabrous radical leaves have unfolded, they are followed, about the end of April or the beginning of May, by one or two leaves which are partly hairy. The latter are in turn succeeded, as the flowering shoot elongates and becomes erect, by leaves which are completely covered with hairs on the lower surface.⁴ The pubescence becomes more dense as the erect stem is ascended. (Pl. LXXXI shows all the successive leaves formed on one flowering shoot. Leaves 1-7 are radical, and leaves 8-16 cauline. Hairy parts show white, and glabrous dark.) The plant

¹ Adamson ('12), pp. 358, &c., gives a good account of various *S. Ulmaria* societies in a Cambridgeshire woodland.

² At least some of the other species of *Spiraea* mentioned in § 3 are also swamp plants: e. g. *S. salicifolia* and *S. tomentosa*. See Britton and Brown ('97), p. 196.

³ I have seen as many as twelve, but this is quite exceptional.

⁴ The flowering shoot usually begins to elongate about the middle of May, by which time most plants already show some hairy leaves.

generally flowers towards the end of July (or earlier on drier soils), by which time all the leaves on the shoot are unfolded.

Thus the leaves of the erect flowering shoots vary markedly in hairiness, according to both their time of unfolding and their position on the stem.¹

(c) *The non-flowering shoots of adult plants* exhibit an even more remarkable periodicity in hair formation. They commence about March by unfolding glabrous leaves in precisely the same way as the erect flowering shoots. Similarly, too, as the season advances, the successive leaves are *increasingly hairy*. This goes on till about midsummer (the actual time appears to vary, possibly with the kind of season, from about the middle of June to the middle of July), when the process is reversed. The new leaves unfolded are now *decreasingly hairy*, until finally glabrous leaves are once more produced on the approach of autumn. The actual number of hairy or partly hairy summer leaves formed on a given shoot appears to depend on its size and vigour. If a shoot is fairly large and vigorous, it may form only a few glabrous leaves, but a number of nearly or completely hairy ones. On the other hand, a small, weak shoot may produce only one or two slightly hairy leaves; all the rest formed during the year being glabrous.²

To sum up, the successive leaves on an erect flowering shoot exhibit a continually rising curve of hairiness, the spring leaves being glabrous and the summer leaves hairy. On the other hand, the non-flowering shoots have glabrous spring and autumn leaves, and (if the plants are sufficiently vigorous) more or less hairy summer ones. In other words, the curve of hairiness rises from zero in spring-time to a maximum about midsummer, once again falling to zero towards autumn.

(d) *Distribution of hairs on the partly hairy leaves.* The series of leaves shown on Pl. LXXXII and LXXXIII, selected from various non-flowering shoots, serves to illustrate the rules governing the localization of hairs on leaves which are not completely hairy. In each leaf, taken as a whole, it is readily seen that *hairiness decreases from above downwards*. Out of many hundreds of leaves examined, I have only met with one or two partial exceptions to this rule. If individual partly hairy leaflets are considered, it is equally obvious that the distribution takes the form of a *marginal band of hairs* (Pl. LXXXII, leaves 2, 3, 5, 7, 11, &c., and Pl. LXXXIII, leaves 1 and 2); with sometimes, but by no means always,

¹ Ascherson and Graebner ('00-'05), p. 438, state that the radical leaves are less hairy than the cauline in certain varieties of *S. Ulmaria*.

² Curious cases are sometimes met with in which a fairly vigorous shoot shows no sign of elongating to a flowering shoot at the usual time. It proceeds to behave like a non-flowering shoot, showing first increasing, then decreasing, hairiness. A few weeks later it suddenly alters its behaviour again; the leaves once more exhibit increasing hairiness, and a belated flowering shoot is formed.

additional bands running inwards from the margin, between the main veins (Pl. LXXXII, leaves 4, 6, 9; also Pl. LXXXIII, leaf 3).¹ The partly hairy leaves on the erect flowering shoots also follow the same rules (Pl. LXXXI, leaves 6, 7, and 8). All the leaves photographed (Pl. LXXXI-LXXXIII) are mature. The hairs would not spread subsequently from the margin over the entire surface.

Broadly speaking, the rule followed in every case is that when a leaf or leaflet is only partially hairy, the hairs are localized principally at those points which are most remote from the main water supply. This point will be dealt with later.

§ 6. COMPARISON WITH OTHER HAIRY PLANTS.

Spiraea Ulmaria is not unique in this curious periodic production of hairs, though it is the most striking case I have seen. Specimens of *S. vestita*, Wall.,² a species quite distinct from *S. Ulmaria*, though closely allied to it, were examined in the Cambridge University and Kew Herbaria. The upper leaves are downy, but in both herbaria specimens exist which show that the lower leaves are only partly hairy. In one or two cases the lowest leaf of all is glabrous. Thus this species apparently follows much the same rules as *S. Ulmaria*. I have also grown *Spiraea tomentosa*, L., from specimens kindly sent me by Professor H. C. Cowles, of Chicago, and Professor J. B. Pollock, of Michigan. This is a shrubby form, with small downy leaves. Here, too, as the buds open in the spring-time, there is a similar succession of glabrous, partly hairy, and hairy leaves.

A number of other marsh herbs resemble these species of *Spiraea* in forming small glabrous leaves in spring-time, followed, as the season advances and the erect flowering shoots are formed, by a steadily increasing production of hairs on the later leaves.³ Such are *Epilobium hirsutum*, *Lysimachia vulgaris*,⁴ *Mentha aquatica*, *Valeriana sambucifolia*, *Scabiosa succisa*, *Eupatorium cannabinum*, *Lycopus europaeus*, &c.

But the phenomenon is not confined to marsh plants. I noticed a specimen of *Rubus discolor*, W. and N., growing partly shaded by trees in the New Forest, in which the proximal leaves on the lateral shoots were invariably much less hairy than the distal ones. Again, I examined the cultivated Raspberry (*Rubus idaeus*, L.), without finding any trace of

¹ The distribution is not always quite so regular as shown in the series of leaves photographed; though it is so in most cases. Sometimes an interveinal band is incomplete: in this case its innermost portion is often present as a group of hairs in a fork where two veins meet (Pl. LXXXIII, leaf 2). It will be shown later that hairs are developed also on the main veins themselves. Cf. Renner ('08), p. 128, who states that in many leaves in which the lamina is folded in the bud, both on the midrib and lateral veins, hairs are developed especially on the veins and the edges of the leaf, e.g. *Fagus sylvatica* and *Carpinus betulus*.

² *S. vestita*, Wall. MSS. = *S. Kamtschatica*, var. *himalensis*, Lindl. Cf. Lindley ('41), t. iv, and Hooker ('79), p. 323.

³ Yapp ('08), p. 691.

⁴ Yapp ('09), Text-fig. 1, p. 278.

diminished hairiness in the lower leaves. But Mr. E. J. Salisbury informs me that in the wild Raspberry, when the canes are growing in thick clumps, the lower leaves are considerably less hairy. Specimens kindly sent by Mr. Salisbury confirm his observation.

Thus we are evidently dealing with a widespread phenomenon.

§ 7. SEASONAL DIFFERENCES IN LEAF STRUCTURE.

Various authors have called attention to the periodicity of growth exhibited by shoots.¹ The leaves increase in size and the internodes in length (and also in the length of their cells) from below upwards. Such increase is followed by a corresponding decrease after the maximum is reached (cf. Pl. LXXXI and Text-fig. 5). It has been shown above that a similar periodicity of hairiness obtains in the non-flowering shoots of *Spiraea*

TEXT-FIG. 3. Sections of (A) a 'sun' leaf, and (B) a 'shade' leaf of *Spiraea Ulmaria*. $\times 350$.

Ulmaria. The leaves of the erect flowering shoots, on the other hand, exhibit a more or less continually rising curve of hairiness. It will now be shown that corresponding seasonal differences of structure occur in the successive leaves formed on these erect flowering shoots.²

The possible range of structure may first be indicated. Text-fig. 3 shows sections taken through extreme 'sun' and 'shade' leaves. A is from a cauline leaf of a fully exposed plant, and B from a radical leaf of a plant grown in deep shade and a constantly humid atmosphere (under a bell-glass).³

¹ Moll ('76), Pfeffer ('03), Tammes ('03), Groom ('08), &c.

² The method of investigation was as follows: The successive leaves on selected shoots were preserved in alcohol, care being taken not to remove any leaf from the plant till it was fully mature and several later leaves had unfolded. Sections were taken from corresponding portions of the terminal leaflet. Another portion of the same leaflet was cleared in eau de Javelle and mounted in water as a transparent object. In this state the size and relations of the epidermal, palisade, and other cells could be studied, and the number and size of the stomata ascertained. The cells remain of approximately the same size as during life. The latter point was determined by taking a contact print of a living leaf on photographic paper. The leaf was then treated as above, when it was still found to correspond in size with the photographic print. Thus the number of stomata per unit area given later may be taken as practically the same as in a living leaf.

³ Cf. the figures given in Hesselman ('04), p. 419.

TEXT-FIG. 4. Three leaves from one erect flowering shoot of *S. Ulmaria*, var. *denudata*. The months indicate time of unfolding. Below each leaf are shown successively (a) part of its upper epidermis, superposed on palisade cells, (b) part of lower epidermis, with stomata, and (c) section of leaf lamina. Intercellular spaces are black. Shaded cells are at a somewhat different level to the others. Leaf outlines $\times$ about $\frac{3}{8}$; all other drawings $\times$ 350.

We have seen that two types of leaf (glabrous and hairy), with intermediate transitions, occur on each shoot. As was perhaps to be expected, the glabrous low-growing leaves were found to possess a more or less definite 'shade' structure; while the upper, exposed hairy leaves approximated to the 'sun' type. There is a gradual transition (often fluctuating as regards individual leaves) in structure between the two extremes.

The glabrous radical leaves, which are unfolded about March, have large epidermal cells, with more or less sinuous lateral walls (especially those of the lower epidermis). The cuticle is thin. The stomata are large and relatively few in number. The mesophyll is composed of large, loosely arranged cells, with large and abundant intercellular spaces (Text-fig. 4, leaf 2). As more leaves are unfolded the following progressive changes may be observed. The epidermal cells (both upper and lower) of the successive leaves become gradually reduced in size, and their lateral walls less sinuous. The cuticle of the upper epidermal cells is thicker, though in this plant it is always fairly thin. The stomata become progressively smaller, and at the same time considerably more numerous per unit area.¹ The lower surface of the leaves is more and more hairy. The mesophyll is more compact (especially the upper palisade layer), its cells are smaller, and the intercellular spaces are gradually reduced to a minimum (Text-fig. 4, leaves 10 and 18).

The general question of relation of structure to environment will be discussed later. It may, however, be remarked here, that while the above relative differences were found in the successive leaves of each shoot examined, the actual structure of any given leaf depends partly on its position on the shoot, and partly on the general nature of the habitat. Thus the most lacunar leaves, with the fewest stomata, &c., are the radical leaves of plants grown under conditions of extreme humidity and shade. The converse also holds true (cf. Text-fig. 3). Again, the observed differences depend only to a certain extent on the actual size of the leaf lamina. Thus, a 'shade' leaf has not only a larger surface area, but also larger epidermal cells, fewer stomata per unit area, &c., than a *corresponding leaf* from a plant grown under fully insolated conditions (see Text-fig. 5). On the other hand, if the leaves formed on a single shoot are considered, a curve showing the periodicity in size of lamina would exhibit a very distinct rise and subsequent fall (both sides of this curve are steeper in shade than sun plants, cf. Text-fig. 5). But a curve showing the progressive changes of structure would be a continually rising one. Thus two leaves from opposite ends of a shoot may be approximately equal in size, yet possess a totally different structure (Text-fig. 4).

¹ Dufour ('87), p. 407, states that stomata are more numerous on leaves grown in sun than in shade, while Eberhardt ('03), pp. 151-2, says that in humid air the size of epidermal cells is increased, and the number of stomata decreased, as compared with the effect of dry air; cf. Fig. 4. p. 81.

Some of the more important features may now be dealt with in detail.

(a) *The stomata.* These are slightly raised, even in the more exposed leaves of *S. Ulmaria*, var. *denudata* (Text-figs. 3 and 4). They are for the

SUN SERIES

SHADE SERIES

TEXT-FIG. 5. Selected leaves from two flowering shoots, to show (a) periodicity of leaf size, (b) difference in actual size of 'sun' and 'shade' leaves, and (c) narrowing of leaflets of upper leaves. Certain leaves of each series have been omitted (see numbers of those selected). In each case the largest and smallest are shown. All $\times \frac{1}{5}$.

most part confined to the lower surface of the leaf. The only exceptions to this are (1) a few at the sides of the larger veins, and (2) groups of very small stomata, which are crowded on the upper surface of the leaf-teeth, immediately above the endings of the more important veins. On determin-

ing the numbers of stomata per unit area, it was at once apparent that an increase occurred in successive leaves. Unfortunately, while the numbers on the glabrous leaves are readily ascertainable, the dense pubescence of the majority of leaves renders accurate counting impossible. Many methods of surmounting this difficulty were tried, but none proved really successful.¹ Finally, the var. *denudata* was used, though this is also hairy to a certain extent. It is from this plant that the only complete series of counts were obtained. A few actual examples may be given.

SHOOT A² (Type form). A 'shade' plant, i. e. grown in ordinary garden soil, under currant bushes, and sheltered by a high wall on the south side. The shoot produced a total of 24 leaves. Of these, the first two were quite glabrous. A few extremely short hairs appeared on the main veins of the *third* leaf. The hairs gradually increased in number and length until the eighth leaf, when it was difficult to count the stomata; above this it was impossible.

Leaf No.	1	2	3	4	5	6	7	8
No. of stomata } per sq. mm. ³	221	221	224	226	240	255	302	about 348

SHOOT B (Type form). Grown under distinctly drier and sunnier conditions than A. In all, 14 leaves were produced. Very short hairs again began on the *third* leaf. The stomata could not be counted beyond the sixth leaf.

