The Physiological Anatomy of *Spartina Townsendii*.

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With seven Figures in the Text.

INTRODUCTION.

SPARTINA is a small genus of very characteristic grasses, mainly natives of the Atlantic seaboard of America, where they are to be found abundantly in salt marsh and estuary. *Spartina cynosuroides*, the freshwater Cord Grass, penetrates inland to the Missouri River, and in the Western States it forms a large part of the grass of sloughs and wet marshes. In Europe only four representatives occur, if we regard *S. Townsendii* and *S. Neyraui* as one species.

S. juncea is restricted to the western portion of the Mediterranean, whither it was introduced probably by shipping. Of the other three the oldest known is *S. stricta*, which Stapf regards as undoubtedly indigenous. It has the widest distribution of the European forms, but, notwithstanding its long establishment, it is becoming scarce on the south coast of Britain owing to the rapid spread of a later species. *S. alterniflora* was recorded first from the neighbourhood of Bayonne at the beginning of last century, and later it was discovered at the head of Southampton Water, down which it spread until its progress was checked by the remaining species, *S. Townsendii*, about whose origin and first appearance considerable uncertainty exists.

In his Flora of Hampshire, published in 1883, Townsend gives the first record of this species as 1878, when it was collected in the neighbourhood of Hythe, Southampton Water, by the brothers Groves, who described it shortly afterwards as a distinct species. But there is no doubt that it existed earlier, although overlooked. A specimen in the Warner Herbarium at University College, Southampton, collected near Hythe in 1870 and labelled *S. stricta*, is undoubtedly *S. Townsendii*. This carries it definitely

back to that date, but there is reason to believe that it occurred even before that time. The older accounts of the Spartan grasses vary much, and in Sowerby's 'Grasses' (1861) the opinion is expressed that the plants of *S. alterniflora*, collected near Southampton, were so like *S. stricta* that they could not be regarded in any other light than as intermediate varieties. But *S. stricta* is a fairly constant species showing remarkably few variations. Therefore the probability is that the doubtful specimens were in reality plants of *S. Townsendii*, which in many of its characters is intermediate between *S. stricta* and *S. alterniflora*. Unless the plants were examined carefully *in situ*, and at the flowering season, the appearance of this new plant might be overlooked for several years, mixed as it was with a very similar species, and growing in places not readily accessible. This view would help us to understand better its present extent and profusion.

Townsend's Spartan grass has been characterized by its phenomenal success on the shelving mud banks along the entire western shore of Southampton Water, whence it has spread with amazing rapidity over the available and suitable mud flats between Selsey Bill and St. Alban's Head, which form the natural boundaries of the sunken valley of the old Frome or Solent River. Here the numerous creeks and estuaries, harbours, and salt marshes from Poole to Chichester are well protected, while tertiary formations have supplied abundant mud. Again, the various stages of the progress eastward and westward have been short and favoured by eddying currents, which have helped largely in fruit dispersal. On both sides of these limits, where chalk ridges reach the sea, there are extensive stretches of shingle beach and cliff, broken by few suitable openings, with the result that for the time being the natural spread seems checked.

The value of this grass in fixing and in reclaiming shifting and unsightly mud banks has been recognized, and already attempts have been made to utilize it. Plants placed in the Medway have made considerable progress; others have also become acclimatized at both Blakeney Point and Wells Marsh in Norfolk. More recently the experiment has been extended northwards to the mud flats of the Forth and Don mouth.

At the present time it is the dominant species in the south of England. *S. stricta* survives in a few quiet backwaters, while *S. alterniflora* is disappearing fast before its more vigorous competitor, whose adaptation and success may be gauged by a glance across the Spartan beds from Cadland to Calshot, or from Lymington Harbour to Hurst Castle Bay.

It is inevitable that such an extensive and thick vegetation should affect the deposition of silt near river mouths, and hence tend towards a quicker levelling up. At present there exist no reliable data with regard to the rate, but it is hoped that a series of accurate survey measurements may be made at different stations along Southampton Water.

Apart from its usefulness, the grass presents interesting ecological features, and the present study was undertaken in the hope that it would throw some light on its adaptation to a life of periodic submersion, as well as form an introduction to a contemplated series of experiments on its physiology. The distribution and spread of the plant has been treated fully by Stapf, who is still carrying out his observations on its ecology.

EXTERNAL MORPHOLOGY.

