Transpiration in Succulent Plants.

BY

E. MARION DELF.

With one Figure in the Text.

CONTENTS.

	PAGE		PAGE
INTRODUCTION	409	(6) Glands	422
I. TRANSPIRATION IN RELATION TO		(7) Capacity for Superficial Absorption	423
STRUCTURE	410	(β) Water-storing System	425
(a) Transpiring Surface	410	(1) Distribution of Water-storing	
(1) Reduction in Leaf Surface	410	Tissues	425
(2) Transpiring Surface in Relation		(2) Acidity or Salinity of the Cell-sap	425
to Succulence	410	(3) Nature of Cell-sap and the Succu-	
(3) Protective Means :		lent Habit	426
1. Cuticle	412	(4) Conservation of the Water Supply	428
2. Wax	415	(γ) The Conducting System	433
3. Hairs	415	II. TRANSPIRATION IN RELATION TO	
(4) Stomata :		HABITAT	435
1. Distribution	416	(1) In Desert Plants	435
2. Power of Regulation of		(2) In Plants of Warm, Damp,	
Transpiration	417	Tropical Regions, as in Man-	
3. Protective Adaptations	420	groves and Epiphytes	436
(5) Aqueous Tissue :		(3) Halophytes	437
1. Nature and Function	420	(4) Halophytic and Alpine plants	438
2. Occurrence	421	III. SUMMARY	440

INTRODUCTION.

SUCCULENT plants are largely characteristic of dry, sandy, or rocky regions, where the physical conditions seem to favour rapid transpiration, whilst the water supply is limited, or in some way precarious. They are, however, also found in very different situations, as, for example, the epiphytes of a typical tropical forest where the atmosphere is warm and damp. Other succulent plants inhabit maritime districts, especially the neighbourhood of salt-marshes, and others, such as many of the Crassulaceae, though commonly found in stony or rocky places, thrive equally well in ordinary soil, and may then be freely associated with mesophytes. We may thus distinguish, according to their habitat, four main classes of succulent plants, which may be briefly designated as (1) *Desert Plants*, (2) *Rock Plants*, (3) *Epiphytes*, (4) *Halophytes*.

We are naturally led to ask how far the succulent habit is to be regarded as an adaptation to environment in all these cases; and in the

following pages this question will be discussed in its bearing on the problem of transpiration, firstly in relation to structural features, and secondly in relation to habitat.

I. TRANSPIRATION IN RELATION TO STRUCTURE.

Succulent plants have a number of anatomical features in common which are undoubtedly connected with the process of transpiration. We shall consider the character of (*a*) the transpiring surface, (*β*) the storage system, and (*γ*) the conducting system, from the physiological point of view.

(*a*) The Transpiring Surface.

In plants of extremely dry habitats there is often a notable reduction in leaf surface, the stem itself taking on the bulk of the work of assimilation and transpiration; there is therefore, presumably, a corresponding diminution in the total water loss, although not necessarily in the actual rate of transpiration, per unit area of surface. Examples of this are seen in the thorny almost leafless stems of desert species of *Euphorbia*, and the equally thorny swollen stems of *Opuntia*, *Echinocactus*, and some other genera of the Cactaceae. The same tendency to eliminate the leaf as a distinct organ is seen in the halophytic genera *Salicornia* and *Arthrocnemum*, where the leaves are reduced to mere fleshy lobes almost entirely adnate to the stem.

A large number of plants, however, have fleshy leaves or succulent stems without any such extreme reduction of surface, as, for example, the majority of epiphytic or halophytic plants; these are often termed semi-succulents.

It is commonly assumed that the percentage water content of a plant is in itself a criterion of its degree of succulence;¹ but I have reserved this phrase to indicate the water content per unit area of surface.² In this sense the degree of succulence of a plant is of some interest for problems of transpiration, and a number of determinations from my own experiments are given in Table I.

The method employed was that of finding the fresh weight of a leafy shoot, estimating the surface area, and drying at 100° C. until a constant weight is obtained. The greatest difficulty lay in the determination of the surface areas. For large-leaved forms the outline of the leaf was carefully traced on paper ruled in millimetre squares; when a number of leaves had to be traced in succession, they were kept in a damp chamber or floated on water until just before use, in order to minimize the shrinkage in surface due to loss of water in transpiration, which has been demonstrated to take place even before withering becomes perceptible.³ In the case of small-leaved forms the procedure was varied to suit the particular type of leaf.

¹ Cp. Aubert.

² Delf, E. M.: Transpiration and Behaviour of Stomata in Halophytes. *Annals of Botany*, 1911.

³ Cp. Thoday, D.: Experimental Researches on Vegetable Assimilation and Respiration, V. *Proc. Roy. Soc., B*, vol. lxxxii, 1909.

In the case of *Suaeda* and *Salsola* the method employed was that described in my paper on 'Transpiration and Behaviour of Stomata in Halophytes' ('Annals of Botany', xxv, p. 487); for *Salicornia* the micrometer screw method detailed in the same paper (p. 487); whilst the small leaves of *Mesembryanthemum crystallinum* were estimated both by the micrometer screw and celluloidin method,¹ and the mean between the two determinations (which usually differed by from 1–3 per cent.) taken as a fair approximation to the true surface area. In all cases the stem was included in the determinations both of areas and of dry weights.

The succulence of the leafy shoots of *Salsola Kali* and *Arenaria peploides* is probably somewhat underestimated, for the only material available had been sent by post from some distance, and although kept in water for some time before using were probably not fully turgid at the time of the experiment. The shoots of the remaining examples were obtained direct from healthy plants cultivated in the garden at the James Allen's Girls' School, Dulwich,² where there is an artificial salt-marsh, which is watered at intervals with a 1–2 per cent. solution of Tidman's sea-salt, and also an artificial sand-dune, and pebbly sea-shore, in a very flourishing condition. It was ascertained, by means of the thallium sulphate test, that the plants used had a very considerable salt content, but they probably show a somewhat less succulence than that of plants in their natural habitat, especially in the case of variable plants, such as *Aster Tripolium* and *Arenaria peploides*.³

TABLE I.

Water Content per sq. dm. in some typical Succulent and Mesophytic Plants.

	Plant.	Water Content %.	Surface Area.	Water Content in grm. per sq. dm. ('Degree of succulence').
I.	<i>Mesembryanthemum edule</i>	96.3	70.54	12.6
	" <i>crystallinum</i>	97.7	3.28	6.2
	<i>Suaeda maritima</i>	90.3	40.38	10.0
	<i>Salsola Kali</i>	86.6	17.16	6.9
	<i>Salicornia annua</i>	89.5	24.43	6.5
	<i>Arenaria peploides</i>	89.2	12.34	5.5
II.	<i>Plantago maritima</i>	95.2	84.76	4.8
	<i>Aster Tripolium</i>	91.5	92.18	3.7
	<i>Sedum Sieboldii</i>	93.6	26.87	3.4
	<i>Atriplex portulacoides</i>	88.9	54.14	3.3
	<i>Cakile maritima</i>	91.8	14.96	2.8
	<i>Eryngium maritimum</i>	85.0	90.72	2.5
III.	<i>Glaucium</i>	89.0	46.50	2.1
	<i>Statice Limonium</i>	81.2	141.78	1.7
	<i>Saponaria officinalis</i>	78.4	82.28	1.4
	<i>Mercurialis annua</i>	77.0	45.14	0.95

¹ Delf, E. M. : Loc. cit., pp. 488, 489.

² By kind permission of the Head Mistress, Miss Howard; and of Miss L. J. Clarke, the senior Science Mistress, in whose laboratory these determinations were also made.