Leaf No.	1	2	3	4	5	6
No. of stomata } per sq. mm.	239	283	273	350	360	372

SHOOT C (var. *denudata*).⁴ Grown in a garden, fully exposed to sun. In all, 21 leaves were produced. A very few short, straight hairs appeared on the main veins of the *fifth* leaf. These slowly increased in number and length on the remaining leaves. In this variety, however, the leaves never become densely hairy, though in a few cases stomata counting was somewhat difficult.

<i>Leaf No.</i>	1	2	3	4	5	6	7	8	9	10	11
<i>No. of stomata</i> } <i>per sq. mm.</i>	393	303	313	322	313	352	482	440	543	678	807
<i>Leaf No.</i>	12	13	14	15	16	17	18	19	20	21	
<i>No. of stomata</i> } <i>per sq. mm.</i>	776	856	945	934	928	1095	1188	1293	1083	1090	

Thus there is a gradual though fluctuating rise in the number of stomata through the successive leaves of the entire shoot. The numbers themselves are worthy of comment. Not only are the absolute numbers of

¹ Hesselman ('04), p. 419, states that he, too, was similarly baffled by this same species.

² The same shoots will also be referred to later as Shoots A, B, and C.

³ The stomata counts, in this and the following cases, were taken from the terminal leaflet, cleared as previously described. As a rule, the numbers represent the mean of ten counts taken from different parts of the leaflet (lower surface only). The larger, and as far as possible even the smaller, veins were avoided.

⁴ The leaves used for Text-fig. 4 are from this shoot.

stomata on the upper leaves extraordinarily high,¹ but the range from about 300 to nearly 1,300 per sq. mm. for different leaves of the same shoot is equally remarkable. It may be that *Spiraea Ulmaria* is exceptional in the latter respect. But it would be worth while comparing the successive leaves of a number of other plants, for if the phenomenon is at all general, the numbers already published for a large number of species² might need considerable revision. The highest number previously recorded appears to be 1,000 per sq. mm. in *Psidium Guyava*, which Parkin and Pearson³ mention as being very remarkable in this respect.

The glabrous autumn leaves resemble the glabrous spring leaves in structure as well as appearance. Thus the number of stomata in the former is usually between 200 and 300 per sq. mm. Further, in the case of tall radical leaves, there is often considerable difference between the upper and lower leaflets, the latter possessing a more pronounced 'shade' structure than the former.⁴ Thus the lower leaflets may be less hairy, and have fewer stomata and more lacunar mesophyll.

E. g. the sixth leaf of Shoot A had 255 stomata per sq. mm. on the terminal leaflet, and only 213 on the lowest leaflet. Again, in a partly hairy leaf (the fourth on the shoot) collected at Wicken Fen, the terminal leaflet had 395 stomata per sq. mm. ; the

TEXT-FIG. 6. Stomata from different leaves. For description see text. $\times 535$.

second pair of leaflets, 333 ; the fourth pair, 269, and the lowest pair of all, only 176. In other cases, however, the differences were less than these.

But the number of stomata is not the only thing to be considered. From the point of view of transpiration, the size of the stomata, and more particularly of their pores, is as important as their number. Text-fig. 6 shows stomata taken from three different leaves. A is from a radical leaf of a plant grown in deep shade, under a bell-glass, i. e. in saturated air and weak illumination. The pore is widely open. The leaf had an average of 255 stomata per sq. mm. B is from the second leaf of Shoot C, with 303 stomata per sq. mm. Here the pore is smaller, but still much larger than that of C, which is taken from the eighteenth leaf of the same shoot (C),

¹ Shoot C was not unique in possessing such numerous stomata. In all, three shoots of var. *denudata* were examined, and in each case the stomata on the upper leaves exceeded 1,000 per sq. mm. In one shoot 1,252 were recorded, and in another, grown in shade, but otherwise exposed, 1,112.

² Cf. Morren ('63), Weiss ('65), and other authors. Miss Delf ('11), p. 500, has recently recorded a similar rise (from 97.5 to 236.25 per sq. mm.) in the number of stomata on successive internodes of *Salicornia annua*.

³ Parkin and Pearson ('03), p. 443. Jost ('07), p. 38, states that in extreme cases there may be as many as 625 (*Olea*) or 716 (*Brassica rapa*) per sq. mm.

⁴ Boodle ('04), pp. 663-4, records an instance in which the upper, exposed pinnae of a leaf of *Pteris aquilina* had marked xerophytic characters, which were absent in the lower, sheltered pinnae.

with 1,188 stomata (cf. Text-fig. 4). Many of the stomata on the upper leaves had even smaller pores than C. Moreover, abortive stomata, or what appear to be such (Text-fig. 6, D), with no actual pore at all, are very frequently found. These are much more common on the leaves with numerous stomata than on the lower leaves, and have been included in the countings given above.

The question at once arises, so far as the stomata alone are concerned, will the transpiration from the numerous small stomata of the upper leaves be greater or less, per unit area of leaf surface, than that from the fewer but larger stomata of the lower leaves? If very much greater, it would seem possible that any economy of water effected by the production of hairs and other xerophytic devices in the upper leaves might be rendered nugatory by the numerical increase of stomata. Appended below are rough calculations,¹

¹ Unfortunately, the only measurements available at the time of writing this paper are taken from the stomata of leaves fixed and cleared in the manner described above. As, however, the several leaves were treated in exactly the same way, it is probable that the respective sizes of the stomatal pores bear much the same relations to each other as when fully open in nature. Still, the measurements, &c., given must be taken as approximations only.

Regarding the stomatal pores as ellipses, the areas of the pores shown in Text-fig. 6, B and C (i. e. from the second and eighteenth leaves), are 0.0000136 sq. mm. and 0.0000036 sq. mm. respectively. As the second leaf has 303 stomata per sq. mm. of leaf surface, the total area of the stomatal openings amounts to about 0.00412 sq. mm., i. e. 0.41 % of the whole lower surface of the leaf. In the eighteenth leaf, however, which has 1,188 stomata per sq. mm., a considerable number of the stomata are abortive. Moreover, the pores of many of the remainder are smaller than the one figured (see Text-fig. 6, C and D). It has been estimated (roughly) that the number of effective stomata on this leaf may amount to about 80 % of the whole. On this assumption, the total area of stomatal openings would be about 0.00342 sq. mm., or 0.34 % of the lower leaf surface; that is, actually less than in leaf 2.

For calculating the amount of water vapour which could be transpired through the stomata of the two leaves respectively, the formula given by Brown and Escombe ('00, p. 276) for the absorption of CO₂ may be used. It is assumed that the air in the intercellular spaces of the leaves is saturated with water vapour, and the free air outside the leaves two-thirds saturated. The measurements are calculated at 18° C. and 760 mm. The formula in question is:

$$Q = \frac{k\rho \cdot A \cdot y \cdot 3,600}{l + x}$$

where Q = the amount of water vapour (in c.c.) transpired per hour per sq. cm. of lower leaf-surface, and

(1) in the case of leaf 2:

k = diffusivity of H₂O vapour at 18° C. in C.G.S. units = 0.248.

ρ = difference of pressure of H₂O vapour inside and outside leaf, in atmospheres = 0.0067.

A = area of pore of stoma = 1.36×10^{-7} sq. cm.

y = number of stomata per sq. cm. = 30,300.

l = length of stomatic tube = 0.0010 cm.

$x = \frac{1}{8}\pi \times \text{diameter of circle of same area as elliptical pore of stoma} = 0.00016 \text{ cm.}$

Hence, $Q = 21.2$ c.c. of water-vapour transpired per hour per sq. cm. of lower leaf surface.

(2) For leaf 18, the differences will be:

$A = 3.6 \times 10^{-8}$ sq. cm.

y (reckoning 80 % of the total number as effective) = 95,000.

$l = 0.000714 \text{ cm.}$

$x = 0.000084 \text{ cm.}$

In this case, $Q = 25.4$ c.c. of water vapour transpired per hour per sq. cm. of leaf surface.

It will be seen that there are several possible sources of error in such a calculation as the above.

from which it seems probable that the difference is not great. Thus, considering the stomata alone, and under certain specified conditions (the same for the two cases), it is calculated that for Shoot C transpiration from the second leaf (Text-figs. 4 and 6, B) might amount to 21.2 c.c. per hour per sq. cm. of leaf surface. From the eighteenth leaf (Text-figs. 4 and 6, C) the corresponding amount would be 25.4 c.c. per hour per sq. cm. The difference is not very pronounced; so as the upper leaves possess a dense covering of hairs, more compact mesophyll, &c., it may safely be asserted that, in spite of the numerous stomata, they are, on the whole, distinctly more xerophytic than the lower leaves (see § 13). The argument here is from leaf structure alone; the ultimate test is of course the measurement of actual transpiration (see § 12).

(b) *Thickness of leaves, &c.* The leaves of *Spiraea Ulmaria* are fairly thin, varying in total thickness (excluding the hairs) from about 78 to 140 μ . Curiously enough, the thickest leaves on a shoot are invariably the glabrous spring leaves. In these the individual cells are large and loosely arranged. On passing up the stem, the successive leaves show a gradual shrinkage in the size of these cells,¹ which at the same time become more tightly packed together (see Text-fig. 4). The leaves thus exhibit a progressive reduction in thickness. The upper leaves, in fact, may almost be said to be shrunken miniatures of the lower. This of course applies to structure, not to surface area of the lamina. It is chiefly in this variation in size of the individual cells that the plasticity of the leaves of *Spiraea* consists, rather than in any marked change in the number of layers comprising the leaf, or the proportions assumed by the various tissues. There are, however, some changes in these proportions, which may now be instanced, and a few average measurements given (in μ).

	Total thickness of leaf, between veins.	Depth of cells of upper epidermis.	Depth of cells of lower epidermis.	Depth of palisade.	Depth of spongy mesophyll.	Ratio of palisade to spongy mesophyll.
SHOOT A (referred to above)—grown in shade:						
Leaf No. 2	138.0 μ	22.0 μ	15.5 μ	54.5 μ	46.0 μ	1.2 : 1.0
„ 18	78.0	15.5	8.0	31.0	23.5	1.3 : 1.0
SHOOT B—grown in light of moderate intensity:						
Leaf No. 2	140.0	19.5	15.5	60.0	45.0	1.3 : 1.0
„ 12	104.0	18.0	8.0	47.0	31.0	1.5 : 1.0
SHOOT C—fully insolated:						
Leaf No. 2	135.0	19.5	15.5	57.0	43.0	1.3 : 1.0
„ 18	80.5	17.0	8.0	31.0	24.5	1.3 : 1.0

These figures illustrate the general shrinkage referred to above. Further, the lower epidermal cells decrease in depth in the upper leaves,

But it is probable that the difference in transpiration could not be very much greater, and might even be considerably less than that calculated here.

I am indebted to Professor G. A. Schott for assistance in making this calculation.

¹ This has already been noted for the epidermal cells and stomata.

much more than those of the upper epidermis (cf. also the sections and surface views in Text-fig. 4). The latter cells remain relatively large in the upper, exposed leaves, especially at the leaf margins.

(c) *Palisade tissue.* The above table shows that the ratio of the total depth of the palisade *tissue* to that of the spongy mesophyll is remarkably constant. The variation, however, in the ratio of the length of a palisade *cell* to its breadth is considerably greater. As one would expect, the palisade cells of 'shade' plants tend to be relatively shorter and broader than those of 'sun' plants. In addition to this, in an individual leaf, those palisade cells which are most remote from the larger veins are relatively longer and narrower than those situated near to the veins. Again, taking a lower and an upper leaf from each of the three shoots previously used, we get the following average measurements (expressed in μ):

	<i>Length of palisade cell.</i>	<i>Breadth of palisade cell.</i>	<i>Ratio of length to breadth.</i>
SHOOT A—shade:			
Leaf 2 (a) near vein . . .	30.0 μ	15.5 μ	1.9 : 1.0
(b) remote from vein	32.0	11.5	2.8 : 1.0
Leaf 22 (a) near vein . . .	19.0	9.5	2.0 : 1.0
(b) remote from vein	18.5	6.5	2.8 : 1.0
SHOOT B—moderate sun:			
Leaf 4 (a) near vein . . .	27.5	9.5	2.9 : 1.0
(b) remote from vein	35.5	8.0	4.4 : 1.0
Leaf 10 (a) near vein . . .	24.0	8.5	2.8 : 1.0
(b) remote from vein	31.0	7.0	4.4 : 1.0
SHOOT C—full sun:			
Leaf 2 (a) near vein . . .	30.0	12.5	2.4 : 1.0
(b) remote from vein	36.5	10.0	3.6 : 1.0
Leaf 18 (a) near vein . . .	20.0	9.5	2.1 : 1.0
(b) remote from vein	24.0	7.5	3.2 : 1.0

This table shows clearly (1) that the actual dimensions of the palisade cells are less in the upper than the lower leaves; (2) that the palisade character is best developed at some distance from the larger veins;¹ and (3) that the palisade character is least marked in shoots grown under shade conditions.

§ 8. DEVELOPMENT OF THE LEAVES, AND TIME OF ORIGIN OF THE HAIRS, PALISADE CELLS, &c.

In order to appreciate the effect of environment on the production of hairs, it is necessary to follow to some extent the development of the leaves themselves. Comparatively little appears to have been written on the later stages of leaf development.² A brief account will therefore be

¹ Stahl ('83), p. 35, records the same fact for the sun leaves of the Beech and the Bilberry. This is analogous to the development of the interveinal bands of hairs in partially hairy leaflets.

² Goebel ('05), p. 302 et seq., and others have described the distribution of growth during development, &c. The former points out (p. 305) that 'in general, parts which have the earlier functions to perform appear the earliest'. Mer ('83), p. 111, has given a very brief account, unaccompanied by figures, of the order of development of the tissues of the lamina itself.

given of the order and time of appearance of certain of the tissues of which the lamina is composed.