Rhizome. Spartan grass owes its power of rapid extension mainly to its characteristic rhizomes, which vary in length from a few inches to over a foot, rarely exceeding one-quarter inch in diameter. Their length is dependent for the most part on the type of soil and the available space. They travel horizontally through the mud at a depth of from $2\frac{1}{2}$ to 4 inches, but frequently in the young stages they show positive geotropism and penetrate downwards for a short distance. Near their point of origin they are firm, with short hollow internodes. The greater portion of their length, however, is soft and flexible, the whole structure being adapted for penetrating a soft substratum. Short scale leaves are found in the bud stage, but the mature rhizome is invested merely by colourless sheaths devoid of blade and ligule. After proceeding for a short distance, rooting more or less freely at the nodes, the tip turns upwards and gives rise to aerial branches. New rhizomes are produced sympodially, and in the early stages there is nothing to distinguish them from the aerial shoots, except that the latter remain for a longer time within the sheath and are given an upward tendency. The creeping axes are shorter in a stony substratum, and hence it may also be that the question of the available space plays a part in determining the tendency and consequently the ultimate formation of culm and rhizome.

Culm. The erect cylindrical aerial axis, covered almost entirely by numerous investing leaf-sheaths which enhance its rigidity, reaches a height of from 2 to 4 feet. The first shoot arising from the upturned rhizome tip is usually the dominant one. Secondary culms spring distichously from its basal portion. Of these the lower and outer generally grow more quickly, checking the development of the higher ones. Only at the margin of the clump or belt is it possible for plants to develop all or most of their aerial shoots.

Leaf. The leaves are also distichous. The first three or four are practically scales. As soon, however, as the axis rises above the ground short green-tipped blades appear, increasing in size as the stem is ascended, until they reach a length of twelve to eighteen inches. The lowest blades are thrown off at an early stage, separating at the articulation. This helps to distinguish this species from *S. alterniflora*, in which the lower blades are retained longer and wither gradually. A short soft-celled ligule, tipped

with hairs, encircles the stem and prevents water or mud from lodging between it and the sheath. The long smooth pale-green sheath clasps the axis firmly, completely surrounding it for the greater part of its length and passing into the blade through the pulvinar articulation. The lower blades form angles of from 45° to 60° with the stem, while the upper ones are more erect. The angle increases with submersion. During the fall of the tide the leaves swing up and down in the surface film until they are suddenly released and spring into position.

The adaxial surface of the blade is increased enormously by from forty to fifty ridges and furrows running from just above the pulvinus to the apex. These provide an increased assimilatory surface in addition to protection for the stomata. The papillae and waxy coating on this surface give it a velvety and glaucous appearance.

Root. The roots are adventitious and divided into two distinct sets. One type is long, relatively thick, smooth, and practically devoid of branches. This fixing form grows normally to a depth of six to twelve inches, serving to anchor the plant firmly in the soft mud. While its root-cap is large, root-hairs rarely, if ever, occur. The other type is shorter, thinner, and much branched, possessing a poorly developed root-cap and very sparse root-hairs on the youngest branches. Generally this latter form springs from, and clusters round the basal joints of the aerial axis, forming a densely woven, horizontal matting which aids largely in transforming the soft mud banks into comparatively firm turf. Similar tufts of branched roots spring from the rhizome nodes also. Their function is mainly absorptive. Both kinds of roots frequently show negative geotropism, probably an adaptation to the continuous silting.

ANATOMY.

Epidermis. The adaptation of the plant to alternate aerial and aquatic existence is marked by peculiar and special epidermal structures wherein it differs from any other grass genus examined. The two most striking features are the very distinctive hydathodes and the forked accessory stomatal papillae, both of which are undescribed as far as we can ascertain.

A distinct waxy coating covers all exposed portions above ground, giving the glaucous appearance. This is most pronounced on the adaxial surface of the leaves, where the epidermis is thinner, shows less cutinization, and is covered by numerous papillae as in Fig. 1, *I*. These conical or peg-like projections also show little cutinization. On the narrow cells of the ridges they run along in pairs which frequently become coated over in the old fully developed leaves, as in Fig. 1, *I*, *pa'*. This adds to the protection of the most exposed portions. The epidermal cells along the sides of the grooves are wider, and the number of papillae consequently greater. These, however, undergo no change. The papillae aid the waxy

coating in preventing water from adhering to, and wetting the upper surface. Their efficiency may be gauged by the fact that leaves, submerged in the laboratory for more than twenty-four hours, were quite