³ Cp. Lesage, P. : Recherches expérimentales sur les modifications des feuilles chez les plantes maritimes. Revue Générale de Botanique, 1890.

The plants fall roughly into three groups which may be termed 'succulent', 'semi-succulent', and 'mesophytic', respectively. The plants belonging to the first group possess from 5 to 12 grm. water content to every square decimetre of surface; to this class belong, probably, the xerophytic succulent Cactaceae (*Opuntia*, &c.). The same degree of succulence may be attained by large and small leaved forms, such as *Mesembryanthemum edule* and *Suaeda maritima*; by adnation of the reduced leaf (as in *Salicornia*, and to a less extent in *Salsola*), or by the development of aqueous tissue in each separate leaf, as in *Arenaria peploides* or *Plantago maritima*. The plants belonging to the second group comprise most of our British halophytic plants, many rock plants, and would probably also include many subtropical or tropical epiphytes, and plants typical of the Mangrove swamps. These have from about 2 to 5 grm. water content per sq. dm. surface. The third group includes only typically mesophytic plants, such as *Saponaria* and *Mercurialis*, and perhaps also a few exceptionally thin-leaved halophytes like *Statice*, in which the aqueous tissue is limited to the region of the midrib, and in which the epidermis is provided with small excretory glands. *Frankenia* and *Tamarix*, two other somewhat thin-leaved halophytic genera, at least in some of their species, are also provided with epidermal glands, and it is possible that the excretion of salt which is said to take place through these glands may account for the absence of the succulent habit.

Whether reduced or not, the transpiring surface is protected by a definite tissue, the epidermis, which may be more or less cuticularized. Haberlandt¹ describes an experiment in which he demonstrates the protective power of the epidermis in succulent plants. Two pieces of an Aloe leaf were covered with wax, except for a definite area, equal in both cases. The epidermis was carefully stripped from the exposed surface of one piece, but was left intact on the other; both pieces were then exposed to the air for three hours. The pieces were then weighed and the stripped leaf was found to have lost 524 mg., whilst the uninjured piece had lost only 2 mg. In this case the epidermis has a well developed cuticle, but there is, no doubt, a considerable amount of protection derived from even a slightly cuticularized epidermis.

Many succulent xerophytes have a thick cuticle and relatively little water loss, as the work of both Schimper² and Volkens³ shows. Holtermann also found some Cactaceae with thickly cuticularized epidermis in which the transpiration was almost imperceptible. In alpine plants, according to Leist and Bonnier,⁴ the outer wall of the epidermis is more strongly

¹ Haberlandt: Physiologische Anatomie, p. 96.

² Schimper, A. F. W.: Ueber Schutzmittel des Laubes gegen Transpiration, besonders in der Flora Javas. Monatsber. der Akad. Wiss. in Berlin, xl, 1890.

³ Volkens, G.: Zur Flora der ägyptisch-arabischen Wüste, auf Grundlage anatomisch-physiologischer Forschungen, 1887.

⁴ Leist and Bonnier: Quoted by Dr. A. Burgerstein, in 'Die Transpiration der Pflanzen', 1904.

cuticularized than that of the same species living on the plains; and here again the function of the cuticle appears to be primarily protective rather than mechanical, as Fleischer¹ believed. Wiegand² suggests that cuticularization is particularly characteristic of plants which are exposed at all times to the danger of too great transpiration; whereas a thinner cuticle with a covering of hairs is more often found in plants in which transpiration must be reduced at times, and yet must remain unhindered when the air is damp, and transpiration therefore rendered difficult.

Schimper claimed that a thickened cuticle, as well as other xerophilous adaptations, is to be found in most epiphytes,³ in Mangrove plants,⁴ and in the plants of the Solfataras,⁵ or regions bordering a fumarole. He stated that in the first case the precarious water supply rendered protection against too rapid evaporation necessary; in the second case the presence of chlorides, and in the third case of sulphates in the soil, renders the process of absorption so difficult that the transpiration also must be diminished by means of xerophilous adaptations. According to the more recent observations of Holtermann,⁶ however, this is by no means always the case. The epiphytic vegetation was found to occur, at least in Ceylon, mostly in damp tropical or subtropical forests; the plants found in such localities showed little or no cuticularization of the epidermis, and they were, as a matter of fact, found to be capable of very rapid transpiration; such are, for example, many species of *Ficus*, *Peperomia*, *Drymoglossum*, many Bromeliaceae, and some Orchidaceae. A few epiphytic orchids which were found growing in a dry atmosphere had a thickened cuticle, but these were distinctly exceptional. In *Sonneratia*, *Rhizophora*, and other plants of the Mangrove formations there was similarly but little development of cuticle, and, at times, a rapid rate of transpiration. In *Agapetes vulgaris* and *Rhododendron retusum*, the two most characteristic plants of the Solfataras of Ceylon, there was also absolutely no protection against excessive water loss.

Aubert⁷ measured the rate of transpiration of a number of succulent and mesophytic plants and came to the following general conclusions:

1. With equal surfaces, succulent plants, such as many Crassulaceae and species of *Mesembryanthemum* which have a thin cuticle, transpire more freely than many mesophytes with a thick cuticle (*Hedera Helix*, *Picea excelsa*); with equal fresh weights, however, the succulent types transpire less than these.

¹ Quoted by Dr. A. Burgerstein, loc. cit., p. 205.

² Wiegand: Relations of Hairy and Cutinised Coverings to Transpiration. Bot. Gaz., 1910.

³ Schimper, A. F. W.: Die epiphytische Vegetation Amerikas, 1888.

⁴ Schimper, A. F. W.: Die indomalayische Strand-Flora, 1891.

⁵ Schimper, A. F. W.: Ueber Schutzmittel des Laubes gegen Transpiration, besonders in der Flora Javas, 1890.

⁶ Holtermann, Dr. C.: Der Einfluss des Klimas auf den Bau der Pflanzengewebe, 1907, pp. 138, 61, 73.

⁷ Aubert, E.: Turgescence et transpiration des plantes grasses. Ann. des Sci. Nat., Bot., 1892.

2. The Cactaceae transpire less than any plants examined, whether reckoned on equal surfaces or equal fresh weights.

The work of both Stahl¹ and Rosenberg² points to the fact that many European halophytes possess the power to transpire freely, as judged by the cobalt paper test. I have shown,³ and have often observed, that in many of our British salt-marsh plants the transpiration may be much greater for equal transpiring surfaces than in a typical mesophytic plant; in others the value approaches, but rarely falls below, that of the typical mesophyte under similar conditions at the time of the experiment. The figures in Table II give some of these results; but since the observations were made of necessity at different times,⁴ the transpiration is estimated per hour per square decimetre, relative to the loss of a water surface measured at the same time under the same experimental conditions, the latter value per hour per square decimetre being taken as 100 in each case; the variations in transpiration due to the purely physical effect of the environment are now eliminated, as Livingston⁵ pointed out. Throughout the experiments the transpiration observed is that of detached leafy shoots with no water supply; the cut end was sealed immediately after being severed from the plant, and the fresh weight at once obtained; the shoot was then allowed to transpire, hung up in the air of the laboratory, away from any draught or direct sunlight, and the water loss during the first hour or two hours of withering determined by means of an accurate balance. The values obtained will be somewhat below those of the normal plant, since, in all the plants examined, the stomata close within the first half-hour of experiment, and also because the transpiration falls off as the water content of the whole plant falls below the normal.

TABLE II.

Relative Transpiration per hour per sq. dm.