If a winter bud of *Spiraea Ulmaria* be examined about November, it will be found that the stipular bud-scales are well developed. The most advanced foliage leaves (the glabrous ones of the following spring), however, have only reached a stage approximately equivalent to that shown in Text-fig. 7 (this figure is taken from a hairy leaf). The leaves remain practically in this condition throughout the winter, and are little further developed by the following March, when the bud begins to expand. Multicellular mucilage hairs are abundant, especially on the upper surfaces of the veins. But the long cutinized hairs¹ which form the characteristic pubescence of the later leaves are at this stage absent from the entire bud. It is

TEXT-FIG. 7. Section through part of a young developing leaf, while in the bud. The still meristematic portions (i. e. the interveinal parts of lamina) are shaded. $\times 360$.

important to notice that *few, if any, of these cutinized hairs are developed in the bud until after the first foliage leaves have expanded and become functional.*

The development of one of the hairy leaves may now be followed. In every case the larger veins are the first parts of the lamina to develop, and are relatively large and well differentiated at a time when the rest of the lamina is still meristematic (see Text-fig. 7). On a leaf such as this, which is destined to become hairy, the first hairs are formed early. They appear

¹ At least three kinds of hairs occur on the leaves of *Spiraea Ulmaria*: (1) capitate mucilage hairs, which appear to function mainly in the bud (in *Spiraea* they wither soon after the leaf expands); (2) short bristly hairs found scattered on the upper surface and at the margins; and (3) the long, unicellular, twisted, cutinized hairs, of which the pubescence clothing the lower surface of the leaves is composed. It is the last kind which is to be understood when 'hairs' are referred to in the remainder of this paper.

on the larger veins at approximately the same time as the protoxylem, and while the leaf is still completely enclosed in the bud (Text-fig. 7). At this time the remainder of the lamina is meristematic, though the upper and lower epidermis and several layers of mesophyll are distinguishable.

A somewhat later stage is diagrammatically represented in Text-fig. 8, A. The first seven leaves of the shoot had expanded, but the leaf figured was still completely enclosed in the bud. The interveinal parts of the lamina

TEXT-FIG. 8. A, transverse section through part of an apical bud, showing several leaflets of a single developing leaf. Meristematic portions shaded black. B, a single leaflet just emerged from the bud. C, a still later stage. All $\times 16$.

are developing, and in consequence assuming a looped appearance. They are still meristematic, and as yet bear no hairs. The mesophyll is undifferentiated, and there are neither stomata nor intercellular spaces. The smaller veins have not yet been formed. In the main veins the protoxylem alone is lignified, but the veinal hairs are now so numerous that they form a fairly dense packing below and between the veins.

Text-fig. 8, B is taken from the terminal leaflet of the ninth leaf of the

same shoot as 8, A. This leaf had emerged from the bud, and so was in contact with the outer air. It was a little further expanded than leaf 6 in Text-fig. 2. By this time more xylem tracheae have matured, and many of the finer veins, also bearing hairs like the main veins, have been differentiated. Many stomata have appeared, and also intercellular spaces in the mesophyll, but the latter are small, and few of the former quite mature. The uppermost layer of mesophyll has begun to take on the character of palisade tissue (this is most marked at the tops of the loops), and in places even a second row of palisade cells has begun to form. Thus at this stage, i. e. very soon after the leaf emerges from the bud, and before it is fully expanded, all the chief tissues are recognizable. But the leaf has not as yet attained either its full size or thickness.

A still later stage is seen in Text-fig. 8, C, which represents a section through the lowest leaflet of the same leaf as 8, B. (N.B.—The leaflets, like the leaves, develop and unfold in regular acropetal succession; see Text-fig. 2, leaf 5.) The leaf has now nearly reached its final thickness. The smallest veins are present, also the cuticle and two layers of palisade. The stomata are more mature and the intercellular spaces larger.

The ultimate degree of expansion of the cells and tissues, and also the question of whether the lamina shall become flat or remain more or less crinkled or folded, depends chiefly on the external conditions.

The general distribution of pubescence on the leaves has been discussed earlier in this paper. It is now clear that the earliest hairs appear on the main veins, while the leaf is still in the bud. Subsequently, when the leaf is emerging, or has just emerged from the bud, the next hairs to be formed are those on the finer veins at the leaf margins or between the main veins; that is, on those parts most remote from the main veins, and which are the first to be exposed to the air as the leaf unfolds.¹ Development of the pubescence may now be arrested, as in the partly hairy leaves or leaflets; or it may proceed further until even the finest veins are covered with hairs. In many cases hairs are even formed on the ultimate parenchyma 'islands' bounded by the finest veinlets.

To sum up, the main veins of the lamina, together with the hairs they bear, reach a high state of development in the bud. On the other hand, the hairs on the finer veins, and those which occur over the parenchyma 'islands', only appear when the leaf has emerged from the bud; i. e. when some parts of it are already in direct contact with the outer air. This is also true of the palisade tissue, the intercellular spaces of the mesophyll, the cuticle, and the stomata.

We are now in a position to discuss :

¹ In the case of the interveinal bands of hairs, it is the *upper* surface which is most exposed, while the hairs are actually developed on the *lower*. Cf. Text-fig. 8, B.

§ 9. THE EFFECT OF ENVIRONMENT ON THE PRODUCTION
OF HAIRS AND PALISADE CELLS.

(a) *Historical.* Many of the older observers noticed that plants not infrequently varied in hairiness according to habitat. Thus Linnaeus¹ mentioned *Plantago Coronopus* as being 'in humido foliis glabris integris, in sicco hirsutis dentatis'.¹ De Candolle² said that lymphatic (i. e. non-glandular) hairs 'are in general rare in plants which grow in the shade, or in rich and moist places'; while 'they are more abundant, generally, in those which grow in warm and dry places, much exposed to the sun'. Kraus³ instanced potato shoots as being less hairy or even glabrous when grown in very moist air than in dry air.

During the last thirty years a considerable literature has arisen, dealing with the influence of external factors, not only on the development of epidermal structures such as hairs, stomata, &c., but also on the differentiation of the mesophyll, and especially of the palisade tissue. One of the earlier works of this period was the classic paper by Stahl,⁴ published in 1883, in which the action of light is regarded as the factor determining the structure of 'sun' and 'shade' leaves.

In the same year Mer⁵ found that light and also dry air favour the production of palisade tissue, while shade and humidity produce the reverse effect. The same is true also of hairs on aerial stems.⁶ A well-watered soil hindered the formation of both stem- and root-hairs, while both were produced if the soil were drier.

Vesque and Viet⁷ proved that light, accompanied by more or less dry air, increases the development of palisade tissue, and the number and length of hairs on leaves. In a later paper, Vesque⁸ says that the result of a large number of cultural experiments shows that a marked development of palisade tissue can always be referred to the action of transpiration.

Kohl⁹ stated that changes of relative humidity in the atmosphere surrounding growing organs are capable of inducing the formation or suppression (as the case may be) of palisade cells. Again, he found¹⁰ that in the case of hairy species of Compositae or Labiatae, not only the number of hairs, but also their length, is determined to a great extent by the amount of transpiration from the organs themselves. The less the transpiration, the fewer and shorter the hairs.

Dufour¹¹ found that the dimensions of leaves developed in light of high intensity are greater in all respects (and the palisade tissue is more pronounced) than those of leaves grown in shade.

¹ Linnaeus ('63), p. 219.

⁴ Stahl ('83).

⁷ Vesque and Viet ('81), p. 176.

¹⁰ Kohl, l. c., p. 103.

² De Candolle ('41), p. 98.

⁵ Mer ('83), p. 112.

⁸ Vesque ('83), p. 489.

¹¹ Dufour ('87), pp. 406-8.

³ Kraus ('76), p. 153.

⁶ Mer, l. c., p. 117.

⁹ Kohl ('86), p. 93.

Eberhardt¹ showed that plants grown in dry air tend to be more hairy, and their leaves thicker (in consequence of the great development of palisade), than those grown either in normal or in very humid air.

Zinger,² in an interesting paper on some European species of *Camelina*, shows that in *C. microcarpa* and the different varieties of *C. sativa*, a gradual transition from a xerophytic to a hygrophytic type can be traced, with marked differences in respect of palisade tissue, hairiness, &c. These differences are strictly correlated with the conditions of illumination and moisture in the respective natural habitats.

Lesage³ found that when plants were grown in a saline soil, or solutions in which the salts reached a certain concentration, they developed more palisade than when grown in ordinary soil or very dilute salt solutions. Later⁴ he subjected growing plants to periodic variations of atmospheric pressure. Those which had been exposed to the periodic lowering of pressure had (if leaves of the same age, &c., were compared) more marked palisade than the control plants grown under ordinary air pressure.

Similar results to those of the above-mentioned authors have been obtained by other experimenters.⁵

Although the question of root-hairs scarcely comes within the scope of this paper, it may be mentioned that their formation also is largely dependent on the water supply. Schwarz⁶ found that no root-hairs were formed in very wet soil. Further, that as the water content of the soil decreased, root-hairs increased correspondingly. Finally, however, when the soil attained a certain degree of dryness, root-hairs were again suppressed.

If the above results be analysed, it will be noticed⁷ that *in general*,⁸ both palisade cells and the epidermal hairs of aerial shoots (and to some extent at least, root-hairs) are most fully developed under conditions which either promote transpiration or hinder absorption; namely, under conditions which impose on the plant some necessity for increased economy of water.

The results of the writer's own work on *Spiraea Ulmaria* and other marsh plants may now be given.

(b) *Field observations on Spiraea, &c.* It has been stated above that even the type-form of *Spiraea Ulmaria* produces both glabrous and hairy

¹ Eberhardt ('03), pp. 149-52.

² Zinger ('09), pp. 340-9.

³ Lesage ('89), p. 204, and ('90), p. 170. Cf. also Boodle ('04, second paper), p. 41.

⁴ Lesage ('94), p. 255.

⁵ e. g. Géneau de Lamarlière ('92), p. 483 et seq., Lothelier ('93), p. 520, &c. Cf. also Burgerstein ('04), pp. 47-53, and the additional literature cited by him.

⁶ Schwarz ('83), p. 14 et seq. Cf. also Sorauer ('86), pp. 95-6, and Mer ('83), p. 117.

⁷ Cf. Lesage ('94), and Burgerstein ('04), pp. 51 and 53.

⁸ Of course plants vary much in plasticity. Stahl ('83), pp. 5-10, instances cases of pronounced shade and sun plants which have little or no power of adapting themselves to sunny and shady habitats respectively.

leaves. As a rule, these occupy in nature the more shady and humid, and the sunnier and drier positions respectively. This is true as regards both time and space; i. e. whether we consider the leaves in relation to the annual march of the seasons, or the vertical distribution of humidity and light in the vegetation. The curves in Text-fig. 9 represent the mean evaporation and light intensity for several years. Both curves rise to a maximum in July and then fall steadily towards autumn. Further, I have shown that in marshes there is a rapid rise in the average evaporation as the

TEXT-FIG. 9. Curves of mean evaporation [continuous line] and light-intensity [broken line]. The former shows the mean monthly evaporation for twenty-five years in London [see Mill ('10), p. 56]. The latter represents the mean maximum light-intensity at Vienna for three years only [taken from Wiesner ('07), p. 52].

successive strata of the vegetation are ascended.¹ Lately, I have also determined by experiment that the same is true of light-intensity.

If the degree of hairiness could be conveniently represented by means of curves, it would be found that the curves of actual hairiness in *Spiraea Ulmaria* follow very closely the mean curves of evaporation and light-intensity, both in space and time. Thus, (1) in the erect flowering shoots, the glabrous spring leaves are formed near the ground, at a time of

¹ Yapp ('09), p. 287 et seq. Dachnowski ('11), p. 146, has recently confirmed my evaporation results, in the case of the bog vegetation of Cranberry Island.

year (about March) when the average evaporation is slight and the light-intensity low. As the season progresses and the curves of evaporation and light rise steeply (Text-fig. 9), and further, as the shoot itself grows upwards into drier and lighter strata, the leaves exhibit continually increasing hairiness (Pl. LXXXI, and Text-fig. 10). (2) The curve of hairiness of non-flowering shoots rises steadily to June or July; subsequently falling till glabrous leaves are once more reached in autumn. This corresponds very closely indeed to the curves in Text-fig. 9. Finally, (3) the same general relations obtain even in the case of individual partly hairy leaves. Just as

TEXT-FIG. 10. Diagrammatic section through a group of plants of *Spiraea Ulmaria*, showing relation of glabrous and hairy leaves to strata of varying humidity. Glabrous leaves, black with white veins; hairy leaves, white with black veins. (June.) $\times$ about $\frac{1}{4}$.

successive leaflets occupy higher and less humid levels, so they exhibit increasing hairiness from below upwards (Pl. LXXXII and LXXXIII, and Text-fig. 10).

The same relations are broadly true of other hairy marsh plants,¹ and also for the structural variations described earlier in this paper. These field observations are at once seen to agree with the general experimental results quoted above. They suggest considerable responsiveness, on the part of *S. Ulmaria* and other plants, to even slight variations in the environment.

¹ See § 6; also Yapp ('08), p. 691.

(c) *Experiments on Spiraea, &c.* In the first instance I was easily able to confirm the researches of Vesque and Viet, Kohl, and others,¹ on the effect of humidity on hair production in certain plants. E. g. in *Epilobium hirsutum* and *Mentha aquatica*, the formation of hairs was completely inhibited by growing the plants in a damp atmosphere; the converse being true of a dry atmosphere. The case of *S. Ulmaria*, however, proved to be somewhat different. A large number of plants of this species were grown, some at the Cambridge Botanic Garden (through the kindness of Mr. R. I. Lynch), and others at Aberystwyth. A wide range of habitats was secured by varying the following factors: (1) soil, (2) soil-moisture, (3) humidity of air, (4) light-intensity, and (5) degree of exposure or shelter.²

The experiments extended over a period of four years, so that while the same individual plants were used, several generations of shoots were observed.