FIG. 1. 1. Epidermis of upper surface of leaf-blade, showing simple papillae (*pa* and *pa'*); hydathode (*hy*); and special stomata (*st*). 2. Epidermis of abaxial surface with ordinary stoma; pits (*p*); and hair (*h*). 3. Epidermis of abaxial surface of leaf-sheath immediately below the articulation: silica-cell (*si*); saddle-cell (*sa*). 4. Epidermis of articulation region, showing thick-walled pitted cells with very wavy outline. 5. Radial longitudinal section through 3: nucleus beneath silica body (*n*). 6. Enlarged surface view of the two types of short cells.

dry when taken out and shaken slightly. The normal period of natural submersion rarely exceeds a few hours.

The number of variations in the epidermis of different portions of the plant are merely changes rung on an essentially simple ground-plan, either of long cells alone, or more often of long cells alternating with

short ones, singly or in pairs. Their radial walls may be straight, but more frequently they present an undulating margin, most pronounced in positions of great strain like the pulvinar region, as in Fig. 1, 4. The inner surface of the sheath, protected by being pressed firmly against the stem, has thin, straight walls, while the outer epidermis (Fig. 1, 3 and 5) is coated with a thick development of cuticle. The adaxial surface of the blade is cutinized slightly, whereas the abaxial side has a strong, resistant layer which not only protects the mesophyll, but adds materially to the rigidity of the leaf. The poor development of this coating on the upper surface is compensated by the protection afforded by the furrows, and by the curling of the leaves when the water-supply is limited or transpiration excessive.

Long cells. These occur alone only in protected regions like the inner epidermis of the sheath and along the sides of the leaf-grooves. In most other parts they alternate with short cells, and possess strongly thickened outer and radial walls with numerous round or elongated pits (Fig. 1, 2, 3, and 4). Over the articulation between sheath and blade the thickening is most pronounced, forming strong radial flanges or girders between elongated large pits (Fig. 6). Freedom of movement at this point is facilitated by the shortened cells, whose folded fan-like walls (Fig. 1, 4) are capable of lengthening with a kind of bellows-action.

The most interesting of these long cells are the *motor-cells* (Fig. 4, 2, *m.c.*), which were first described for grasses by Duval-Jouve, who regarded them mainly as silica-containing cells, to which he gave the name '*cellules bulliformes*'. In *Spartina Townsendii* they form belts three cells wide running along the bottom of the furrows of the blade. They are clear and colourless, containing little solid matter but abundant water easily given up. While their inner and radial walls are very thin and collenchymatous, their outer walls differ only slightly from the adjoining epidermal cells. They are well developed towards the middle of the blade, being much deeper than the other cells along the furrows, but towards the margin little difference is seen. This accounts for the leaves rolling up completely only when excessive drying takes place.

Short cells. These show greater variation and are of two distinct types, one containing no silica or only traces, the other with a relatively massive, definitely shaped silica body. The former, which occur singly or in pairs between long cells, may be regular, but frequently they become saddle-shaped, cruciform, biscuit-shaped, or even dumb-bell-like (Fig. 1, *sa*). They invariably show less thickening than the adjacent long cells, and no pits are present on their outer walls. More interesting, however, is the second type containing a distinct silica mass. Each is accompanied by a short cork-cell placed always on the side towards the base of the plant, and forming a kind of saddle, in the hollow of which

the silica-cell lies, partly embraced by the upcurved ends. This is shown in Fig. 1, 3, 4, and 6. This type appears wedge-shaped in longitudinal sections of the leaf. The blunt end is outwards (Fig. 1, 5, *si*) and covered by a very thin wall, difficult to distinguish owing to its delicate structure and the refraction of the mass beneath. The silica body occupies the greater part of the cell. It is invested by a thin layer of protoplasm and blocks the entire upper and wider end of the cell cavity by which its outline is determined. It is easily recognizable both by the presence of small included air-bubbles, and by its resistance to stains. These cells develop from ordinary short, rectangular ones, and are most abundant in the upper outer epiderm of the sheath, where, immediately below the articulation, they equal the long cells in number. They cease at the point

FIG. 2. 1. Surface view of special type of stoma with forked papillae (*f.pa*); simple papillae (*pa*). 2. Transverse section through swollen vesicular ends of guard cells. 3. Transverse section near the middle and thickened portion of guard cells (*gc*).

where the break appears later. A few occur along the ridges of the blade and on the peduncle, but none have been found on the rhizome, the stem, or the first-formed leaves. Their distribution lends strong support to the view that they add to the rigidity of the plant, which is aided largely by the closely investing leaf-sheaths, on whose outer surface they are most numerous.