Water	100
<i>Salsola Kali</i>	64.1
<i>Mesembryanthemum edule</i>	66.9, 47.6
<i>Atriplex portulacoides</i> . .	61.7
<i>Salicornia</i>	32
<i>Sedum spurium</i>	36.0
„ <i>Sieboldii</i>	49.6
<i>Saponaria officinalis</i> . .	27.6, 7.4
<i>Vicia Faba</i>	26.0
<i>Aster Tripolium</i>	22.4

¹ Stahl, E.: Einige Versuche über Transpiration und Assimilation. Bot. Zeit., 1894.

² Rosenberg, O.: Über die Transpiration der Halophyten. Öfvers. af Kongl. Vetenskaps-Akad. Förhandlingar, Stockholm, 1897.

³ Delf, E. M.: Transpiration and Behaviour of Stomata in Halophytes. Annals of Botany, xxv.

⁴ These figures are taken mostly from unpublished experiments made during the months of August and September, 1911.

⁵ Livingston, B. E.: The Relation of Desert Plants to Soil Moisture and Evaporation.

A large number of succulent plants, therefore, show but little development of cuticle, and can endure a rapid rate of transpiration per unit area of surface without harm.

Many succulent plants, however, in addition to the possession of a more or less developed cuticle, have a coating of wax which acts as a further protection against water loss. Garreau¹ offered experimental evidence as to the protecting power of wax coverings in the case of *Centranthus ruber*, *Syringa vulgaris*, *Sedum verticillatum*, and some others, where the rate of transpiration was increased from 1.5 to 3 times by removing the wax. Frequently the wax not only coats the free surface of the epidermal cells, but also blocks the apertures of the stomata more or less completely. Dr. F. Darwin² has shown that, generally speaking, the stomata of a plant tend to become aggregated in the areas covered by the wax or bloom. Thus, if bloom be only found on one side of a leaf, the stomata are often either less numerous or altogether lacking on the side which is not thus protected. The association of stomata with a wax covering may, however, also be connected with the prevention of the blocking of the stomata by rain or heavy dew, since the maintenance of gaseous exchange is of great importance in the economy of the plant.

A wax covering is chiefly characteristic of plants inhabiting dry regions, as the observations of Schimper, Volkens, and others show. Holtermann³ found that in Ceylon those epiphytes which lived in the warm damp air of the tropical forests were glabrous, whereas those which were found in exposed, sunny places were frequently coated with wax. Wiegand,⁴ from his experiments with artificial surfaces, concluded that a wax covering would form an equally effective protection whether in still air or in wind.

Most halophytes which live in damp or marshy situations are glabrous, as, for example, *Rhizophora*, *Salicornia*, and *Aster Tripolium*. *Suaeda maritima* is an exception, for the small leaves are covered with a fine bloom, and it is often found in marshy places. *Psammophilous* halophytes are frequently covered with wax if sclerophyllous, or very slightly succulent, as in *Elymus* and *Eryngium maritimum*; but if succulent the leaves are commonly glabrous, as in *Cakile maritima*, which also has only a very slight development of cuticle.

Hairs, whether glandular or protective, are not common in succulent plants; they are, indeed, much more characteristic of sclerophyllous vegetation. We may, however, instance *Sempervivum arachnoideum*, a succulent alpine plant, the rosettes of which are clothed, and perhaps also protected by long loose hairs. Some species of *Avicennia* are hairy, and *Evolvulus*

¹ Quoted by Dr. A. Burgerstein in *Die Transpiration der Pflanzen*, 1904, p. 39.

² Darwin, Dr. F.: *Stomata and Bloom*. Journ. Linn. Soc., 1887.

³ Holtermann: *Der Einfluss des Klimas auf den Bau der Pflanzengewebe*, 1907.

⁴ Wiegand: *Relations of Hairy and Cutinised Coverings to Transpiration*. Bot. Gaz., 1910.

alsinoides is a littoral plant from the drier coastal regions of Ceylon, which is stated by Holtermann to have a number of small, succulent, and yet hairy leaves. According to Wiegand¹ a hairy covering is a relatively much more effective protection against transpiration in windy than in still weather; whilst in damp air it yet allows of a considerable amount of transpiration.

Many species of *Atriplex* are covered with short, closely set hairs, which form an almost continuous sheet of large thin-walled cells covering the much smaller cells of the epidermis, except for narrow chinks above the stomata. According to Volken's these hairs readily give up their water in time of need to the cells below, and then their walls collapse, and the empty cells thus form a very complete protection for the whole transpiring surface; the hairs can probably also absorb water from rain or dew, or they may be replenished from within when the roots are able to absorb freely. Some species of *Mesembryanthemum*, as *M. crystallinum*, *Forskalii*, and *nodiflorum*, have a number of swollen papillae which, according to Hagen,² have a protective function. The papillae are thin walled and appear to be filled with a mucilaginous cell-sap, which does not easily allow of evaporation; we shall see that these papillae probably also function as absorbing hairs for rain and dew.

TABLE III.

Distribution of Stomata in Succulent and Mesophytic Plants.

	Plant.	Habitat.	Stomata per sq. mm.		
			Upper Surface.	Lower Surface.	Average.
I.	<i>Mesembryanthemum edule</i>	dry, rocky	60	80	70
	<i>Suaeda maritima</i> . . .	damp, saline	63	63	63
	„ <i>fruticosa</i> . . .	sandy, saline	37	37	37
	<i>Salsola Kali</i> . . .	„ „	(stem) 71	—	71
	<i>Salicornia annua</i> . . .	marshy, saline	„ 104	—	104
	<i>Plantago maritima</i> . . .	„ „	143	231	187
	<i>Arenaria peploides</i> . . .	marshy or sandy	49	80	65
	(Hunstanton) „ (cultivated) . . .		134	194	164
II.	<i>Aster Tripolium</i> . . .	marshy or dry, saline	94	87	90
	<i>Sedum album</i> . . .	dry	94	87	90
	„ <i>Sieboldii</i> . . .	„	88	71	79
	<i>Cakile maritima</i> . . .	sandy, saline	127	163	145
	<i>Eryngium maritimum</i> . . .	„ „	243	149	196
	<i>Glaucium maritima</i> . . .	stony, saline	117	88	102
III.	<i>Statice Limonium</i> . . .	moist, saline	143	109	126
	<i>Saponaria officinalis</i> . . .	moist	60	349	204
Czech's Figures.	<i>Populus nigra</i> . . .	dry	Whether upper or lower surface unspecified		135
	„ <i>alba</i> . . .	damp			315
	<i>Brassica lyrata</i> . . .	dry			400
	„ <i>palustris</i> . . .	damp or marshy			609
	<i>Veronica Chamaedrys</i> . . .	dry			175
	„ <i>Beccabunga</i> . . .	aquatic or marshy			248

¹ Wiegand : Relations of Hairy and Cutinised Coverings to Transpiration. Bot. Gaz., 1910.

² Burgerstein : Die Transpiration der Pflanzen, p. 224.

It was established by Czech,¹ and has been confirmed by Volkens and other observers, that, in general, the stomata of plants growing in wet or even damp situations are more numerous per unit area than are those of dry places. Thus *Veronica Chamaedrys* was found to have 175 stomata per sq. mm., whilst *Veronica Beccabunga* had 248. So far as I have been able to observe, this holds true also for succulent plants, those from dry regions, such as some species of *Mesembryanthemum* and *Sedum*, having considerably fewer than have those, such as *Salicornia*, from marshy places. Table III gives the distribution of the stomata of such plants as I have observed, and also a few of Czech's figures for comparison.