On the whole, the effect of varying habitats on the hairiness of *Spiraea Ulmaria* was less than had been expected, the character being apparently one of a certain degree of fixity. Differences of soil, soil-moisture, light-intensity, and exposure produced no effect whatever on the normal periodicity of hair formation. Under no conditions could the normally glabrous spring or autumn leaves be induced to become hairy,³ while in all cases the upper leaves on the flowering shoots produced hairs.

But though external conditions had comparatively little controlling effect on the actual formation of hairs, in certain instances they exercised considerable influence on the frequency, and especially on the length of the hairs. This was the case with shoots grown under glass shades, i. e. in still, humid air. When (a) these were exposed to full sunlight,⁴ the effect was

¹ Vesque and Viet ('81), Kohl ('86), &c.

² At Cambridge the plants were potted in either (a) pure peat, (b) loam, or (c) a mixture of peat, loam, and sand. The pots were then divided into two sets. One set was placed in a fully insulated part of the garden, the other in a shady spot, never reached by the direct rays of the sun. Soil-moisture was varied by submerging (partly or completely) certain pots in water. Others had good drainage, but were copiously watered, while a third set were only watered at infrequent intervals. A final differentiation of habitat consisted in placing glass shades over some of the drained and also undrained pots. The aerial shoots were thus developed in a still, humid atmosphere, under varying conditions of light, soil-moisture, &c.

At Aberystwyth plants were grown in various situations in a garden, some in deep shade, others in the open, &c. Others were kept in the laboratories, and also on the roof of the College, which is situated close to the sea, and exposed to great gales of wind.

³ Cf. Vesque ('84), p. 21, who says that he had never succeeded in inducing a single hair to form on a really glabrous plant: though theoretically he thought it should be possible, as 'les plantes glabres ont dû précéder historiquement'.

⁴ As determined by experiment:—

(1) The shade plants (b) were grown under light-intensity =	1.0
(2) „ sun „ (a) „ „ „ „ „	= 4.5
(3) In the free air outside the glass shade (a) „ „	= 4.9

Thus, a little light is cut off by the glass shade, or by the moisture which condenses on its

comparatively slight; the leaves appearing to be nearly as hairy as those grown in the open. The hairs, however, were distinctly shorter. *The greatest diminution of hairiness was induced when low light-intensity was superadded to stillness and humidity of the air.* Thus (b) flowering shoots grown in weak light under glass shades still produced more or less hairy leaves, but the hairs were straight and very short. The lower cauline leaves appeared to be more easily influenced than the upper.

A curious inhibition of hairs occurred on plants which had been protected from cold, &c., during the winter. A number of plants were kept indoors continuously for some years, in the Cool Fern House and the Cool Pit at Cambridge, and the Laboratories at Aberystwyth. In all cases the rhizomes of these plants remained horizontal, and each year produced a crop of radical leaves of the glabrous spring or autumn type.¹ In a few instances patches of hairs occurred on a leaf, but for the most part the leaves were entirely glabrous. On the other hand, plants brought indoors towards the close of the winter produced normal erect flowering shoots with hairy leaves.

Another experiment which resulted in decreased hair formation is recorded on p. 847.

Spiraea Ulmaria, var. *denudata*, Boenn., like the type form, commences in spring-time by forming glabrous leaves. These are followed by increasingly hairy leaves as the erect flowering stem elongates. But here the hairiness begins somewhat later, and is chiefly confined to the larger veins of the leaves; the general pubescence, so characteristic of the type, being absent. In nature I have found many transitional forms intermediate between *S. Ulmaria* and its variety *denudata*.² Thus individuals are sometimes found with an unusual number of glabrous radical leaves. In others, one, two, or even more of the cauline leaves may also be glabrous. Finally, plants occur in which only the leaves at the extreme top of the flowering shoot are markedly hairy. But in all cases, whether in the type, or its var. *denudata*, or in any of the numerous intermediate forms, the lower leaves are glabrous. On the other hand, the cauline leaves are (in varying degrees) increasingly hairy as the flowering shoots are ascended.

inner surface. The method used was based on the following: If a solution of potassium iodide be mixed with dilute sulphuric acid, and exposed to light in the presence of oxygen, the iodine liberated is a measure of the total light received during the time of exposure (see Manchester ('93), p. 88 et seq.). This method, to which Professor Weiss called my attention, has the advantage of recording the *total light received*, and not merely the intensity at a given moment. Like other photometric methods, it has the disadvantage of recording only the chemically active rays. For a discussion of the utility of such methods for botanical researches, see Rübel ('08), pp. 5-7.

¹ Gates ('10), p. 677, similarly found that the internodes of *Oenotheras* grown in a tropical greenhouse did not elongate, the plants thus remaining (for the entire time of the experiment, i. e. twenty months) in the rosette condition. Cf. also the experiments of Klebs ('10), p. 552 et seq., on *Sempervivum*.

² Trow ('11), p. 58, also states that *S. denudata* occurs in Glamorganshire, together with many intermediate forms connecting it with the type.

The var. *denudata*, as well as several intermediate forms, has been grown for some years. The results show that the individual, in its successive generations of shoots, retains to a considerable extent its peculiar characteristics, even under varying habitat conditions. For example, *S. denudata* has never been induced to become really hairy, even when grown in dry, sunny, exposed situations.

The results recorded in this section show that (1) the production of glabrous and hairy leaves in *Spiraea Ulmaria* and certain other marsh plants closely follows in nature the mean curves of evaporation and light-intensity; but that (2) *S. Ulmaria* possesses a more limited plasticity, in respect to hairiness, than that exhibited by such species as *Mentha aquatica*, &c.

§ 10. THE LOCALIZATION OF WITHERING IN LEAVES EXPOSED TO WIND, ETC.

Before discussing the causes of hair formation, certain parallel phenomena must be mentioned. As stated above (p. 820), the partially hairy leaves and leaflets of *Spiraea* exhibit a definite localization of the hairs (cf. Pl. LXXXII and LXXXIII). It was early noticed¹ that when *Spiraea* plants with glabrous leaves were exposed to winds sufficiently strong to cause partial withering, the distribution of the withered parts coincided very nearly with the distribution of hairs on the partly hairy leaves of the same species. Exposure withering thus begins round the margins of the leaflet, and sometimes, though not always, extends inwards in the form of bands between the main veins. Subsequently observations were made on the localization of withering in the leaves of many other plants. These, which for the most part confirm the results of Schröder,² published in 1909, may now be summarized (cf. Text-fig. 11).

Leaves which are allowed to wither naturally in still air lose their colour gradually, and either more or less uniformly or else irregularly. On the other hand, the effect of exposure to strong winds, &c., is to cause first a marked withering of projecting apices, e. g. the apex in linear leaves,³ &c., leaf-teeth, or the various tips of lobed leaves (see Text-fig. 11, A, B, and E). Next, in other than linear leaves, the withering extends round the margin of the leaf, and sometimes, though by no means always (even the same species may vary in this respect, cf. Text-fig. 11, C and D), between the larger veins (Text-fig. 11, B-G).⁴ The process may now stop, or it may

¹ Yapp ('08), p. 691.

² Schröder ('09), pp. 85, &c. Apart from this paper the literature on the withering of leaves is scanty. Hansen ('01), p. 32, and ('04), p. 34, calls attention to the withering of leaf apices and margins through wind. Hasenclever ('79), and Oliver ('93), p. 22, show that acid gases will cause discoloration of the apices and margins of leaves. Cf. also Stahl ('09), pp. 134-5.

³ Cf. Yapp ('08, second paper), p. 65.

⁴ My attention was called by Professor F. W. Oliver to the exceptional case of *Polygonum*

TEXT-FIG. 11. To illustrate localization of withering in leaves exposed to wind, &c. Withered portions, black with white veins; uninjured parts, white with black veins. A, *Plantago lanceolata*; B, *Quercus Robur*; C and D, *Fagus sylvatica*; E, *Crataegus Oxyacantha*; F, *Populus* sp.; G, *Rosa* sp.; H and J, *Polygonum cuspidatum*. J is a section through an unfolding leaf: the black parts here are not yet withered, though they may wither later. A-H, $\times \frac{2}{3}$; J, $\times 4\frac{1}{2}$.

continue until only the tissue immediately surrounding the larger veins remains green; ¹ finally this too may wither and die.

Further, a similar localization is seen in other connexions. Thus anthocyan in young leaves in spring-time is frequently confined to the tissues at the apex of the leaf, round the margins, and between the larger veins.

Lidforss ² figures leaves of *Viburnum Tinus*, in which certain portions have been killed by frost. These portions are the margins, and to some extent the interveinal regions. On one occasion the present author noticed an autumn leaf of *S. Ulmaria* which had been injured by frost. Not only did the frozen portions show a similar localization in the individual leaflets, but the different leaflets exhibited decreasing injury from above downwards (cf. the hairiness described on p. 820).

Again, Professor T. H. Macbride, of Iowa, told me in 1909 that *Myxomycetes* often confine their attacks to just these same regions of a leaf.

It is obvious that those regions of the leaf lamina which show a special tendency to form hairs (in *Spiraea*), to wither on exposure to strong winds, &c., &c., are physiologically different from the remaining parts. So far as their water supply is concerned, it may be pointed out that they are usually thinner and more exposed than the parts immediately surrounding the larger veins. They are thus more liable to lose water. Further, they are themselves just the regions of the lamina which are most remote from the water supply coming up from below and passing along the main veins.

§ 11. THE CAUSES OF THE FORMATION OF HAIRS AND PALISADE CELLS.³

Hairs on aerial shoots and palisade cells have a good deal in common. Both are elongated in a direction more or less at right angles to the surface of the organ which bears them. The production of both is favoured (at least in many cases) by the same external conditions (see § 9). Root-hairs

cuspidatum. If in exposed situations, the leaves of this plant are often marked in the spring-time with red bands, parallel to the midrib, and therefore crossing the larger lateral veins. Later, these red bands may disappear, or, if windy weather ensues, the tissue may wither and actual lesions occur (Text-fig. 11, H). This and other Polygonaceae (e.g. *Rumex* spp.) are the only instances I have seen in which the withered areas cross the larger veins, instead of lying between them. It is to be noted that the injury occurs in those parts which are exposed during the unfolding of the revolute leaves (Text-fig. 11, J). If withering is delayed until the leaf is mature, it is then localized round the margins in the normal manner.

¹ In certain cases, e.g. leaves of *Acer*, *Populus*, &c., fallen leaves may be found with the larger veins dead and brown, and the interveinal tissues green. This is the exact converse of exposure withering. It is due, so Mr. G. Massee informs me, to the action of certain parasitic Fungi, which attack only the leaf veins.

² Lidforss ('07), Taf. I.

³ A short paper on this subject was read at the Portsmouth meeting of the British Association, Yapp ('12), p. 565.

also may to some extent be included in the parallel. Probably all three elements play an important part in relation to the water supply of the plant (cf. § 12). They may therefore be considered together, though the main concern of this paper is with the leaf-hairs of *Spiraea*.

In the first place, in so far as the plant is plastic, is it possible to determine the nature of the stimulus to which the plant responds by the development of these special elongated cells?

Kraus¹ explained the formation of hairs on potato stems in dry air by supposing that decreasing humidity hindered growth in length. In consequence, said he, turgor increases in the transverse direction, and the epidermal cells grow out in the form of hairs.

Mer² supposed that the appearance of both stem- and root-hairs is due to the accumulation of nutritive substances caused by a slowing down of growth. Vesque³ adopted Mer's view, though he thought it complicated matters to include root-hairs in the hypothesis.

Jungner⁴ suggested a theory respecting the formation of hairs on certain xerophytes of alpine regions, extending it to include those of deserts and salt steppes. Although acknowledging that the plants are exposed to strong evaporation, he assumed that transpiration is depressed during the early stages of leaf development. Consequently the pressure of turgor in the cells is high, and, the air outside being rarified, the turgid cells grow out in the direction of least resistance.

Turning now to theories of palisade formation, Stahl⁵ supposed that intense light retarded the growth in length of the veins of developing leaves. The young assimilating cells then expand in the only direction possible (i.e. that perpendicular to the leaf surface), and in consequence assume the form of palisade cells.

Mer⁶ attributed a marked development of palisade cells to active nutrition resulting from the action of light in dry air.

Vesque⁷ regarded transpiration as the chief factor inducing the formation of palisade tissue. Kohl,⁸ who held the same view (and applied it also to hair formation), further pointed out that transpiration affects turgescence, and turgescence regulates the growth of cell membranes.

Of these theories, that of Kohl (and of Vesque so far as palisade cells are concerned) agrees best with the known facts (cf. § 9). All the evidence available suggests that any marked development of these peculiar elongated elements is in some way associated with *decreased turgor* rather than the *increased turgor* postulated by Kraus and Jungner. This evidence is as follows:

1. *The experiments of many observers*, which show that in general these

¹ Kraus ('76), p. 153.

² Mer ('83), p. 115.

³ Vesque ('83), p. 495.

⁴ Jungner ('94), pp. 233-4.

⁵ Stahl ('83), p. 34.

⁶ Mer, l. c., p. 112.

⁷ Vesque, l. c., p. 489.

⁸ Kohl ('86), pp. 95 and 103.

elements are developed especially under conditions which either promote transpiration or hinder absorption (see p. 835). For *S. Ulmaria*, &c., in particular, we have seen that in nature the curves of hairiness follow very closely the mean curves of evaporation, &c. It is obvious that such external conditions can only act by inducing internal changes in the cells themselves. Kohl (l.c.) has already suggested that changes of turgor may be important in this connexion.