Stomata. The stomata belong to the characteristic grass type. The walls of the middle portions of the guard cells are so thickened that the cavities connecting the swollen ends are reduced to narrow passages, as in Fig. 2, 3. The slit is slightly longer than these rigid bridges, which are carried bodily apart by the swelling of the vascular thin-walled ends (Fig. 2, 2).

The most active stomata are those situated on the adaxial surface of the leaf over the loose chlorenchyma, where they are more numerous than in any other part of the plant. There they occur in two, rarely

three, close rows on each side of the laminar furrows. These rows (Fig. 4, 2) are about two cell-widths apart, and almost corresponding distances from the motor-cells forming the bottom of the groove, and the line of hydathodes nearer the angle of the ridge. The stomata are of exceptional interest on account of the unique structure and placing of the papillae on the subsidiary cells. The papillose epidermis of this surface has been noted already. There are two massive papillae on each subsidiary cell, placed opposite the end of the stomatal slit (Fig. 2, 1 and 3). These expand at the top into two, three, or more rarely four, short branches which are strongly lignified, like the thickened walls of the guard cells. Frequently there is a simple papilla between them, corresponding to the middle of the pore. All bend over the guard cells, forming a fringe round and over the stoma as in Fig. 2, 1.

A small piece of leaf immersed in water showed a tiny air-bubble captured by these furcate papillae. Doubtless when the leaves are submerged the entangled air-bubbles prevent the entrance of water through the slits, and in this way the most active stomata are prevented from admitting water into the air-spaces at a time when they are open or partly so. This apparatus, along with the simple papillae and the waxy coating, goes a long way towards an explanation of the plant's adaptation for its dual existence.

The normal type of stoma occurs sparsely over all chlorenchyma. They are abundant on the inner epiderm of the sheath, but then it presses so tightly against the stem that no water gains entrance. Although their appearance on the rhizome sheaths is more surprising, the absence of chlorophyll prevents the manufacture of osmotic substances, and consequently the guard cells are inert.

Hydathodes. Hydathodes of a type apparently hitherto undescribed take the place of the water pores found in many submerged plants, being distributed widely in definite tracts in the active chlorenchyma, usually near large water-storing cells. On the upper surface of the leaf they are arranged in a row (Figs. 1 and 4) along each side of the furrow, about two or three cell-widths from the ridge angle, and one or two from the upper line of stomata. Here the epiderm consists of long cells alone, and the hydathodes are placed between every two or three of these in longitudinal series. On the abaxial surface of the leaf-blade and sheath they form a similar line in the large-celled tissue between the sclerenchyma bands over the bundles. They are absent from the rhizome, the invested portion of the stem, and the inner surface of the sheath, but occur abundantly on peduncles, and even glumes in the more-pronounced assimilatory bands, although always near fairly large cells with watery content. They are placed invariably between the ends of two long cells which become slightly narrower as they approach one another (Fig. 3, 1). However, instead

of meeting their corners project outwards again and meet the walls of the lateral cells, forming a cylindrical cavity whose rim in surface view is very thick, with the inner side smooth and circular, while the outer is wavy, varied, and even pitted (Fig. 3, 1). The hydathodal space is bounded therefore partly by four cells, along whose lines of contact are four vertical ridges or flanges, with the intermediate portion facing each cell thinner walled.

A transverse section of the leaf shows a flask-shaped organ, as in Fig. 3, 2, with the neck projecting into the epidermal cavity described, and the swollen basal portion embedded in the underlying tissue; a radial longitudinal section differs inasmuch as the basal part is elongated and boat-shaped, as in Fig. 3, 3. The cap portion of the hydathode has a distinctly stratified, mucilaginous wall, fitting the cavity tightly yet free from its walls. Although in the adult plant it is usually on a level with the surface or slightly below it, in the very young stages it projects a little distance beyond.

It rests on a strongly lignified and cutinized collar (Fig. 3, 2, *c*) which marks the region where the thin-walled swollen base abuts on the retreating sloped lower corners of the adjacent epidermal cells. This collar is so strongly developed as to give the impression of a thick partition at this point. This is accentuated by a slight projecting ridge on its inner upper surface.