According to Burgerstein² the degree of opening of the stomata affects the amount of transpiration far more than the actual number present. Leitgeb³ was the first to call attention to the power of the stomata to open and close, and regarded it as a means for regulating the amount of transpiration. This view has been widely accepted, but has been objected to recently by Lloyd,⁴ who found that in *Fouquieria splendens* and in *Verbena ciliata* the 'rate of transpiration may undergo sudden and wide changes, without the accompaniment of a sufficient change in the dimensions of the stomata to account for them on the theory of stomatal regulation of transpiration.'⁵ According to Lloyd the capacity for diffusion of the stomata of *Fouquieria* is well in excess of what would be required for the greatest observed transpiration rate, and he therefore concludes 'stomatal regulation of transpiration does not occur, though of course conservation of the contained water follows on complete closure of the stomata. It is open to doubt, however, if this condition ever obtains.' On the other hand, some experiments of Dr. F. Darwin, a preliminary account of which was given at the meeting of the British Association, 1910, and a further account of which is now in the press, lead to the conclusion that in many plants, if they can be observed by a sufficiently delicate method, stomatal movements are found to correspond closely with changes in the rate of transpiration caused by alteration in external conditions. It is clear, therefore, that the whole question of stomatal regulation requires further investigation.

So far as the power of movement of the guard cells in the stomata of succulent plants is concerned, we have but little direct evidence. In xerophytic succulents the stomata may be so much sunken or overlaid by cuticle that they seem to have little or no scope for movement. Stahl,⁶ however, states that the stomata of xerophytes all possess the power to close, and they are, therefore, presumably capable of the reverse action.

¹ Burgerstein : Die Transpiration der Pflanzen, p. 210.

² Burgerstein : *ibid.*, p. 211.

³ Leitgeb : Beiträge zur Physiologie der Spaltöffnungsapparate, 1886.

⁴ Lloyd, F. E. : The Physiology of Stomata.

⁵ Lloyd, F. E. : *ibid.*, p. 137.

⁶ Stahl : Einige Versuche über Transpiration und Assimilation, 1894.

In a paper recently published by Linsbauer¹ on the physiological anatomy of the epidermis of some Bromeliaceae, it is shown that the stomata are surrounded by at least two pairs of subsidiary cells, which are arranged as though to protect the guard cells from contraction when the neighbouring aqueous tissue collapses. In the case of *Quesnelia* the stomata were found to be completely closed, owing to the formation of a membrane across the outer respiratory cavity. In many of the Bromeliaceae the arrangements of the stomata and of the air passages in the leaf seemed to be such as to ensure the best ventilation with the minimum of transpiration.

In all the succulent plants which I have examined the stomata appear to be capable of movement, but I have frequently found the stomata of species of *Sedum* and of various fleshy halophytes in the closed condition, especially when the sun was on these plants and the weather dry. Stahl² asserted, chiefly from the results of experiments made on the transpiration of halophytes grown in an artificial salt-marsh, that the stomata of these plants are not capable of closing. Stahl used the cobalt paper test, relying chiefly on the time of coloration of the dried paper; but the careful observations of Rosenberg,³ using the same method and confirmed by means of direct microscopic examination, show conclusively that this is not the case, at least when the plants are growing in their natural habitat. Rosenberg suggested that the inactivity of the stomata observed by Stahl was due to the culture conditions. However, in the artificial salt-marsh at Dulwich I have frequently observed that the stomata of halophytes possess the power of closing, and they appear to me to be especially sensitive to air of low humidity. The stomata of *Salicornia annua* and of *Aster Tripolium* also close in darkness.⁴

So far as I have seen, the stomata of succulent plants close during the earliest stages of withering, and this appears to me to be an adaptation to conserve the water supply as far as possible during time of need. Lloyd⁵ states that in *Fouquieria splendens* and in *Verbena ciliata* 'the beginning of closure occurs somewhat later than initial wilting, and seems to be a result of water loss by the leaf as a whole. There is no adaptive closure, meaning by this a closure in anticipation of wilting.' On the other hand, Rosenberg⁶ found that when he observed the transpiration of the leaves of some halophytes (as *A. triplex*, *Cakile maritima*, *Plantago maritima*) immediately after detaching from the parent plant, a distinct drop in the rate of trans-

¹ Linsbauer: Zur physiologischen Anatomie der Epidermis und des Durchlüftungsgewebes der Bromeliaceae, 1911. Anz. Kais. Akad. Wiss. Wien, mathemat.-nat. Klasse, ix.

² Stahl, W.: Einige Versuche über Transpiration und Assimilation, 1894.

³ Rosenberg, O.: Ueber die Transpiration der Halophyten. Öfvers. af Kongl. Vetenskaps-Akad. Förhandlingar, Stockholm, 1897.

⁴ Delf, E. M.: Transpiration and Behaviour of Stomata in Halophytes, 1911.

⁵ Lloyd: The Physiology of Stomata, 1907.

⁶ Rosenberg: Ueber die Transpiration der Halophyten, 1897.

piration was to be detected by means of the cobalt paper test ; this may be fairly interpreted as due to closure of the stomata prior to wilting. Other plants were brought into the laboratory and there the test was repeated. No such slowing down of the transpiration was then observed immediately after detaching ; and microscopic examination showed that the stomata on the whole plant had closed. I have myself ascertained by direct experiment that the stomata of *Mesembryanthemum edule* closed within fifteen minutes after detaching a healthy leaf on which the stomata were initially open ; and in the case of *Aster Tripolium* and *Plantago maritima* the stomata closed in five to seven minutes after detaching a leaf. In neither of these cases could any sign of withering be detected until some time after the stomata had been observed to close. Moreover, in the case of *Mesembryanthemum edule*, the leaf is well supplied with centrally placed aqueous tissue. When such a leaf withers the cells of the aqueous tissue gradually collapse, beginning from the innermost and slowly extending to the more peripheral cells. All the cells of the aqueous tissue show signs of collapse before the palisade tissue appears to suffer at all from want of water ; and the epidermis of a detached leaf only shows wrinkling after many hours' exposure to drought, because the actual volume of the leaf is slowly diminishing. It appears to me impossible, at least in this case, to regard the closure of the stomata within the first fifteen minutes after detaching as due to 'the loss of water in the leaf as a whole' ; on the other hand, it seems probable that the closing of the stomata so promptly is, in this and probably also in many other cases, an adaptation which reduces the transpiration of the leaf to the least possible under the particular physical conditions experienced at any time.

How far the stomata of succulent plants are able to regulate transpiration is, however, a very difficult question. I am inclined to think that the limiting power of the stomata may be much greater than has been supposed. Even in the apparently closed condition of the guard cells some regulation of the size of the outer respiratory cavity may be demonstrated, as the following experiment with *Salicornia* shows.

Two healthy similar shoots of *Salicornia annua* were chosen, and the cut ends sealed with a wax mixture. Both shoots were placed under the same conditions, one being used to determine loss of water during transpiration, and the other to determine the condition of the stomata during the course of the experiment. It was observed that the stomata appeared closed even before the shoots were cut ; the guard cells, however, showed a wide rift above the closed pore. The average dimensions of the stomata and the loss due to transpiration are shown in Table IV. At the end of the first hour the shoots were removed to a more shaded place, and this probably accounts mainly for the diminution in size of the rifts, since, owing to the abundant aqueous tissue, an exposure of three hours could hardly affect

seriously the water content of the epidermal and guard cells. It will be seen that a change in dimensions of the rift of 20 per cent. was accompanied by a change of 28 per cent. in the rate of transpiration; it is suggested that the two processes are therefore closely connected.

TABLE IV.

Transpiration and Behaviour of Stomata in Salicornia annua.