2. *What may be termed topographical evidence.* It has been shown (§§ 5 (d) and 10) that under certain conditions the margins of leaves and the thinner areas between the main veins exhibit phenomena which the other parts of the leaf do not. Also that these parts are not only especially liable to lose water, but are situated furthest from the water supply coming up from below. Thus it is easy to understand that any shortage in the supply of water to the leaf will affect these regions first and most severely. That such is the case is evidenced by the localization of withering from exposure to wind.¹ These considerations suggest that the marked localization of hairs (and to some extent palisade cells, see p. 830) in the same regions of the leaf may also be connected with a diminished water supply. This is, of course, especially so in view of the known effects of certain external factors (see 1 above).

3. *Evidence derived from leaf-development in Spiraea.* As regards the hairs, we must distinguish between those formed in the bud and those formed during the unfolding of the leaf (see § 8).

It has been shown that, while the earliest leaves are entirely glabrous, the later ones become progressively more hairy, the hairs on the larger veins being formed while the leaf is still in the bud (see Text-figs. 7 and 8). This increasing hairiness of the larger veins of the developing leaves occurs *pari passu* with the general increase of transpiration from the shoot. The latter is of course due partly to the increase of transpiring surface as more leaves are unfolded, and partly to the march of the seasons. Knowing the effect in general of a dry habitat on hairiness, it is difficult to avoid the suggestion that this increase of hairiness may be connected with a diminution of the water supply to the apical bud. This may readily be brought about by a partial deflexion of the water current into the continually increasing number of mature leaves. In this way the cells of the young developing leaves will find it increasingly difficult to maintain themselves in a complete and constant state of turgor. If this be so, it may be regarded as another case of what Wiesner² has called 'correlative transpiration'. Under this term he includes all cases in which strongly transpiring organs deprive others (which transpire little or not at all) of water. Such displacements of water not infrequently bring about striking results. Thus

¹ Hansen ('04), p. 43, &c., discusses the withering of leaves as a result of withdrawal of water by wind.

² Wiesner ('05), p. 477 et seq.

Wiesner (l. c.) observed the production of anisophylly in *Aesculus* under the influence of correlative transpiration. Again, Schimper,¹ Haberlandt,² and others found that the lower leaves of certain plants yielded up their water to the younger leaves when subjected to drought. Two cases which approach that of *Spiraea* very nearly are recorded by Smith and Balls. Smith³ produced evidence to show that during the day-time transpiration from adult bamboo culms may be so great as to draw off the supply of water from the growing culms, thus slowing down their rate of growth. Similarly, Balls⁴ found that in summer-time in Egypt the growth of the stem of cotton plants and others (e. g. *Helianthus*) was completely arrested whenever direct sun was shining on the plant. This he showed to be due to the consumption of all the available water in transpiration from the already unfolded leaves. The water supply was thus the limiting factor in stem growth. These instances add to the probability that a similar disturbance of the supply of water to the apical bud takes place in *Spiraea Ulmaria*, and that this disturbance affects the production of hairs in the bud.

But most of the leaf hairs, as well as the palisade cells, actually elongate after the leaf emerges from the bud, and while it is unfolding in direct contact with the outer air (p. 833). At this stage cuticular transpiration must be an important factor.⁵ Owing to its veneration, the parts directly exposed to atmospheric influences when the leaf first emerges from the bud are the larger veins (which are already covered with hairs) and the delicate leaf margins (cf. Text-figs. 8 and 2, leaf 6). Naturally, therefore, the loss of water by cuticular transpiration will be most severely felt by the latter. As the leaf still further unfolds, and if the transpiration is sufficient, the next parts to experience a shortage of water will probably be the interveinal areas, because it is here less easily replenished. It is precisely in these regions that the hairs are localized in the partly hairy leaves. Finally, when the water supply is still further diminished, the lower surfaces of the unfolding leaves become completely covered with a dense pubescence.

Thus the formation of both the hairs on the larger veins, as well as those on the smaller veins and other parts of the lamina, may be correlated with a diminished water supply to the developing leaves. In the former it seems probable that correlative transpiration plays the most important part. In the latter, loss of water by cuticular transpiration comes into play, coupled with (as before) a strictly limited supply of water from below.

Further, the fact that all the cells of the upper leaves are much smaller than those of the lower (cf. Text-fig. 4) suggests development under conditions in which there is a partial deficiency of water. In other words, it is

¹ Schimper ('88), pp. 37-8.

² Haberlandt ('09), p. 368.

³ Smith, A. M. ('06), p. 325.

⁴ Balls ('10), p. 6, and ('11), pp. 229-30.

⁵ F. von Hoenel ('78) showed that very young developing leaves actually transpire more than mature ones. This he attributed entirely to cuticular transpiration.

probable that the upper part of a normal *Spiraea* shoot has, during development, a less constantly maintained turgor than the lower,¹ and that the water supply is the limiting factor in the growth in size of the cells.

But now arises a difficulty. Although turgor is no longer regarded as the direct cause of the stretching growth of cell-walls,² it is none the less a condition of such growth.³ It is difficult to conceive how either hairs or palisade cells can elongate unless they are turgid. And yet we have seen that they are most strikingly developed under conditions when turgor may be expected to be at a minimum. The difficulty, however, is more apparent than real. In nature the external conditions are never constant. No matter how active transpiration may be at certain times, periods frequently recur (e.g. at night-time or on still, humid days) when turgor is fully restored.

The course of events then is probably somewhat as follows: transpiration during the day-time, increasing with the number of leaves unfolded, and (at least until midsummer) with the march of the seasons, gives rise to a diminished turgor in the cells of the developing leaves. This disturbance of the water supply to the yet plastic cells acts to certain of them as a stimulus (merely, of course, an initial or proximate one), in response to which the cells assume an elongated form.⁴ But the actual stretching growth of the cells can only take place when they once more become turgid. This occurs when transpiration falls at night-time, &c.⁵

Boodle,⁶ in his suggestive paper on the Bracken Fern, has made a similar suggestion with regard to the factors determining leaf structure. He says 'it may possibly be some such factor as strong periodic fluctuations in the turgescence of the cells of the leaf (due to scarcity of water when transpiration is most active) which determines in the immature leaf of the Bracken whether the leaf shall be xerophytic or not; and the same may apply to other plastic species'.

The case seems clearly one of stimulus and response, and the somewhat mechanical theories referred to above appear to be inadequate.

¹ Cf. Pfeffer ('03), p. 120. Miss Delf ('11), p. 501, states that the upper internodes of *Salicornia* had not only more numerous stomata than the lower, but also much smaller epidermal cells. This she regards as indicating that neither they nor the guard cells had attained their full size; and this notwithstanding the fact that the stomata were fully formed and open. Whatever the case may have been in *Salicornia*, the upper leaves described for *Spiraea* were certainly mature, in spite of the small size of their cells.

² As Wortmann ('89), p. 293, &c., and others supposed it to be. Cf. the discussion of this question in Sokolowa ('98), p. 179 et seq.

³ Cf. Pfeffer ('03), p. 118 et seq.; also Sachs ('87), p. 565.

⁴ In this case the stimulus appears to induce the cells to assume a special *form*. In many of the cells of these upper leaves it is chiefly the *size* of the cell which is affected, owing to the stretching growth of the cell-walls being less.

⁵ It seems certain that such fluctuations in the moisture content of leaves do actually occur, at least in mature leaves. Cf. Thoday ('09), p. 19 et seq., also Livingston and Brown ('12).

⁶ Boodle ('03), pp. 665-7.

There yet remains, however, one factor to be briefly considered, i. e. *light*. We have seen that in *Spiraea* a humid atmosphere has relatively little effect in preventing hair formation unless coupled with light of low intensity. Many observers have regarded light as the determining factor, especially in the formation of palisade tissue. In practice it is extremely difficult to satisfactorily control habitats in such a way as to distinguish clearly between the effects of light and relative humidity: two factors very closely associated in nature. Critical researches in this direction are much needed. In the absence of these it is impossible to say anything definite as to the mode of action of light. Failing evidence to the contrary, the writer somewhat inclines to the view of Vesque and Viet:¹ i. e. that light acts by influencing transpiration. Even in a still, humid atmosphere, intense light would certainly tend to increase transpiration, by reason of its heating effect. This view makes it less difficult to understand why the combined effect of two such apparently different factors should be greater than when either acts alone. At present, however, the possibility cannot be excluded that light may act either as a direct, independent stimulus, or that we may be dealing with a case of 'associated stimuli'.²

So far the case has been made out most clearly for hair production in *Spiraea Ulmaria*. But in the light of our knowledge of the conditions which favour the formation of hairs (including root-hairs) and palisade cells in other plants (cf. §§ 6 and 9), it would seem not improbable that similar factors are at work in these also. In other words, that we are dealing with a more or less general phenomenon.³

An interesting apparent exception to what seems to be the general rule regarding the hairiness of successive leaves of a shoot is the case of certain South-west African plants recorded by Schinz.⁴ In a number of species of *Pseudobarleria*, &c., the first-formed leaves are markedly hairy; the later ones, however, are much less hairy. This is the converse of *Spiraea*. But the more hairy leaves are apparently unfolded towards the close of the hot, dry season; the less hairy ones during the cooler period of rains. So that here, too, hair production shows a dependence on external factors similar to the cases described in this paper.

4. Acting on the assumption that hair formation in *Spiraea* is affected by the amount of water supplied to the apical bud, some experiments were tried on growing shoots. When a number of leaves had been unfolded and were vigorously transpiring they were all cut off, subsequent leaves being also removed as soon as mature. It was thought that the removal of the transpiring surface, after a vigorous water current from the roots had been

¹ Vesque and Viet ('81), p. 175.

² Cf. Darwin ('06).

³ It is of course possible that in special cases the stimulus may be different, either in nature or degree: e. g. when palisade cells are formed in aquatic plants.

⁴ Schinz ('94), pp. 67-70.

established, might result in at least a temporary increase in the supply of water to the apical bud. This, by preventing the stimulus of decreased turgor, might perhaps bring about the formation of glabrous leaves. The results were not uniform, but this was to be expected, as we are dealing with a complex of variable factors. In each experiment, however, one or more glabrous leaves were sooner or later produced high up on an erect flowering shoot, where normally only hairy leaves are found.

One example may be given. A normal shoot was selected, which on May 21, 1907, possessed seven unfolded leaves. Of these, leaves 1-3 were glabrous, leaves 4 and 5 partly hairy, and leaves 6 and 7 completely hairy. These seven leaves were then removed from the plant. At this date leaf 8 (a hairy one) was unfolding. Subsequently, leaves 9 and 10 showed decreasing hairiness, while leaf 11 was quite glabrous. Leaf 12 had marginal hairs, leaves 13 and 14 exhibited increasing hairiness, while leaves 15-17 (the last produced on this shoot) were hairy, though not densely so.

It is difficult to say exactly what the reason is for this abnormal production of glabrous leaves. It may be that it is partly due to nutritive difficulties, for cutting off the leaves removes the assimilating as well as the transpiring surface. But if so, one would scarcely expect the return of hairiness described above. Taken in conjunction with the evidence previously given, the experiments, so far as they go, certainly suggest that the explanation may be, in part at least, the one already offered.¹ Some additional support of this view (i. e. that cutting off the transpiring surface may increase the supply of water to the apical bud) is furnished by an experiment of Balls's.² This author's observations on the cessation of growth of the cotton plant during sunshine have been already cited. He further found that removal of about one-third of the total leaf area in full sunshine caused the terminal shoot to resume growth at once, owing apparently to the decreased loss of water from the plant.

The causes which determine the presence or absence of hairs in *Spiraea Ulmaria* may now be summarized as a whole. Several distinct factors appear to be involved, i. e.:

(a) *Heredity*. It is difficult to assign exact limits to the part played by this. The inherent tendency to form hairs in the first instance is certainly hereditary. But how far the degree of hairiness in var. *denudata* and the

¹ Although the experiments were undertaken more or less with the expectation of arriving at the results actually obtained, there is reason for caution in interpreting these results. On several occasions I found plants in the field, the stems of which had been injured an inch or two above the ground, apparently at an early age. In each case two or three of the cauline leaves immediately above the injury were less hairy than the normal, and in some instances even glabrous. Thus it would seem possible that the abnormal production of glabrous leaves described in the text is in some way connected with the injury caused by the removal of the leaves, rather than with the water supply as suggested.

² Balls ('10), p. 9.

intermediate forms is determined by heredity, or how far it is attributable to individual variation, is at present problematical.

Goebel, in his interesting researches on the various forms of leaves in *Campanula rotundifolia*,¹ found that leaf form depended largely on illumination. In nature the seedling leaves, as well as the first leaves formed on the lateral runners, are always of a petiolate, rotund type. Linear leaves, on the other hand, are only formed on the erect flowering shoots. By lowering the light-intensity, rotund leaves could be induced to form on the flowering shoots in the place of linear ones. But the converse did not hold. Even the strongest illumination, whether continuous or intermittent, was powerless to hinder the formation of rotund leaves on either the seedlings or the runners. Goebel regarded the rotund form of the leaf in these cases as hereditarily fixed.²

Now the glabrous leaves of *Spiraea Ulmaria* are formed in nature under precisely the same conditions as the rotund leaves of *C. rotundifolia*, and the hairy ones correspond in position, &c., to the linear leaves of *Campanula*.³ Further, all attempts to induce the formation of hairs either on seedling *Spiraeas* or on the early spring leaves of mature plants have been unsuccessful. It is therefore probable that glabrousness is a character hereditarily fixed in these leaves, just as Goebel supposes roundness to be in the corresponding leaves of *Campanula*.

(b) *Individual variation.* One of the most obvious expressions of this is seen in the variable number of glabrous leaves formed on a shoot. Usually the number varies from three to five, though in exceptional cases as many as twelve glabrous radical leaves have been observed. Again, in most cases one or more hairy radical leaves are produced before the erect flowering shoot begins to elongate. But individuals are sometimes found (see p. 839) in which even the lowest one or two cauline leaves are glabrous or nearly so.⁴ As these plants occur side by side with normal ones, it seems probable that it is simply a case of individual variation.