The basal portion of the hydathode is elongated parallel to the axis of the plant and has pointed pyramidal ends. It is thin-walled and densely filled with protoplasm, in the centre of which lies a relatively large nucleus. In addition to shape, it is sharply marked off from the surrounding cells by the absence of chloroplasts. The protoplasmic content of the cap is also dense, and stained sections give the impression of its being connected through the narrow neck by numerous strands of protoplasm to that in the lower part. A nucleus has also been observed in the cap, placed sometimes near the tip, sometimes partly hidden by the collar. The more frequent occurrence of nuclei in the cap portion in younger material would strengthen the view that the hydathode consists of two cells whose common wall has been resorbed at an early stage.

FIG. 3. 1. Surface view of hydathode (*hy*), from abaxial surface of leaf. 2. Transverse section of leaf showing hydathode: (*n*) nucleus; (*c*) collar. 3. Radial longitudinal section of abaxial surface of leaf, showing hydathode.

In very young leaves the tip of the hydathode projects a short distance above the surface like a swollen glandular hair. This suggests a possible theory as to its ontogeny. The hairs so abundant in many land grasses would be useless to the plant when submerged. This is partly borne out by the fact that many hairs drop off before the leaves unroll and open. Then the hairs in *Spartina* correspond in position to the short cells between two long ones, just as the hydathodes do, and occasionally they have been observed occurring along the same lines as the latter in young plants. It is possible, therefore, that these excretory organs are really hairs modified to meet a new set of conditions. An extensive examination of the genus is necessary before a definite statement can be made with regard to the point.

These hydathodes differ from any described forms, and are certainly unique in grasses. The nearest approach to them are the secretory cells, discovered by Sauvageau in aquatic Monocotyledons, and described by him in various papers on the structure of the leaves of these. In *Cymadocea aequora*, for example, they are distributed for the greater part along the margins of the leaves; in others they may be scattered irregularly over the surface. These, however, are merely larger epidermal cells whose outer walls remain thin, and become distended and convex, while the inner portions penetrate slightly into the mesophyll. They resemble those described above in function, but lack their more definite structure.

The *Spartina* type of hydathode may undoubtedly be regarded as a kind of safety-valve for getting rid easily and quickly of excess water and mineral salts, both of which, in abundance, are accessible, as a rule, to the plant. Thus fairly rapid loss of these is not dangerous to it, a fact which helps to explain the absence of any kind of epithem acting as a filtration-tissue, as in so many Dicotyledons. This want, common curiously enough to most Monocotyledons, facilitates rapid exudation. Their activity in this respect may be demonstrated very simply by cutting some plants and placing the cut stems in water under a bell-jar. In a few hours an immense number of drops may be seen on blade and sheath. The hydathodes forming the lines along the furrows function so quickly that tiny sparkling drops may be detected in less than an hour. These are much more active than those on the abaxial surface, owing doubtless to their greater proximity both to the large water-storing cells and the special assimilating tissue.

Large quantities of salts, especially sodium chloride, are present in the excreted water. These may be detected by chemical methods in the drops given off, but a more striking demonstration of their presence can be seen in nature. While examining some plants, whose upper leaves and peduncles had been exposed continuously for some days of neap tides to a fairly dry atmosphere, our attention was directed to numerous, small, white, worm-like

castings scattered over these parts of the plants. These were often from 1 to 2 mm. long, occurring over the hydathodal lines and only on the living parts. On examination they proved to be heaps of cubical crystals, mainly of sodium chloride. Rapid evaporation after exudation had enabled the salts to crystalize out, and their accumulation in such castings had been favoured by a continuation of dry weather and the failure of the neap tides to submerge the upper portions of the plants for a few days. The worm-casting-like form of the heaps of crystals, their distribution on the plant, and their absence from withered or dead portions prove conclusively that they were products of excretory activity, not the remains after evaporation of clinging drops of water or spray. What is most surprising is the amount of salts excreted by these small structures.

A shoot of *Spartina* with several leaves, when cut off under water and then transferred to a bell-jar with the cut end dipping in water, shows practically as great an excretion as potted plants placed in similar atmospheric conditions. The cut ends of the vessels are immersed freely in the water, continuity with the supply being secured without the intervention of an active cortical tissue as in the roots. The position of the most active of all the hydathodes in the stellate spongy chlorenchyma, with a thin layer of the same between them and the water-storing cells, precludes the possibility of much local pressure outside the hydathodes themselves. This would seem to throw the onus of their activity upon their own structure and contents, inducing the belief that the excretion is due mainly to some form of protoplasmic activity.