<i>Loss in Weight due to Transpiration.</i>			<i>Average size of Stomata.</i>			
<i>Time.</i>	<i>Light.</i>	<i>Water Loss.</i>	<i>Guard Cells.</i>		<i>Rift.</i>	
			<i>Length.</i>	<i>Diameter.</i>	<i>Length.</i>	<i>Diameter.</i>
11.35 a.m.						
12.35 p.m.	11	0.0194 gm.	9.5	7.2	5.1	1.9
2.35 p.m.	50	0.0140 gm.	7.7	6.9	4.1	1.4
Diminution in rate of Transpiration =			Diminution per cent. =			
		28 %	6	7.7	20	20

As has already been stated, the stomata of xerophytic succulent plants are commonly depressed below the level of the epidermal cells. In many cases they are further protected by wax, as in *Euphorbia Tirukalli*,¹ where a ring-like wall of wax surrounds each stoma; by cuticular projections overarched the guard cells, as in the case of *Aristida ciliata* described by Volkens; or by subsidiary cells, as in the stomata of some of the Bromeliaceae recently described by Linsbauer, to which reference has already been made.

The stomata of epiphytes are, however, often not at all sunken or protected, as in the epiphytes described by Holtermann² from damp, shaded spots in the Ceylon forests. The stomata of *Rhizophora*, *Bruguiera*, *Aegiciras*, and other Mangroves were stated by Schimper³ to be sunken, but in nearly every case examined by Holtermann this was not found to be the case. In many species of *Atriplex* the stomata lie below chinks in the parenchymatous covering of leaves, but are not at all depressed below the level of the epidermal cells. In all the species of *Sedum* and in all the succulent halophytes (excepting two species of *Suaeda*) which I have observed, the guard cells are not at all sunken.

In many cases, especially in the leaves of tropical epiphytes, the transpiring surface is supplied by aqueous tissue interposed between itself and the assimilating cells. The aqueous tissue consists of colourless, usually parenchymatous cells filled with a watery cell-sap, which is often readily given up, both in transpiration and in supplying the assimilating tissue. As the cells of the aqueous tissue are gradually depleted of their water, the thin walls collapse, and the collapsed cells form a more or less complete protection to the cells of the mesophyll. When a further water

¹ Haberlandt, Dr. G.: Physiologische Pflanzen-Anatomie, 1896, p. 397.

² Holtermann, Dr. C.: Der Einfluss des Klimas auf den Bau der Pflanzengewebe, 1907.

³ Schimper, A. F. W.: Die indomalayische Strandflora, 1891.

supply is available, whether from root absorption or from rain or dew, the cells expand again and become again water reservoirs. In the leaves of the epiphytic *Peperomia incana* the delicate cell-walls of the aqueous tissue are strengthened at the corners, where they abut on the palisade tissue, with a horn-like substance, so that a firm framework is interposed between the mesophyll cells and the aqueous tissue when the latter collapses in dearth of water.¹ Occasionally the aqueous tissue is formed of deep, narrow, palisade-like cells, as in *Carappa moluccensis* and *Rhizophora mucronata*. Very often the amount of aqueous tissue increases in volume as the leaf grows in age, and this is accomplished by an often considerable increase in the size of the individual cells. This increase in storage capacity as the leaf attains its full size is of obvious importance in the economy of the plant.

Peripheral aqueous tissue is very characteristic of the leaves of epiphytes and of Mangroves. According to Holtermann² many epiphytic species of *Ficus* and *Peperomia* show well-developed aqueous tissue, whereas terrestrial species of the same genera may be entirely lacking in this respect. If the plant is growing in a very exposed, sunny place, the aqueous tissue will be protected on the outside from excessive water loss, as in *Ficus tomentosa*, by the formation of cuticle and hairs; but in epiphytes of damp regions, and constantly in Mangroves and plants of the Solfataras, the aqueous tissue is little protected, and at certain times may show enormous loss of water in nature.

Volgens³ has described various species of *Atriplex* with water-storing hairs, and also some desert species of *Mesembryanthemum*; to these reference has already been made.⁴ There is no doubt, as Haberlandt insists,⁵ that the presence of mucilage in the cell-sap of the aqueous tissue greatly increases its power of resistance to desiccation, even in otherwise little protected leaves, such as those of *Mesembryanthemum crystallinum*. The mucilage may be distributed throughout the whole of the aqueous tissue, as in *Agave*, or localized in special cells, as in *Rhizophora mucronata*; or it may be associated with storage tracheides, as in the leaves of *Loranthus europaeus*.

Most European succulent plants have an internal but no peripheral aqueous tissue; however, the colourless cells of the epidermis may themselves function to some extent as water reservoirs, as may be observed by actual experiment. For example, in one case observed by me, a leaf of *Aster Tripolium* was picked and at once placed in water. Owing, perhaps, to the dry air of the laboratory, both upper and lower epidermis when

¹ Haberlandt, Dr. G.: Physiologische Pflanzenanatomie, 1896, p. 347.

² Holtermann, Dr. C.: Der Einfluss des Klimas auf den Bau der Pflanzengewebe, 1907.

³ Volgens: Zur Flora der ägyptisch-arabischen Wüste, 1886.

⁴ See p. 416 in present paper.

⁵ Haberlandt, Dr. G.: Physiologische Pflanzenanatomie, 1896, p. 352.

examined next day showed much wrinkling and folding on the outside walls of all the cells except the guard cells, which were perfectly turgid, although all were closed or only narrowly open; the leaf itself did not appear at all limp to the eye or to have suffered from want of water. The whole leaf was then immersed in water, and in less than three hours had increased in weight by 13.7 per cent. The epidermis was again examined, and the wrinkling of the epidermal cells was much less apparent; about half the cells showed no wrinkling at all, and in the remaining cells the folds were clearly less numerous. Here, then, we have a case in which the epidermal cells may be partly depleted and filled again, without apparent injury, as in true aqueous tissue.

Glands are not found as a rule on succulent or semi-succulent leaves and stems. Volkens,¹ however, records the presence of glands on the somewhat fleshy leaves of *Cressa cretica*, *Reaumuria hirtella*, *Tamarix manifera*, and *Frankenia pulverulenta*, which appear to excrete salts, chiefly sodium chloride; these salts seem to have the power of condensing moisture, even from an apparently dry atmosphere, so that the leaves sometimes appear to be covered with moisture when no rain has fallen and, all around, the vegetation is dry. There is some difficulty in supposing with Volkens that the glandular tissue can so far alter in permeability as to first excrete a highly concentrated salt solution, and then absorb only pure water back again; but there appears to be no doubt that the layer of salt may be of value in preventing water loss, for these plants are found in some of the driest regions of the Egyptian-Arabian desert, and can withstand long and severe drought. If, however, the layer of salt be removed from the leaves of a cut shoot, the power of resistance to desiccation is strikingly diminished.

According to Rohlf² the same function is subserved by the glands in the leaves of some desert species of *Statice*; and Holtermann observed in the leaves of *Laguncularia racemosa*, *Acanthus ilicifolia*, and *Aegeciras racemosa* (all Mangrove plants) superficial glands which, when tested with thallium sulphate, showed an abundant salt content, and which sometimes even showed minute crystals of salt visible to the naked eye. Holtermann interprets the function of these glands as excretory, the salt being washed away by the dew, which falls heavily in those regions at night. The excretion of salt by these glands is used as an argument against Schimper's theory that salt accumulates in the leaves of halophytes to a harmful extent. Similar glands are found on the leaves of some European species of *Statice*, *Glaux*, and other halophytes; but these are scarcely succulent in habit, and little is known of the true function of the glands in these plants.