(c) *Effect of external conditions.* This has already been discussed at length, and the conclusion arrived at that hair production is promoted by marked periodic fluctuations in the turgor of the hair-producing cells. It has also been shown that *Spiraea* is plastic only to a limited extent in regard to hairiness. Marked changes in the external conditions are required before any visible response can be obtained. This plasticity is less than that of *Campanula* in respect of leaf form, or than the plasticity with regard to hairiness in such plants as *Mentha aquatica*, &c. The stimulus, then, which

¹ Goebel ('96), ('08), and other papers.

² Goebel ('96), pp. 8-9.

³ There is frequently a slight approach even in the matter of form; see Text-fig. 5 and Pl. LXXXI, which show the tendency in *Spiraea* to form rounder leaflets below and narrower ones above. This is a common phenomenon in plants.

⁴ And this in localities in which var. *denudata* does not occur, so that it can scarcely be a case of hybridization.

decreased turgor appears to afford to the hair-producing cells is probably more of the nature of an accelerating stimulus than an actually determining one.

Further, different parts of the plant vary in plasticity. As mentioned above, the lowest leaves are not plastic, but are persistently glabrous. The upper leaves on the erect flowering shoots, on the other hand, are fairly persistently hairy. The most plastic leaves of all appear to be those occupying an intermediate position, i. e. the lower hairy ones. Many plants are more plastic than *Spiraea* in regard to hairiness; but in all cases hairiness appears to be associated with relatively dry, and glabrousness with relatively humid conditions. Taking these facts into account, it would seem that *Spiraea Ulmaria* is retaining a certain degree of plasticity in regard to hairiness. But at the same time it is tending to become fixed in the direction of response to the average conditions, to which the upper and lower leaves of the species, respectively, have been exposed in nature for many generations.

§ 12. THE PHYSIOLOGICAL EFFECT OF THE HAIRS, ETC.

Most authors agree that a dense covering of dead, cutinized hairs depresses transpiration. This is said to be due to the retarding of gaseous interchange on the transpiring surface, and also, in some cases, to the hairs acting as a screen against intense insolation. According to the distribution of the hairs on the respective surfaces of the leaf, one or other effect will be more marked. But, as Haberlandt¹ has pointed out, there is an absence of critical researches on the subject. At first sight, *Spiraea Ulmaria*, with its glabrous and hairy leaves, would seem to be admirably adapted for such critical researches. But, as we have seen, the progress towards hairiness in the leaves of this species is accompanied by other structural changes. These also cannot but exert an influence on transpiration. The whole question of the relation between leaf structure and transpiration is in a somewhat chaotic condition, different experimenters having obtained diametrically opposed results. Thus, von Hoenel² found that under similar conditions 'shade leaves' transpired more strongly than 'sun leaves'. Gêneau de Lamarlière,³ on the other hand, obtained exactly opposite results. The question is a complicated one, and the author hopes to deal with it more fully and critically in a future paper. For this reason no attempt will be made at the present time to do more than put forward certain *a priori* considerations, and to refer briefly to the work of other botanists.

¹ Haberlandt ('09), p. 116. This author himself performed some experiments on the effect of hairs on transpiration (l. c., p. 138).

² Von Hoenel ('79), quoted by Burgerstein ('04).

³ Gêneau de Lamarlière ('92), p. 542. Cf. also the literature cited in Burgerstein ('04), p. 55 et seq. Also Hesselman ('04), p. 402 et seq.

Wiegand¹ has recently experimented with various materials, so arranged as to simulate the hairy and cutinized coverings of plants, and determined the extent to which they hindered evaporation. From his experiments he concluded that hairy coverings (even when of a thin, strigose nature) markedly retard transpiration in wind, but have comparatively little effect in still air. They also have a marked retarding effect in sunshine. Further, that a waxy (i. e. cutinized) covering is more efficient in reducing transpiration than a hairy one.²

Wiegand's results confirm the previously expressed opinions of Goebel³ and Haberlandt,⁴ that a dense covering of hairs may be especially effective in reducing transpiration when the plant is exposed to strong winds. Haberlandt also refers to their similar action under strong insolation. On theoretical grounds it is to be expected that the hairs would have this effect. Thus, when the leaf is exposed to wind, the effect of the hairs would be to diminish the gradient of density of water vapour outside the leaf, by hindering the removal of the humid air from its surface. The distance between the absorbing surface (the free air outside) and the supply is thus increased, and the rate of flow of water vapour outwards correspondingly diminished.⁵ On the other hand, if the air outside the leaf be perfectly still, the gradient of density would be much the same whether the hairs were present or not. Further, wind passing rapidly over the unprotected surface of a leaf would reduce the pressure just at the entrances of the stomatal apertures, and so tend to suck air (and consequently water vapour) out of them.⁶ This effect also would be prevented by the hairs. Again, when exposed to direct insolation, white, air-containing hairs, such as those of *Spiraea*, must reflect an appreciable amount of light. In consequence, less heat is absorbed, and the transpiration again diminished.

In the case of *Spiraea Ulmaria*, it has been shown that its characteristic pubescence is localized precisely in those parts of the plant which in nature are most exposed to the drying effects of wind, sun, &c. Conversely, the glabrous leaves are those found under conditions where transpiration and the effect of wind are at a minimum. The same is also true of the majority of plants mentioned in § 6. Perhaps the most striking instance of all is

¹ Wiegand ('10), p. 430 et seq. He used blotting-paper as the evaporating surface, laying over this various cotton materials to represent hairy coverings, and bees-wax for cutin.

² Probably Wiegand has exaggerated the differences between the two kinds of covering, as in his experiments the layer of wax would have nothing to represent stomata, while all the cotton fabrics would be abundantly furnished with small apertures.

³ Goebel ('91), p. 18.

⁴ Haberlandt ('09), p. 116.

⁵ Brown and Escombe ('00), footnote to p. 276, suggest that epidermal hairs may lessen the amount of CO₂ absorbed by the leaf when the air is in motion, by preventing air currents from sweeping away the external density 'shells'. The same must apply equally to the transpiration of water vapour.

⁶ This action is similar, as Dr. Schott suggests, to that of a hair-dresser's sprayer, or of a Gifford injector in sucking water into a boiler.

afforded by the intermediate, partially hairy leaves of *Spiraea*. In these the leaflets, and even the portions of leaflets, which are most exposed to the danger of excessive loss of water, are provided with a dense covering of hairs (see Pl. LXXXII and LXXXIII).

Bearing in mind all the facts adduced in this paper, it is difficult to avoid the conclusion that the production of hairs in *Spiraea* and certain other plants, under the stimulus of drought, is of the nature of an advantageous adaptive response. The most important physiological effect, then, of this response would seem to be to prevent undue acceleration of transpiration by air movements and, though to a less extent, insolation.

Turning once again to the question of root-hairs and palisade cells, the chief rôle of the former (i. e. to increase the absorbing surface of the root) seems clear. The functions of palisade cells, on the other hand, have been much disputed. Probably they perform several important physiological functions. The only view which need be mentioned here is that of Areschoug,¹ who regards a well-developed palisade tissue as of importance in reducing transpiration. Areschoug's view has been accepted by many authors, though so far direct experimental evidence is lacking.²

Granted the foregoing, it appears that the stimulus of a decreased supply of water promotes the formation of three different kinds of elongated cells, each of which is physiologically important (at least in certain cases) in connexion with the plant's water supply. At one end of the plant the root-hairs increase the intake of water: at the other the hairs and palisade cells assist in reducing the output of water from the leaves. There would thus seem to be in these cases, as in many others, a more or less definite connexion between the nature of the stimulus and the physiological advantage of the response.

§ 13. THE XEROMORPHY OF *SPIRAEA ULMARIA*.

Spiraea Ulmaria is far from being a pronounced xerophyte. Its leaves are thin and frequently of considerable size. They have a fairly thin cuticle, and generally wilt readily when gathered. Nevertheless the plant exhibits certain xerophytic characters which are practically confined to the upper, more exposed parts of the shoots. These characters are as follows:

1. The lower stomatal surface is covered by a dense pubescence.
2. The upper epidermal cells have a better developed cuticle than those of the lower leaves.
3. The mesophyll is much more compact; the internal transpiring surface being thereby considerably lessened.

¹ Areschoug ('82), p. 520, and ('06), p. 329 et seq.

² Hesselman ('04), p. 428, however, as a result of certain field experiments, is of opinion that palisade tissue does not markedly depress transpiration. Some of his experiments were actually carried out on *Spiraea Ulmaria*. Areschoug has discussed Hesselman's objections in his 1906 paper,

4. The leaf surface is much reduced. It is of course a very common thing to find the upper leaves of the shoots of herbaceous plants considerably smaller than those lower on the stem. But undoubtedly the effect of this diminution in size of the upper, more exposed leaves will be to reduce considerably the output of water from the terminal portions of the shoot. It has indeed been suggested above that this reduction in size of the leaf (or at least of its component cells) is in part due to development under conditions which strictly limit the available supply of water. In *Spiraea*, the leaves which present the greatest transpiring surface are placed in relatively sheltered, humid strata of the vegetation.¹ Though all shoots exhibit periodicity in the size of leaves, the actual sizes of the latter vary greatly according to the conditions under which they are grown (see Text-fig. 5).

5. When *Spiraea* leaves are exposed to strong insolation, they tend to assume the profile position. This is taken up, not by the leaf or leaflet as a whole, but by the two halves of a leaflet separately. A marked ventral curvature of the leaflet is thus produced. This will probably tend to a further reduction of transpiration. The phenomenon is a frequent one in marsh plants as well as others, but need not be fully discussed here, as it will form the subject of a forthcoming paper.

At first sight the more numerous stomata of the upper leaves suggest that they may counterbalance the characters which would otherwise reduce transpiration. But it has been shown (p. 828) that in all probability the possible transpiration per unit area of leaf surface, if the stomata alone are considered, would be little if any more from the upper than from the lower leaves. The balance of characters, then, shows that the upper parts of the shoots of *S. Ulmaria* are distinctly more xerophytic than the lower. But in any case the degree of xeromorphy is slight. The question now arises, is this degree of xeromorphy necessary or even advantageous to the plant?²

It may be regarded as an axiom that where functions such as transpiration are concerned, the need for special regulatory devices in a given species will be determined, not by the average conditions, but by what may be termed the normal extremes which the species is called upon to face in nature. In other words, to be successful, a plant must always be prepared for such emergencies as it may occasionally have to meet during the vegetative season.³

¹ Yapp ('09), p. 281.

² And if a dense pubescence is necessary to the type-form, why is it not equally so to the less hairy variety *denudata*? On this point all that can be said (though it is not advanced as being a complete answer) is that var. *denudata* appears to be a less successful form. It is rare in nature, while the type is common. So far as my experience goes, it usually occurs only in sheltered spots. Culture experiments on the roof of the College at Aberystwyth show that, especially if the soil is wet, it is much less able to endure the effect of wind than the hairy form. Moreover, after all, the hairiness of the two forms is merely a matter of degree.

³ A. R. Wallace ('10), p. 258, goes even further than this. He says: 'A dominant species has

Considering hairiness alone, we have seen that its distribution on the plant is correlated in the most minute way with differences of external conditions; that those parts of the plant which would, if the conditions were severe, tend to lose water most readily, are those which are furnished with this hairy covering; and further, that the hairy type is more successful than the less hairy var. *denudata*. It may therefore be concluded that hairiness in this species is a positive advantage to the plant, and in all probability actually necessary whenever transpiration conditions are unusually severe, e. g. in the event of strong drying winds or prolonged insolation. The same may be said of the other xerophytic devices enumerated above. In other words, *Spiraea Ulmaria* is structurally in complete harmony with its environment.

But so far only the aerial organs have been considered, and it may well be asked, why does a plant rooted in damp soil require these regulatory devices at all? And further, even if the necessity be proved for *Spiraea*, how far does this particular instance afford a clue to the problem of xeromorphy in marsh and bog plants in general? An attempt will be made in the next section to give a provisional answer to these questions.

§ 14. THE PRESENT POSITION OF OUR KNOWLEDGE OF 'SWAMP XEROPHYTES', AND A TENTATIVE HYPOTHESIS.

Xeromorphy in plants growing on wet, peaty soils occurs all the world over.¹ A full historical account of the various theories put forward to account for the existence of these 'swamp xerophytes' need not be given here; but the positions taken up by certain authors will be briefly discussed.

Some writers maintain that the xeromorphic structures in question are, and others that they are not, present-day necessities to the plants which possess them.

The latter point of view may be dealt with first. Schwendener,² Clements,³ and others believe that these structures are primitive characters which have persisted in certain stable species (especially Monocotyledones), in spite of a fundamental change of habitat conditions. Perhaps the most important evidence for this view is the fact that hydrophytic species frequently grow side by side in nature with those possessing xerophytic characters. Even Warming, who believes that the xeromorphy is adap-

become so because it is sufficiently adapted to its *whole* environment, not only at any one time or to any average of conditions, but to the most extreme adverse conditions which have occurred during the thousands or millions of years of its existence as a species.'

¹ Warming ('09), p. 194.

² Schwendener ('89), p. 73.