When the plants are submerged, some such system is necessary to get rid of excess water and salts, and prevent flooding of the air-spaces. A similar danger must be met even when they are exposed by the fall of the tide, for the cushion of air, held by the dense vegetation belt over the moist substratum, is more saturated than the atmosphere immediately above, with the result that transpiration is lessened and an auxiliary method of water-excretion rendered necessary. This is found in the system of hydathodes, which also enables the plant to throw off immense stores of salts.

Rhizome and Culm. Both the underground and aerial shoots conform to the usual grass type. One distinctive feature, associated with the habit of the plant, is the development of air-passages which in the former are large, and separated by radial parenchyma plates only one or two cells in thickness, while in the latter they are smaller and separated by much thicker radial walls. Usually they arise by the development of stellate tissue, and its subsequent disruption; sometimes large rounded cells break down without any appearance of stellate cells.

Leaf. The leaf also shows few variations from the normal furrowed grass type, except in the epidermal characters already described. Forty to

fifty fibro-vascular bundles, one for each ridge, run up through sheath and blade. They are of two kinds (Fig. 4, 1 and 2), alternating with one another. Round each bundle are two rings of cells. The inner consists of smaller cells, regular and very strongly lignified in the larger type, less regular and

FIG. 4. 1. Transverse section through leaf-blade, showing the distribution of hydathodes, air-passages, and sclerenchyma. 2. Portion of 1 very much enlarged: (*pa*) papilla; (*st*) stoma; (*sc*) sclerenchyma; (*hy*) hydathode; (*ch*) chlorenchyma; (*mc*), motor cell; (*c*) partition cell; (*w*) water-storing envelope; (*ap*) air-passage.

only slightly thickened in the second; the other envelope consists of large thin-walled elongated cells. In the young plants they contain chloroplasts, which, as growth proceeds, disappear first from the upper cells, then from those towards the lower surface, and finally from the lateral ones. These

large clear cells (Fig. 4, 2, *w*), from their watery contents and proximity to the bundles, may be regarded as a kind of transfusion-tissue, or water-storage system. Two or three rows of similar large cells extend from this vascular sheath and unite with the subepidermal stereome. These at first also contain chloroplasts, which gradually diminish or even disappear finally. Ultimately these cells have a large water-content. They compose the main part of the mesophyll bridges supporting the bundles, and by their turgidity, combined with the sclerenchyma strands, form girders strong enough to keep the leaf erect even when unrolled.

The chlorenchyma consists of irregular stellar cells, curiously elongated like a palisade layer, with radiating lateral arms and large intercellular

FIG. 5. 1. Longitudinal section through junction of leaf-blade and sheath: (I) parenchyma cushion; (II) thickened pad of articulation with split (*sp*); (III and III') sclerenchyma sheath surrounding reduced vascular bundle; (*l*) ligule; (*sc*) sclerenchyma; (*vb*) vascular bundle. 2. Enlargement of regions (I) and (III), showing type and distribution of supporting tissue, and pitting. The large colourless soft-walled cells under the convex thin-walled epidermis represents the active part of the pulvinus.

spaces, as in Fig. 4, 2, *ch*. It extends along the furrow to a little way below the bottom of the groove, between the water-storage ring and a short median line of two or three circular cells (Fig. 4, 2, *c*), whose walls approach collenchyma in structure, in this respect corresponding to inner walls of the motor-cells below whose median line they lie. The partition cells probably both help to strengthen the hinge arrangement and aid the motor-cells to absorb and to give up water. They terminate on the air-passages which run between the bundles through sheath and blade.

The air-passages arise from blocks of rounded cells with few or no chloroplasts. The cells become stellate and finally collapse, forming the lacunae (Fig. 4, 2, *ap*), which are interrupted by transverse diaphragms.

These latter are most numerous in the sheath, where they can be seen readily through the epidermis, owing to the enclosed tubes of air.