It is well known that many plants are capable of absorbing water over

¹ Quoted by Dr. A. Burgerstein : *Die Transpiration der Pflanzen*, 1907.

² Quoted by Dr. A. Burgerstein : *ibid.*

their whole surface ; but it has long been a matter of dispute how far this power is of importance to the plant in nature. The work of Wille¹ and others shows that the proportion of water thus absorbed, relative to that taken up by the roots, is mostly so small that the surface absorption can be of but little meaning biologically.

However, there is no doubt that such surface absorption may be of the utmost value ; rootless epiphytes, indeed, depend wholly on this method for their water supply, and in such cases adaptive mechanisms for collection and storage of water are often found, as, for example, the spoon-shaped leaves of some Bromeliaceae and the absorbing hairs of *Usnea tillandsioides*.

Aerial roots form additional organs of absorption in many epiphytes, especially in the epiphytic Aroids and tropical orchids. These are fleshy, greenish roots which stand out from the surface of the plant and are covered with a parchment-like layer of aqueous tissue, several cells deep. The cells of the aqueous tissue are usually thin walled, isodiametric, and lined with a delicate spiral of cellulose ; often the walls are perforated, so that when water reaches the surface it is sucked in rapidly by capillary attraction. It has even been suggested by Schimper and Goebel² that the aqueous tissue, or velamen, as it is here frequently termed, has the power to absorb water vapour and nutritive gaseous compounds, such as ammonia, from the air ; a very probable suggestion, although not yet substantiated by actual facts.

A number of other plants, however, show a considerable power of surface absorption, the value of which has been perhaps under-estimated. The papillate hairs of certain species of *Mesembryanthemum*, to which reference has already been made, are of some interest in this connexion, for they appear to have a marked power of absorption in addition to their capacity for retaining and storing water. Some cuttings of *M. edule* and *M. crystallinum* had been received by me from Cornwall, where both plants grow freely in a semi-wild state. They had been packed loosely in a cardboard box and were obviously suffering from want of water when unpacked. *M. edule* is a glabrous species with somewhat thickened cuticle and slightly sunken stomata. *M. crystallinum* has papillate leaves with little or no cuticle, and small unprotected stomata, and it therefore seemed worth while to compare their power of surface absorption. A shoot of each was chosen with about the same number of healthy uninjured leaves ; they were detached and weighed accurately after the cut end of each had been sealed up with an adhesive wax mixture. The shoots were then immersed in water, and dried and weighed at intervals. The results given in Table V show that *M. crystallinum* has an absorption from three to seven times as great as *M. edule*. Both these species live in dry, rocky places where there is a limited

¹ Burgerstein, Dr. A. : Die Transpiration der Pflanzen, p. 232.

² Haberlandt, Dr. G. : Die physiologische Pflanzenanatomie, 1896, p. 201.

water supply, and *M. crystallinum* transpires, as I have observed, at about the same rate, relative to the amount of surface, as a typical mesophytic plant, such as *Saponaria*, so that there must often be a need of water. In the above experiment the shoot of *M. crystallinum* was flaccid at first, but appeared to be quite turgid after five hours in water, and therefore, since dew often falls heavily, and lasts for longer than five hours, this plant may well be benefited by the absorptive power of the hairs. In *M. edule*, however, the absorption is so slight that dew formation could hardly be of value except in checking transpiration for the time.

TABLE V.

Absorption of Water by Transpiring Surfaces in Mesembryanthemum.

Time.	<i>Mesembryanthemum edule.</i>		<i>Mesembryanthemum crystallinum.</i>	
	<i>Absorption % of Initial Weight.</i>	<i>Absorption % per hr.</i>	<i>Absorption % of Initial Weight.</i>	<i>Absorption % per hr.</i>
5 hrs.	0.47	0.09	1.7	0.34
23 hrs.	2.7	0.11	16	0.7
3 days	10.7	0.15	27	0.38

Holtermann¹ asserts that the Mangroves of Ceylon appear to have the power of absorbing rain and dew, since the leaves were always fresh and turgid in the early morning after a rainless but dewy night, following a hot day in which they had all perceptibly flagged. However, as Burgerstein² points out, this is not necessarily due to surface absorption of the dew; it may simply be that the presence of the dew checks transpiration and so allows the water absorbed by the roots to accumulate within the plant until the tissues are again turgid. In those Mangroves and desert plants provided with salt glands the superficial absorption appears to be of real biologic importance, and is regarded by some as an adaptive mechanism for increasing the resistance of the plant to drought.

Burgerstein,³ who has made an exhaustive study of the whole question of superficial absorption of water, came to the conclusion that any part of the plant, whether heavily or slightly cuticularized, and whether provided with stomata or not, was yet capable of water absorption to some extent. However that may be, the presence of cuticle is a distinctly retarding factor, and in the absence of hydathodes or glandular hairs the surface absorption of a much cuticularized surface is practically nil. The presence of wax or bloom which makes the leaf practically unwettable is also a character which prevents any appreciable surface absorption, and those succulent plants which have bloom are not those which can absorb freely. The hairs

¹ Holtermann, Dr. C.: Der Einfluss des Klimas auf den Bau der Pflanzengewebe, 1907.

² Burgerstein, Dr. A.: Die Transpiration der Pflanzen, 1904.

³ Burgerstein, Dr. A.: Übersicht der Untersuchungen über die Wasseraufnahme der Pflanzen durch die Oberfläche der Blätter, 1891.

which clothe the surface of many Chenopodiaceous plants may be absorbing, but this has not yet been experimentally demonstrated.

I¹ have suggested that species of *Salicornia* and *Aster Tripolium*, which are very sensitive to dry air and which are subject to a variety of conditions physically, may derive real benefit from their well-marked power of surface absorption. The same suggestion was made independently by Miss A. C. Halkett,² whose experiments bear this out to some extent.

(β) The Water-storing System.

We come now to the question of the system of water-storing tissues which are essentially characteristic of succulent plants. We have already seen that many epiphytes and mangroves have a superficial storage tissue, which perhaps also affords protection to the chloroplasts from the intense sunlight; many of these also have internal water-storing tissue, so that the assimilating cells are covered both above and below by aqueous tissue, as in many species of *Peperomia*. In fleshy leaves the water-storing tissue often gradates insensibly into spongy mesophyll cells with very scattered and pale chloroplasts; it is, however, sometimes localized in thick fleshy petioles. In stems the aqueous tissue is often located in the cortex, either completely encircled by the chlorophyll-containing cells, as in *Salicornia*, or interrupting the assimilating tissue in places, as in *Salsola*, where the stem shows streaks of transparent tissue between the chlorophyllous tissue; the epidermis above the transparent streaks has no stomata. Water is also stored in tubers or corms, as in epiphytic orchids, and in the species of *Sauromatum* popularly known as 'Monarch of the East'. In these cases the plant can live for long simply on this reserve, and in the last case the whole flowering spadix and the single large leaf are produced at the expense of the corm, which shrinks greatly as development proceeds.

In many cases the aqueous tissue contains a highly acid or highly saline cell-sap, which produces a high osmotic pressure internally. This may serve to facilitate surface absorption in plants, such as *Mesembryanthemum crystallinum* and *Salicornia*, but it certainly tends to retard evaporation, for water evaporates less readily from stronger than from weaker solutions; thus Aubert³ found that in *Sedum dendroideum* the acid content increases as the young leaf becomes adult, and those leaves which had the maximum acid content had also the least transpiration. In many cases, in addition to the acid cell-sap, mucilage passages or cells occur, as in the Cactaceae, which are even more retentive of water; for example, with *Opuntia*, Aubert

¹ Delf, E. M.: Transpiration and Stomatal Behaviour in Halophytes. *New Phytologist*, 1911.