³ Clements ('05), p. 126.

tive, says in this connexion: 'Finally, it may be noted that there are not only moors inclining to xerophily, but also others leaning rather to hydrophily, and that, in addition to the structural types and forms of leaves mentioned, there are others which apparently show no signs of xerophily, *and cannot be shown to be in harmony with this habitat.*'¹

Several *a priori* arguments may be urged against the view advocated by Schwendener and Clements. The widespread occurrence of the phenomenon; the existence of varying degrees of xeromorphy in different types of marsh and bog vegetation, these being correlated with marked differences of soil, &c.; the fact that many of these species 'can grow both on extremely dry, warm soil, and on extremely cold, wet soil';² and finally, the probability that xeromorphy, unless advantageous, would actually handicap marsh plants in their competition with other species—all suggest that such xerophytic devices are in some way related to a need imposed on the plant by the nature of the habitat. Further, the argument from proximity of position, which has been so frequently employed, depends on the tacit assumption that plants growing together are necessarily under the same conditions. This is most certainly not the case. Indeed, the present author believes himself to have shown that, so far as the water supply of marsh plants is concerned, few of the species have to face precisely the same set of physiological problems.³

Various authors have discussed the question of whether a bog is to be regarded as a hygrophytic or xerophytic habitat. In this connexion it may be pointed out that only in the more extreme cases, and particularly (so far as xerophytes are concerned) those in which the plant associations are open, can habitats⁴ as such be said to be markedly hygrophytic or xerophytic. In the great majority of closed, mixed associations, the mutual relations of the various species are such as to profoundly modify the general character of the habitat for each other; some plants being exposed, others sheltered, and so on.⁵ In this way, according to the growth forms of the species, and in varying degrees according to the general characters of the habitat and of the vegetation, the same habitat may be xerophytic to one species and hygrophytic to another. This is probably to some extent what Warming had in mind when he wrote the passage quoted in the introduction to this paper. The emphasis here laid upon this point of view is not out of place, for there is some danger that it may occasionally be lost sight of in the comparative study of vegetation in its broader aspects. This is especially so in view of the stress laid on the generally accepted ecological classification of plants into xerophytes, mesophytes, hydrophytes,

¹ Warming, l. c., p. 196. The italics are mine.

² Warming, l. c., p. 194.

³ Yapp ('09), pp. 306-8.

⁴ Using the term in its broad sense, i. e. to indicate the general physical environment of plant associations, rather than merely of individual plants.

⁵ Cf. Yapp, l. c., p. 279.

&c. Such a classification is admittedly useful, but it should not be forgotten that it is all a matter of degree, and that communities composed entirely of marked xerophytes, &c., are probably comparatively rare. Thus, though climatic and edaphic factors are the most important, in that they determine the general character of the vegetation, the inter-relationships of the various species also play a definite, if less conspicuous part, even in the case of relatively dwarf vegetation. But all this does not explain the paradox that certain of the plants rooted in the wet soil of marshes and bogs apparently need to exercise economy in respect to their water supply. We must therefore consider the theories put forward by authors who regard the xeromorphy of these plants as induced by the nature of the habitat.

It is at once obvious that either atmospheric or edaphic factors, or both, may be concerned. The present writer's researches have dealt mainly with the former, while most other observers have confined their attention to the latter.

i. *Edaphic factors* may be taken first, the following comprising the more important suggestions put forward:

1. *Actual physical drought.* Volkens¹ thought the important factor was the drying of the superficial layers of peat during summer. He pointed out that in some moorland and marsh habitats the soil is wet all the year round, while in others the upper layers become dry in summer. Studying the Carices in particular, he concluded that the more xerophytic species are largely confined to the second class of habitats. Davis² and Burns³ have come to a similar conclusion from their observations on the lowering of the water table during droughts in North American peat-bogs.

2. *The low temperature of wet soils* may, it is suggested, check root activity, and so reduce the absorption of water. Kihlman⁴ regarded this factor as of great importance in northern regions, especially when coupled with drying winds. Goebel⁵ came to the same conclusion with regard to the mountainous parts of Venezuela. Transeau⁶ found, as the result of laboratory experiments, that a cold substratum caused a reduction in size of both roots and leaves, and induced the formation of xerophytic characters in the latter. The effect was more marked when, in addition, the soil was badly aerated. He is of opinion that substratum temperatures are of prime importance in northern latitudes, but that they are inadequate to account for xerophytic structures in bog plants in Southern Michigan.⁷

3. *Paucity of oxygen in the soil.* Transeau's experiments showing the effect of a deficiency of oxygen have already been quoted. Again,

¹ Volkens ('84), p. 24.

³ Burns ('11), p. 119.

⁵ Goebel ('91), Teil ii, p. 11.

⁷ Transeau, l. c., p. 36.

² Davis ('06), p. 160.

⁴ Kihlman ('90), p. 107 et seq.

⁶ Transeau ('06), p. 22 et seq.

Warming¹ remarks that an insufficient supply of oxygen may obstruct respiration, and so depress the functional activity of the roots. The researches of Kosaroff,² too, show that the absorption of water is retarded by suppressing the supply of oxygen to the roots. In this connexion it may be noted that the roots of many 'dry-marsh plants' tend to assume a markedly horizontal position, especially when growing in wet peat. This is very striking in the case of the tap-roots of certain Umbelliferae. The phenomenon may well be correlated with the paucity in oxygen of the water-logged soil.³

4. *The presence of free humus acids.* Schimper⁴ attributed the need for xeromorphy in the plants of peat-moors to the action of humus acids in impeding the absorption of water by the roots. This was accepted by Warming and others as 'the weightiest cause of the physiological dryness of the soil'.⁵ But the importance of free humus acids has been disputed by Livingston,⁶ Transeau,⁷ and Dachnowski.⁸ Indeed, according to the recent important researches of Baumann and Gully,⁹ it is extremely doubtful whether, in the so-called free humus acids of sour peat soils, we are dealing with organic acids at all. These authors attribute the acid character of such soils to adsorption by the colloidal cell-walls of plants, especially *Sphagnum*. They produce evidence to show that the cell-walls bring about decomposition of salts in solution, a greater proportion of the base than of the acid being adsorbed. The acid reaction, then, is due to the presence of free hydrogen ions yielded by the acid after the removal of the base.

5. *The presence of bog toxins*, which act on the roots of plants much as do drying media. The existence of such substances in bog water and bog soils has been rendered probable by the work of Livingston,¹⁰ and later of Dachnowski.¹¹ These authors published a series of suggestive papers from 1904 onwards. They conducted many careful culture experiments, using polymorphic lower plants as indicators. They both conclude that inhibition from bogs of plants other than those possessing xerophytic characters is largely due to the presence of these injurious substances, which are soluble in water. Dachnowski¹² states that the toxicity of bog water can be corrected by various means: e. g. by the addition of certain adsorbing agents, and also by aeration. The latter acts, according to him, by slowly oxidizing the toxic substances, and not directly on the living roots, as supposed by other authors.

6. *The great water-retaining power of peat.* Of all soils peat has

¹ Warming ('09), p. 195.

³ Yapp ('08), pp. 74-5.

⁵ Warming, l. c.

⁷ Transeau ('06), p. 25.

⁹ Baumann ('09), and Baumann and Gully ('10).

¹¹ Dachnowski ('08, '09, and '10).

² Kosaroff ('97), quoted by Jost ('07), p. 32.

⁴ Schimper ('03), pp. 15 and 111.

⁶ Livingston ('05), p. 351.

⁸ Dachnowski ('10), p. 327.

¹⁰ Livingston, l. c.

¹² Dachnowski ('08), p. 134, &c.

the greatest water capacity. It would therefore seem probable that an appreciable amount of the water actually present will not be available for absorption by the plant. With a view of determining what the actual percentage of non-available water may be in moorland soils, Crump¹ has conducted a number of interesting wilting experiments. He calculates that certain plants (e. g. *Eriophorum angustifolium*) are unable to absorb more than about 48 per cent. of the total water present.

The above are some of the more important suggestions that have been made with respect to edaphic factors. But, as both Livingston and Dachnowski point out, our knowledge of the chemistry of bog water and bog soils is still very incomplete.

ii. *Atmospheric factors.* Certain authors deny the importance of these. E. g. Dachnowski,² referring to the xerophytic characters of bog plants, says, 'None of these features are correlated with atmospheric influences.' Elsewhere, however, he seems to admit that they may play a part.

On the other hand, both Kihlman and Goebel (see 2 above) emphasize the importance of drying winds, especially when accompanied by coldness of soil.

The present author³ has shown that even in the comparatively dwarf vegetation of a marsh, great and constant differences of relative humidity exist in the different aerial strata. Thus the leaves of plants which occupy the lower strata are, on e. g. dry and windy days, exposed to transpiration conditions far less severe than leaves growing in the upper strata of the vegetation. More recently Dachnowski⁴ has obtained similar results in the bog vegetation of Cranberry Island. The position, then, of the transpiring organs of the various plants must be of considerable importance.⁵ Indeed, a slow absorption of water can only be prejudicial in so far as it is liable to be accompanied by excessive transpiration from the aerial parts.

Another factor that has to be taken into account in this connexion is the length of the vegetative period of the different species. So far, for instance, as the danger arising from limitation of absorption by reason of low soil temperatures is concerned, it is obvious that, in temperate latitudes, this will be experienced to the greatest extent by evergreen plants during the winter or spring time. Schimper⁶ was the first to emphasize the connexion between the coldness of the soil and the xerophytic structure of the leaves of evergreen trees and shrubs in temperate regions. Früh and Schröter⁷ similarly attribute the need for such structure in the plants

¹ Crump ('12).

² Dachnowski ('11, second paper), p. 34. Cf. also ('10), p. 338.

³ Yapp ('09).

⁴ Dachnowski ('11), p. 146.

⁵ Kearney ('01), p. 442, in his survey of the Dismal Swamp Region, points out that the tall, reed-like plants of freshwater marshes protect the smaller, more hygrophytic forms against excessive transpiration.

⁶ Schimper ('90), pp. 15-17.

⁷ Früh and Schröter ('04), p. 15.

of a *Hochmoor* partly to difficulties of absorption, and partly to the prevalence of the evergreen habit.

A TENTATIVE HYPOTHESIS.

Much remains to be done before the causes which have contributed to the production of xeromorphy in bog and marsh plants can be stated with exactitude. In particular, our knowledge of the physical chemistry of peat soils is still very incomplete. It is also uncertain as yet to what extent the stomata of marsh plants are capable of normal movement.¹ Again, the osmotic properties of the cell-sap of marsh and bog plants would be worth investigating. But the problem is gradually becoming less obscure. As seen above, many possible factors have been suggested by different authors, each factor in turn being assigned a position of paramount importance.

Probably the truth is that a number of factors, both edaphic and atmospheric, are operative. Further, it is probable that while some factors are of greater importance than others, the importance of any given factor will vary according to circumstances. As regards edaphic factors, the general trend of evidence, a good deal of it experimental, renders it increasingly probable that the soils of peat-marshes and bogs are to a certain extent, if not physically, at least physiologically dry to plants. But the factor, or combination of factors, which renders absorption difficult is not the same in all cases. For example, low soil-temperatures probably play a part in far northern latitudes, at high altitudes, and in the case of evergreen plants during the winter-time. But the same factor may be entirely inoperative in the case of plants which only produce leaves during the summer-time; and especially in the bogs and marshes of warmer latitudes. Again, the presence of toxic substances or the lack of oxygen (whether this acts directly, or merely by oxidizing injurious compounds) may possibly affect chiefly the more deeply rooted plants.² On the other hand, plants rooted on or near the surface may secure abundant oxygen, but are exposed to the danger of physical drought if the water table is lowered to any considerable extent. Further, it is probable that chemical, and perhaps also physical, differences between the soils of bogs and marshes (i. e. *Hochmoore* und *Flachmoore*) respectively, are largely responsible for the fact that xeromorphy is more prevalent in the plants of the former than in those of the latter (but see below). Doubtless in many cases two or more soil factors, often in different combinations, co-operate.³ At the same time, we know little of the ultimate causes which limit the absorption of water by the roots.

But edaphic factors alone cannot suffice to account for the fact that xerophytic and hygrophytic species so frequently occur side by side in

¹ Cf. Darwin ('98), p. 552, and the literature there cited. Also Früh and Schröter ('04), p. 14.

² Cf. Yapp ('08), pp. 74-5.

³ Cf. Warming ('09), p. 195.

nature. It is here that atmospheric factors become important. Granted that the characters of the substratum are such that the rate of absorption of water is slow, then the atmosphere will play a differentiating rôle. A reduction in the amount of water absorbed does not injuriously affect the plant, provided that transpiration is reduced in the same ratio. The latter is effected in one of two ways, according to the position of the aerial parts of the plants. (1) For the taller plants, the shoots of which occupy the upper strata of the vegetation, and are therefore liable to exposure to strong winds, insolation, &c., xeromorphy may well be a necessity; and even more so if the plants are evergreen. (2) On the other hand, the leaves of the smaller plants occupy the lower strata, where they are protected from wind, and transpire into a constantly humid atmosphere. As is to be expected, these lower strata do actually contain the more hygrophytic species, e. g. *Hydrocotyle vulgaris*, &c., and also the hygrophytic seedlings and lower leaves of other species. Conversely, the more xerophytic species, e. g. *Cladium Mariscus*, or parts of shoots (cf. *Spiraea Ulmaria*), are those occupying the most exposed positions.

So far as atmospheric factors are concerned, the less dense the vegetation, and the larger the proportion of plants of an evergreen habit, the more xerophytic may the vegetation be expected to be. In this country these two conditions obtain to a greater extent in bog than in marsh vegetation. It is therefore not surprising, seeing that atmospheric and (probably) also edaphic factors are in general more favourable, that the vegetation of peat-marshes should contain a larger proportion of hygrophytic species than that of bogs; and, conversely, that the latter should support a greater number of xerophytic types.

The general nature of the habitat is of course important, but having made due allowance for that, the whole matter really resolves itself into a consideration of the different problems of individual species.¹ And if this be so in any given marsh or bog, much more is it true when we come to compare different types of swamp vegetation and different latitudes and climates.

As an example, two species of marsh plants may be briefly compared: *Spiraea Ulmaria* is a plant of the drier parts of marshes. Its roots grow in moist but not water-logged soil. Probably they rarely experience lack of oxygen, and absorption in the well-aerated soil is unlikely to be much impeded by toxic substances. The vegetative period is comparatively short (about March to October), so that coldness of soil will scarcely play a very important part in these latitudes. On the other hand, it is liable to suffer from actual drought through lowering of the water table. The aerial parts have been discussed at length in this paper, and it has been shown that the exposed leaves exhibit a definite if slight degree of xeromorphy,

¹ Cf. Yapp ('09), pp. 306-8.

while the sheltered leaves are more hygrophytic in character. Probably the chief danger to this species is the drying effect of wind, especially when coupled with a temporary desiccation of the surface layers of soil.