The inner surface of the sheath is continued upwards in a short ligule (Fig. 5, 1), terminating in a brush of fine hairs. The solid portion consists of moderately thin-walled, slightly elongated cells. The surface next to the stem, to which it is applied closely, has a smooth epiderm like the inner side of the sheath, while that towards the blade consists of cells, as in Fig. 7, with the long diameter nearly at right angles to the surface, and their outer walls notched, uneven, and mucilaginous. As the leaf-base is not always at the same angle to the stem, it seems likely that this upper surface of the ligule acts as a pulvinus in preventing its being torn away from the stem. The large, clear, colourless cells of the whole structure are adapted for holding water, which is retained, even under unfavourable conditions, by the mucilaginous coating. In this more or less turgid condition the ligule is pressed tightly against the stem, preventing the entrance of either water or mud, while the clefts (Fig. 7, *cl*) at its base permit the blade to sway freely without jerking the ligule suddenly away.

Pulvinus and Articulation. Immediately above the insertion of the ligule there is a thickening of the blade, due to the greater development of the mesophyll at that point. Under this short, convex stretch of epiderm, which shows little cutinization or thickening, lies a mass of soft-walled cells with slight almost invisible pitting. In longitudinal section they present the outline shown in Fig. 5, 2. Beneath this cushion the cells become thickened, distinctly pitted, twisted, and fibrous, forming a solid sheath round the bundle, which is slimmer at this point, and minus the water-storing envelope. This investing mass of mechanical tissue is thickened near the middle of the pulvinar region, from which it thins away upwards and downwards, as in Fig. 5, 1, III and III'. The sclerenchyma strands under the epidermis of the ridges above this region pass in under the soft tissue to meet the central supporting mass, while those under the abaxial epidermis stop short where the articulation bulges out on the dorsal side. This joint (Fig. 6) is marked by a darker, more glossy surface, where the epidermal cells are short, with thickened pitted outer walls and very wavy radial ones. Beneath this bulging portion is a pad of thick-walled cells with large pits; on the inside it abuts on the central supporting sheath. Above and below are the ordinary mesophyll cells.

Transversely along the middle line of the abaxial surface of the joint a split appears later, cutting across the strengthened pad without any definite order. This split forms a pseudo-articulation on which the leaf-blade swings more freely for some time before it falls off.

The soft-walled tissue on the adaxial surface acts as a pulvinus. When the plants are submerged and contain abundant water, these cells are turgid and the leaf-blade is bent back, but when they are exposed to a drying

FIG. 6. Longitudinal section through regions (II) and (III') of Fig. 5, *x*, showing the thickened dorsal pad through which the split or pseudo-articulation appears later. The epidermis is strongly thickened and cutinized. Silica-cells (*sz*), abundant on the upper part of the sheath, stop at the point of splitting. Saddle cells (*sa*.) accompany them.

FIG. 7. Longitudinal section through the ligule with notched thin-walled mucilaginous cell (*m*); and clefts (*cl*).

atmosphere, part of the water is given up and the leaf becomes more erect, making it easier for the motor-cells to roll the leaf, and thus check transpiration from the upper surface. The latter danger is also lessened by a smaller surface being presented to the sun's action when the leaves are more upright.

Plants placed in water in the laboratory and then allowed to dry showed a pulvinar movement of ten to fifteen degrees. This is larger than occurs normally in nature. Freedom of movement at the articulation is facilitated by the thinning of the bundles there and by the migration of the stereome from a subepidermal position towards the centre, while sufficient mechanical support is given to the pulvinus by the thickened central sheath of sclerenchyma with its dorsal pad.

Fixing Roots. The fixing roots are much thicker than the absorptive ones and are never branched. The epidermis and the layer beneath it finally decay, so that the persisting exodermis represents the original third layer, contrary to the usual Monocotyledon rule. The layer next to the latter consists of smaller cells also sclerified. Then follow five or six rows of compact parenchyma, the outer cortex, ultimately, showing moderate sclerification. Cubical crystals occur in abundance in these layers. The inner cortex consists of a large number of rows of extremely regular parenchyma with rectangular air-chinks at every corner. Even in old fixing-roots the regularity and embryonic appearance of these cells are retained, so that the sections appear like the young roots of many Monocotyledons. Lacunae, of the type more common in the absorbing roots, also occur, either all along except at the tip and near the insertion, or at irregular intervals.

Absorbing Roots. At first these are anatomically the same as the young fixing roots, but are even then considerably thinner as a rule, owing to the smaller amount of cortex. In the adult roots all the inner cortex, except that at the actual growing-point, shows numerous well-marked radially elongated air-passages, stretching from the inner edge of the outer cortex to within two or three cell-rows of the endodermis.