² Halkett, A. C.: Some Experiments on Absorption by the Aerial Parts of Certain Salt-marsh Plants. *New Phytologist*, 1911.

³ Aubert, E.: Turgescence et transpiration des plantes grasses. *Annales des Sciences Nat. Bot.*, 1892.

found that the rate of transpiration increased steadily from the young shoot to the old, until the quantity of mucilage and gums began to become important. From that time the transpiration steadily fell off, until in the adult segments it was almost negligible.

Aubert's work further shows that the presence of organic acids is intimately connected with the succulence of the plant; thus a number of different species of *Sedum* arranged in order of their acid content per gramme fresh weight were found also to be arranged roughly in order of their fleshiness. This is intelligible when we remember that both organic acids and the sugars which are derived from them in metabolism are osmotically active substances, and would exert a high attraction for water.

In the Cactaceae the organic acid is mostly present as salts of malic acid; in the Crassulaceae mostly as free or combined isomalic acid, together with traces of tartaric acid, whilst the species of *Mesembryanthemum* examined gave abundant oxalates together with traces of mineral acids. The observations of Wolff¹ and others show that in halophytes malic acid is present in small amount, in addition to chlorides.

It has been suggested by Diels² that it is the presence of organic acids in halophytes which prevents the harmful accumulation of salts in the aqueous tissue of those types which do not possess secretory glands. The succulent habit is then regarded as connected with the formation of organic acids in restricted respiration, rather than with the biologic necessity of reducing transpiration, in order to avoid harmful accumulation of salts brought up by the ascending sap.

This theory was based upon a series of experiments, in which it was found that if a normal halophytic plant, such as *Cakile maritima* or *Salicornia*, was kept for some time in distilled water, or in a very dilute solution of chlorides, a gradual diminution in the percentage chloride content of the plant took place. Since the plants were, as far as possible, uninjured, the whole root system having been transferred to the solution, the inference was that the chlorides had in some way interacted with the organic acids and passed out from the plant in a form not thus far detected experimentally.

Unfortunately, all the calculations made were reckoned on equal initial fresh weights, no allowance having been made for changes in water content during the course of the experiment, owing to the effect of the transference to water or salts, or owing to changes in the physical conditions affecting the rate of transpiration. In a critical account of Diels's theory, Benecke³ drew attention to these omissions, and further recorded some experiments made by himself, following Diels's method as nearly as possible, but ob-

¹ Wolff: Quoted by Burgerstein, loc. cit.

² Diels: Die Entchlörung und der Stoffwechsel der Halophyten. Pringsheim's Jahrbücher, 1906.

³ Benecke, W.: Ueber die Dielsche Lehre von der Entchlörung der Halophyten. Pringsheim's Jahrbücher, 1901.

serving the chloride content relative to the total ash content, as well as relative to the fresh weight. Benecke's figures show clearly that, although there is an apparent diminution of chloride content owing to the changes in water content of the plant, there is no change in the actual proportion of chloride present in the ash. The whole theory of diminution and disappearance of the chlorides, through the intervention of organic acids, thus stands at present unsubstantiated by facts.

Lesage¹ was the first to show clearly that it is the saline character of the habitat which appears to chiefly cause the succulent character of the leaves of halophytes. No less than ninety species found near the coast were examined, representing thirty-two families. Of these fifty-four had leaves thicker by the sea than when inland, twenty-seven were indifferent, and four were thicker inland than by the sea. Of the fifty-four which showed increase in fleshiness from the more saline position, some were oftener found inland than by the sea (and may be termed 'facultative' halophytes), such as *Solanum Dulcamara*, *Plantago Coronopus*, and *Ranunculus sceleratus*, and some were typical littoral forms, as *Beta maritima*, *Cakile maritima*, *Glau-cium luteum*, and *Arenaria peploides*; a few species, although littoral, were indifferent, as *Psamma arenaria*, *Suaeda maritima*, and *Triglochin maritimum*. With the exception of the few species mentioned, there was a distinctly greater fleshiness in the littoral than in the inland forms.

Most of these plants have no definite aqueous tissue, and their succulence is brought about by an increase in the number or size of the mesophyll cells. Thus the mesophyll cells of *Parietaria* appeared to increase in size, those of *Ranunculus sceleratus* increased in the number of layers, whilst *Beta maritima*, *Atriplex portulacoides*, and *Cakile maritima* showed increase in both number and size of the cells. Unfortunately, no mention is made of aqueous tissue as such, although the observation is made that in some cases the chloroplasts become paler and fewer in the plants grown in salty substrate. However, there is little doubt that some of these interior cells with little chlorophyll function as water-storing tissue, especially in plants with fleshy leaves, susceptible to salt content, such as *Salicornia*, *Cakile maritima*, and *Arenaria peploides*; there is little doubt, also, that this colourless water-storing tissue tends to increase in saline situations. Observations were supplemented by culture experiments with *Lepidium sativum* and other plants which could endure saline solutions, when it was found that, in general, the more concentrated the solution the more fleshy were the leaves produced.

Some experiments of Holtermann throw further light on the question of the effect of the salt content of the habitat in the Mangrove vegetation of Ceylon. A number of Mangroves (*Lumnitzera*, *Avicennia*, *Rhizophora*,

¹ Lesage, P.: Recherches expérimentales sur les modifications des feuilles chez les plantes maritimes. Rev. Gén. de Botanique, 1890.

and others) were grown in ordinary soil in the Botanic Gardens at Peradenyia, but were watered with salt solutions of varying strength. After a time the culture plants were compared with the same plants growing in their natural habitat. In nearly every case the aqueous tissue was found to be less developed than the normal in those plants which had been watered with dilute solutions, and it was more strongly developed in those which had been watered with more concentrated solutions of salts. In one instance the leaves of a swamp plant of *Avicennia officinalis* had from four to five layers of aqueous tissue, whereas leaves from a plant cultivated at Peradenyia and watered with a 5 per cent. solution of potassium chloride showed from seven to eight layers. In the case of the flora of the Solfataras, observed by both Schimper and Holtermann, the excessive amount of sulphates in the soil appears to have the same effect in favouring the formation of aqueous tissue as the chlorides in the case of the Mangrove vegetation.

Not only are succulent plants provided with a reserve of water, but very often there is a marked conservation of the water supply, the younger leaves in time of drought being kept continually turgid at the expense of the older; this is probably true of all succulents with the exception of those which, like *Salicornia*, live in very moist habitats. It is also true, although to a much less extent, of a large number of mesophytic plants.

Meschayeff, in 1882, appears to have been the first to call attention to the oecological importance of this movement of water in plants; and subsequently numerous other observations of the same kind were made. Haberlandt hung up cut shoots of *Rhizophora mucronata* without any water supply. After one day the older and yellower leaves became withered, while the remaining leaves, except the youngest, were scarcely withered.

A more careful experiment is that of Burgerstein, who chose a pot plant of *Gasteria vittata*, a plant which has opposite pairs of fleshy leaves. The pot was allowed to stand with no water in a sunny place for six weeks, at the end of which time the earth was quite dry. Six leaves on one side were now cut off and weighed, the water content of each being found separately. The plant was now well watered, so that at the end of a month all the leaves seemed to have recovered their turgidity. The six remaining leaves were then detached and weighed, their water content being calculated as before. In comparing the water content of the full and the nearly depleted leaves, the amount of depletion was greatest at the lowest leaf and fell off regularly to the uppermost, as may be seen from the figures in Table VI.