Cladium Mariscus presents somewhat of a contrast. It is a wet-marsh plant, which is more pronouncedly xerophytic than *Spiraea*. Its roots grow in water-logged soil, and are indeed frequently entirely submerged. It is a relatively tall plant, and not only are the upper parts of its leaves exposed to wind and sun, but they are evergreen. Absorption, then, may possibly be impeded by such factors as lack of oxygen, toxic substances, &c., in the summer time, and by low soil temperatures in winter and spring. At the same time the leaves may be exposed to unduly severe transpiration conditions at any time of the year. Hence it is not surprising that, as is actually the case, *Cladium* should be more decidedly xerophytic than *Spiraea*. The comparison could readily be extended to include such diverse types as *Hydrocotyle vulgaris*, *Andromeda polifolia*, &c., &c.

To sum up, there is every reason to suppose that associations of bog and marsh plants are as much in harmony with their environment as are those occupying other distinctive habitats, such as the various woodland, desert, and other plant associations. But to arrive at this conclusion, it is necessary to take many factors into consideration. In all probability edaphic factors, climatic factors, the growth forms of the plants, with the resulting differences of exposure and shelter, the duration of the vegetative period, and possibly other factors as well, have all contributed to the production of a series of physiologically intricate, and at first sight paradoxical types of vegetation.

Finally, it may be once more emphasized that the xeromorphic structures in question are required to meet, not so much the everyday needs, as the extremes, possibly even only the occasional extremes, which the plants possessing them are called upon to face.

SUMMARY OF RESULTS.

1. The present paper is an experiment in what may be called species-ecology. It is an attempt to see how far the intensive study of a single species, supplemented by observations on others, may help towards an explanation of the problem of xeromorphy in marsh plants.

2. The species selected (*Spiraea Ulmaria*) is a 'dry-marsh' plant, the leaves of which are densely pubescent on the lower surface. This pubescence is subject to a kind of periodicity, and appears only under certain definite conditions. The chief rules governing the appearance of the hairs are as follows: (a) The seedlings, also all leaves formed during the first year, are glabrous. (b) On the erect flowering shoots of adult plants, there is a regular succession of glabrous, partially hairy, and completely hairy

leaves. The earliest radical spring leaves are glabrous, the cauline leaves hairy (see Pl. LXXXI). (c) The non-flowering shoots of adult plants produce only radical leaves. The earliest of these are glabrous as in (b). Subsequently, the successive leaves exhibit increasing hairiness up to June or July, after which they are decreasingly hairy, till finally glabrous leaves are once again produced in autumn. (d) The distribution of pubescence on the partially hairy leaves is interesting. The terminal leaflet is invariably the most hairy, and there is a regular decrease in hairiness from above downwards. Individual partly hairy leaflets generally possess a marginal band of hairs, with sometimes additional bands running inwards between the main veins (see Pl. LXXXII and LXXXIII).

3. In reality this seasonal periodicity in the production of hairs is a widespread phenomenon. *Spiraea Ulmaria* was the most striking case observed, but many other marsh, and also certain land, plants exhibit the same general succession of glabrous, partly hairy, and more or less completely hairy leaves.

4. Similarly, there are marked seasonal differences in leaf structure. The lower glabrous leaves have on the whole a more or less definite 'shade' structure, while the upper, more exposed, hairy leaves approximate to the 'sun' type. The former have large epidermal cells, with sinuous lateral walls, and few but relatively large stomata. The mesophyll is loose, with large intercellular spaces. On passing up the erect stem, the following progressive changes in leaf structure may be observed: the leaf becomes thinner, but the cuticle thicker; the epidermal cells smaller, and their walls less sinuous. The stomata are more numerous but smaller, and the hairs much more abundant. The mesophyll is more compact, and the intercellular spaces are gradually reduced to a minimum (see Text-fig. 4). Speaking generally, the upper leaves show a distinctly greater degree of xeromorphy than the lower. These changes are independent of the actual size of the respective leaves.

5. The variations in the number of stomata are remarkable. There is a gradual though fluctuating rise in the number of stomata through the successive leaves of the entire shoot. In one shoot, for instance, the numbers varied from about 300 to nearly 1,300 per sq. mm. of lower leaf surface. The latter number is the highest yet recorded for any species. At first sight it might appear that these numerous stomata of the upper leaves would neutralize the effect of the xeromorphy referred to above (4). But the stomata of the lower leaves have larger pores, and it is calculated that under similar conditions, and *considering stomata alone*, the possible transpiration from the upper leaves could be but little, if any more, per unit area of leaf surface, than that from the lower.

6. The effect of environment on the development of certain leaf tissues, especially hairs and palisade cells, is considered. The results of many

investigators show that in general these are most fully developed under conditions which impose on the plant some necessity for increased economy of water, i. e. under conditions which either promote transpiration or hinder absorption. *Spiraea Ulmaria* is found to be less plastic than many other species in respect to hairiness. Many experiments show that it is difficult to inhibit the formation of hairs on leaves which are normally hairy, though their number and length can be readily influenced. At the same time, the distribution of pubescence on the plant (described in 2 above) corresponds in the most striking manner with the average physical conditions of the natural environment. Thus the curves of hairiness in *Spiraea* follow very closely the mean curves of evaporation and light-intensity. This is true whether the vertical changes in these factors (due to the density of the vegetation) or the annual march of evaporation and light-intensity are considered (cf. Pl. LXXXI and Text-figs. 9 and 10).

7. The localization of hairs on the partially hairy leaves of *Spiraea* (in particular the marginal and interveinal bands of hairs) shows a marked correspondence with the localization of withering in leaves in general, when such withering is due to the effect of wind, &c. (cf. Pl. LXXXII and LXXXIII, and Text-fig. 11). Anthocyan in young leaves in spring-time, the local effect of freezing, &c., often show a similar distribution. As regards their water supply, these regions of the leaf-lamina (i. e. the margins and interveinal parts) are physiologically different to the remaining parts. They are more liable to lose water, and are also the most remote from the water supply coming up from below.

8. The development of the leaves is described, and it is shown that no hairs are developed in the bud until the first foliage leaves have expanded and become functional. Hairs then appear on the main veins of the developing leaves, and the hairiness of these veins (while still in the bud) increases *pari passu* with the general increase of transpiration from the shoot. But the hairs on the finer veins, and those which occur over the parenchyma 'islands', only appear when the leaf has emerged from the bud; i. e. when some parts of it are already in contact with the outer air (Text-figs. 7 and 8). It is these later formed hairs which are most conspicuous in the mature leaves (see 2 above).

9. The causes of the formation of the hairs, &c., are discussed, and it is shown that a parallel may be drawn between the epidermal hairs of leaves and stems, the palisade cells of leaves, and to some extent root-hairs as well. In so far as the development of these special elongated elements is determined or accelerated by external conditions, it would appear that similar factors are usually operative in all three cases.

Hair formation in *Spiraea Ulmaria* is considered in detail. In this case the factors which determine the presence or absence of hairs on the leaves are probably the following: (a) heredity, (b) individual variation,

and (c) external conditions. It is shown that evidence of many kinds points to hairiness being associated with a diminished, and glabrousness with an abundant supply of water (see 6 and 7 above). In so far then as *Spiraea* is plastic in respect to hairiness, the course of events would seem to be somewhat as follows. As transpiration increases with the unfolding of the leaves in spring-time, the amount of water available for the apical bud becomes diminished. Certain cells of the developing leaves are thereupon stimulated to form hairs. This is a case of what Wiesner has called 'correlative transpiration'. When the partially developed leaf emerges from the bud, its supply of water is still further lessened by cuticular transpiration from its surface (cf. 8 above). The initial stimulus which leads to hair formation is thus afforded by diminished turgor; the actual growth in length of the hair cells, however, cannot take place till turgor is once more restored. This takes place at more or less regularly recurring intervals, especially at night-time. Thus hair production is promoted by marked periodic fluctuations in the turgor of the hair-producing cells. *Spiraea Ulmaria* possesses only a limited degree of plasticity in regard to hairiness. It is suggested that the species is tending to become fixed, in the direction of response to the different conditions to which the upper and lower leaves respectively have been exposed in nature for many generations.

10. With regard to the physiological effect of the hairs, &c., it is concluded that the pubescence prevents undue acceleration of transpiration, and especially that due to air movements and, to a less extent, insolation. It is probable that the stimulus of a decreased supply of water during development promotes the formation of three special kinds of elongated cells, each of which is physiologically important in connexion with the problems of water supply. At one end of the plant the root-hairs increase the intake of water, and at the other the hairs and (probably) the palisade cells assist in reducing the output of water from the leaves.

But the experimental treatment of the subject of the effect of leaf structure on transpiration is reserved for a future paper.

11. Structurally, the leaves of *Spiraea Ulmaria* show considerable differences according to position and time of development. The lower sheltered leaves are hygrophytic, while those which are exposed to wind, strong insolation, &c., are distinctly more xerophytic in character. It is concluded that this degree of xeromorphy of the upper leaves (hairiness, &c.) is a positive advantage to the plant, and probably actually necessary, at least under unusually severe transpiration conditions.

12. The whole position of our knowledge of 'swamp xerophytes' is reviewed, and the conclusion arrived at that all the evidence points to the various bog and marsh associations being as much in harmony with their environment as are those (e.g. woodland, desert associations, &c.)

occupying other distinctive habitats. In other words, xeromorphy is of physiological utility to those bog and marsh plants which exhibit it. It may be regarded as directly related to the needs imposed on the plant by the special nature of the habitat. But in each case the special regulatory devices are required to meet, not so much the everyday needs, as the extremes, possibly even only the occasional extremes which the species has to face in nature.

The environmental factors of a bog or marsh habitat are complicated. No single factor can be regarded as of sole importance in determining the need for xeromorphy. The hypothesis is put forward that, as suggested by so many authors, the soil is to some extent physiologically dry. The degree of physiological drought varies in different cases (e.g. bog soil is doubtless drier to plants than marsh soil), as do the factors or combination of factors which occasion it. But edaphic factors alone cannot account for the fact that hygrophytic and xerophytic species often live side by side in nature. Here atmospheric factors become important. Granted that the characters of the substratum are such that absorption of water is slow, then the atmosphere will play a differentiating rôle. A retardation of absorption is only prejudicial when accompanied by an excess of transpiration. On the whole the more hygrophytic species, or the more hygrophytic stages or portions of other species (e.g. seedlings, or the lowest leaves of herbaceous plants), occupy the lower humid strata of the vegetation. On the other hand, the more xerophytic species, or the more xerophytic parts of others, are those which grow under more severe transpiration conditions; e.g. evergreen plants, and those occupying the drier, more exposed strata of the vegetation.

Thus, in all probability, edaphic and climatic factors, the growth forms of the various species, with the resulting differences of exposure and shelter, the duration of the vegetative period, and possibly other factors, all play their part in determining the need or otherwise of special devices for regulating transpiration in swamp plants. In short, after making due allowances for the general nature of the habitat, the whole matter really resolves itself into a consideration of the different problems of individual species.

The work embodied in this paper was carried out chiefly at Aberystwyth, but, in addition, work was done at certain times at the Cambridge Botanical Laboratory and the Jodrell Laboratory, Kew. In addition, therefore, to various acknowledgements made in the course of this paper, I wish to express my thanks to Professor A. C. Seward, and to Lieut.-Col. D. Prain, for permission to use these laboratories, respectively. Also to Mr. L. A. Boodle, for kindly providing facilities at the Jodrell Laboratory, and for several helpful suggestions and criticisms; to Mr. R. I. Lynch,

Curator of the Cambridge Botanic Garden, for the trouble he took in growing a large number of *Spiraeas* for me, for the purposes of this paper; and finally to my pupil, Mr. C. M. Green, who is investigating some other species of marsh plants, and who has furnished me with information concerning their degree of xeromorphy.

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EXPLANATION OF PLATES LXXXI-LXXXIII.

Illustrating Professor Yapp's paper on *Spiraea Ulmaria*, L.

The plates consist of photographs taken from dried and pressed leaves of *Spiraea Ulmaria*, L., to illustrate the distribution of hairiness. In each case, only the lower surface of the leaf is shown. *Hairy parts are white, glabrous parts dark.*

PLATE LXXXI.

Shows all the leaves formed during one season on an erect flowering shoot. The leaves are arranged and numbered in order of development. Leaves 1-7 are radical, and 8-16 cauline. There is (as always) a gradual transition from glabrous to hairy leaves. The shoot was grown under fully insulated conditions. Note the narrowing of the leaflets in the upper leaves (cf. Text-fig. 5).

PLATE LXXXII.

A selected series of radical leaves. N.B. These were taken from a number of different non-flowering shoots. This series is arranged to illustrate the distribution of hairiness on partially hairy leaves. Note the increase in hairiness of successive leaflets as the individual leaf is ascended: the terminal leaflet is invariably the most hairy. Compare the increase in hairiness of successive leaves as the entire plant (flowering shoot) is ascended—see Pl. LXXXI. In individual partially hairy leaflets the hairs usually form a marginal band, with sometimes (e. g. Nos. 4, 6, and 9) extensions in the form of bands between the main veins (cf. the localization of exposure withering—Text-fig. 11).

PLATE LXXXIII.

Three partially hairy leaves. No. 1 shows the marginal bands of hair; No. 3 the additional interveinal bands. The terminal leaflet of No. 2 illustrates a not infrequent case in which only the innermost portions of the interveinal bands are developed. These now show, in addition to the marginal bands, patches of hairs occupying the forks of the veins.

YAPP.—LEAVES OF SPIRAEA.

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Yapp, R. H. 1912. "Spiraea ulmaria, L., and its bearing on the problem of xeromorphy in marsh plants." *Annals of botany* 26, 815–870.

<https://doi.org/10.1093/oxfordjournals.aob.a089419>.

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