The lacunae, so well developed in this latter type of root and locally in the former, arise as follows: A certain small number of radial rows of cells in the inner cortex show considerable enlargement. The cells of the neighbouring rows, not growing in size much and sometimes even collapsing, meanwhile become stellate, usually four-armed, and the intercellular spaces at their corners thus become enlarged. The radial walls of these rows of stellate cells become considerably thickened, and at points single cells or rows of two or three decay altogether, and only their radial walls plus small traces of their tangential walls attached to them persist round the gap. Each tangential wall becomes split across, and finally numerous narrow, complete radial rifts are formed in the inner cortex by the decay of com-

plete rows of stellate cells. Each space is always bounded by the intact radial walls which form limiting membranes.

The result is that the inner cortex has a small number of radial rows of large intact cells, separated by air-passages, in each of which occur several persistent radial membranes bearing slight vestiges here and there of the tangential walls of the defunct cells. These membranes never occur in the air-passages of the stem, rhizome, sheath, or glumes. Where the rootlets are connected with the absorptive root there is always a sheath of fairly compact, non-stellate cells left, about four cells thick, to surround the inrunning axis as it crosses the cortex.

The Inflorescence. The inflorescence of 3-13 somewhat spike-like axes conforms to the grass type, with one flower to each spikelet. These begin to form very early; although flowering does not usually begin until August and September, their component parts are well established by the end of May. Lodicules are absent and the glumes are compressed, both adaptations to the plant habit.

The surface and the contents of the versatile anthers are slightly mucilaginous as well as the plumose stigmas. The flowers are protogynous and wind-pollinated.

In connexion with the scarcity of hairs on the vegetative portions of the plant, already commented on, their abundance on the glumes is interesting. Of course the inflorescence is subjected to less submersion, but that alone seems an insufficient explanation. Some of the glume-hairs are very large, especially on the keels, and have groups of cells lying against their lower sides. As these latter have numerous pits on their outer walls and also on their inner, they can absorb water readily, and possibly alter the angle of the stiff hairs. In this way they might play a part in opening and closing the flowers. It is also probable that they hold air-bubbles in the spikelets when submerged.

SUMMARY.

Distribution. *Spartina Townsendii* probably occurred along Southampton Water considerably earlier than 1870—the date of the earliest recorded specimen in the Warner Herbarium. Its present natural distribution is limited by Selsey Bill and St. Alban's Head, the boundaries of the sunken valley of the old Frome or Solent River. At those points the chalk ridges reach the sea, and outside them lie fairly long stretches of shingle beach or cliff, broken by a few or no suitable estuaries or mud flats for a considerable distance.

External Morphology. There are two sets of roots. The anchoring or fixing roots are long, unbranched, devoid of root-hairs, and penetrate straight down into the mud; the absorptive roots branch freely, forming a dense, more or less horizontal web. Both types occasionally show marked negative

geotropism, and thus occupy newly deposited strata. The rhizome, whose length varies with the substratum, differs little from the ordinary grass type, as also the erect haulms. Rigidity is aided by the long-continued investment of the stem by the leaf sheaths. The long, rigid, semi-erect leaves belong to the furrowed type, rolling to a limited extent and showing a distinct pulvinar action at the articulation. The ligule also possesses a kind of pulvinus.

Anatomy.—The epidermis shows great local variations in the outline, arrangement, thickening, and structure of its units. Exposed portions have a distinct waxy coating overlying thickened and cutinized walls. The adaxial surface of the leaf-blades possesses papillae which aid the wax in preventing wetting.

The most active stomata, which occur on the sides of the furrows, show interesting auxiliary structures in the form of forked papillae on the subsidiary cells. These bend over the slit, forming a fringe which entangles an air-bubble when the leaves are submerged, and thus prevent the flooding of the air-spaces. The other stomata are of the normal grass type, but in some positions they are inert, owing to the absence of chlorophyll and the small osmotic content of the guard cells.

Numerous hydathodes of a hitherto undescribed type occur along definite tracts in the neighbourhood of large water-storing cells. These excrete large quantities of water and salts in solution. This exudation is due to some form of protoplasmic activity within the hydathode rather than to root pressure.

Hairs are abundant on the young vegetative organs, but most disappear very early. They persist on the glumes, where they may help in the opening and closing of the flower, and also in entangling air-bubbles when submerged.

There is a large development of air-passages in all organs of the plant. Their origin varies in different parts.

The two types of roots show differences in thickening and the degree of air-passage formation. A remarkable feature is the presence of solid portions in the deep penetrating roots, where numerous air-passages would seem more in keeping with accepted views.

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