The same gradual depletion of the old leaves at the expense of the young may be demonstrated more simply by observing the shrinkage in the dimensions of the different leaves on a shoot when allowed to wither. I have made such observations with species of *Mesembryanthemum* and of *Sedum*.

TABLE VI.

Water Content in successive pairs of Leaves of Gasteria vittata.

	Water Content % of turgid leaves.	Water Content % of withering leaves.	Loss during drought.
First Pair (lowest)	86.3	78.6	7.7
Second Pair	90.3	82.8	7.5
Third „	90.8	83.7	7.1
Fourth „	91.1	84.9	6.2
Fifth „	91.3	86.0	5.3
Sixth „ (youngest)	93.4	91.8	1.6

In the case of *Mesembryanthemum edule* a shoot was chosen which had three pairs of expanded leaves and one very small pair, the leaves of which were closely appressed to each other. One leaf of each of the three pairs of expanded leaves was marked with Indian ink along the length and breadth of both upper and lower surfaces. The cross-section of one of these leaves forms an isosceles triangle, so that the marks on the lower surface were made on one flank only. The measurements were made with an accurately divided rule and a lens magnifying ten times. The shrinkage observed calculated as percentages is recorded in Table VII.

TABLE VII.

Shrinkage in Surface of Mesembryanthemum edule when withering.

		1st day. %	2nd day. %	3rd day. %	6th day. %	7th day. %
Lowest Leaf.	Upper Length	4.6	0.3	2.4	(Shrinkage had obliterated marks.)	
	Upper Surface Breadth	3.4	3.6	1.9		
	Lower Length	7.4	0	0		
	Lower Surface Breadth	3.3	0	0		
	Upper Length	0	1.1	0	5.6	2.7
	Upper Surface Breadth	1.9	0.9	0	1.2	2.2
Second Leaf.	Lower Length	1.8	0.7	0.3	4.6	1.6
	Lower Surface Breadth	0	0	0	0	5
	Upper Length	0	0	0	4.0	1.3
	Upper Surface Breadth	0	0	0	1.0	0
Third Leaf.	Lower Length	0	0	0	(marks illegible)	
	Lower Surface Breadth	0	0	0		

It may be seen that the upper leaves were entirely, and the middle pair almost entirely, protected from loss in water content during three days' exposure to warm, dry air. After the third day the lowest leaves shrivelled rapidly, turning yellow, and finally becoming mere empty shrivelled bags; during this time the second pair of leaves first began to suffer seriously,

and the third pair to a less extent. The innermost pairs of leaves grew to double their original size and remained perfectly turgid, as far as could be

seen, throughout the experiment; they were, however, too inaccessible for accurate measurement.

Detached shoot of *Salicornia*
(probably *S. ramosissima*).

Very similar results were obtained with different species of *Sedum*, but with *Salicornia* the behaviour is quite different. A shoot of *Salicornia* was marked as shown in the figure, and the distance between the marks observed as before with a lens magnifying ten times. Only the lengths were observed, for it is almost impossible to obtain an accurate estimate of the diameter of anything as soft as a flaccid *Salicornia* stem. In this plant, as will be seen from the figures in Table VIII, the younger parts suffered first from the

loss in water, and later the older internodes also showed collapse, the whole plant having much less endurance in conditions of drought than *Mesembryanthemum*.

TABLE VIII.

Shrinkage in length of Shoots of Salicornia (probably S. ramosissima) during withering.

		Region.	Loss % per 24 hours.	
			1st day	2nd day
Main Shoot	(1)	Lowest internode	0	0
	(2)	Next above	10	0
Branch	(3)	Lowest internode	0	10.2
	(4)	Next above	3.6	6.7
	(5)	" "	11.9	3.2
	(6)	" "	11.9	3.2

Pringsheim,¹ in a paper dealing with this subject, records some experiments in which the attempt is made to analyse the water output of adult leaves which are both transpiring and supplying water to the growing parts.

¹ Pringsheim, E.: Turgorregulation und Wasserbewegung in welkenden Pflanzen. Pringsheim's Jahrbücher für wiss. Bot., 1906.

In a typical experiment with *Sedum spectabile* six similar shoots were chosen, with as nearly as possible the same number of leaves. On June 20 the ten oldest leaves of three shoots were detached and weighed; no account was taken of the cut surface where the leaf had been attached, since this is unusually small in species of *Sedum*. The detached leaves were left to dry on blotting-paper, together with the remaining three shoots, the fresh weight of which was also found. On July 10 the six lowest leaves of the shoot were quite dry; the detached leaves were withered, but less so than those on the plant. The weight of each set of leaves was again taken, and the initial weight of the cut leaves was calculated in terms of an equal weight of the shoots with attached leaves. The results are shown in the following table, taken from Pringsheim's paper:

TABLE IX.

Leaves of Sedum spectabile, withering.

I. Detached Leaves.	All 10 leaves.	Lowest 6 leaves.	Upper 4 leaves.
a. Initial wt. June 20	7.92 grm.	4.29 grm.	3.71 grm.
b. Wt. July 10	5.23 "	2.74 "	2.49 "
c. Loss % fresh wt.	33.9 "	36.1 "	32.9 "
II. Attached Leaves.			
d. Wt. July 10	1.64 "	0.165 "	1.45 "
e. Loss % fresh wt.	79.5 "	96.3 "	60.9 "
f. Transport of water % fresh wt.	45.6 "	60.2 "	27 "
g. Transport % of Total Loss	57.1 "	62.5 "	46 "

From these figures Pringsheim concludes that the water loss of individual leaves on the plant is greater than when detached, and that the greater part of this water loss is due to displacement within the plant. Very similar results were obtained from experiments with the most varied type of plant, such as *Bryophyllum*, *Cotyledon*, *Mesembryanthemum*, *Tradescantia*, *Rhipsalis*, *Sambucus*, and *Vicia*.

Not less interesting are the observations made by Pringsheim on the osmotic conditions within the same plants, both normally and when withering. It was found that, with very few exceptions, the older leaves had a lower osmotic pressure than the upper; for example, in leaves of *Sedum spectabile*, the osmotic equivalent expressed in terms of a standard 10 per cent. solution of potassium nitrate was found to be—for leaves

5-5½ cm. long (oldest)	18-20 per cent.
3 " " (younger)	24-26 " "
2-2½ " " "	30 " "
1-1½ " " "	38 " "

The osmotic equivalent was thus greatest at the growing point, falling off quickly and remaining fairly constant for the adult leaves.

In a few plants no difference could be detected, as in *Rochea falcata*, where all the leaves are fleshy, and in *Phaseolus*, where the leaves are mesophytic, the youngest leaves had a lower osmotic equivalent than the older ones. In these exceptional cases, however, there appeared to be no water transport from the older leaves to the younger during withering.

Wiesner suggested that the water transport was due to the correlation between the young growing parts and the older leaves, the need of the actively growing parts forming a kind of mechanical check on the water loss of the older leaves by evaporation. Pringsheim remarks that this theory would not account for the fact that adult attached leaves transpire from the same fresh weight more strongly than similar detached leaves under the same conditions, and suggests that there is an internal regulating mechanism which adjusts the osmotic condition of the cell-sap throughout the plant, according to circumstances. In support of this theory, Pringsheim describes a number of experiments on the osmotic conditions of withering plants. Not only is there found to be what may be termed an 'osmotic gradient' in the normal plant, but this gradient is, in many cases, more or less maintained during withering; a few of Pringsheim's results are quoted in Table X.

TABLE X.

Osmotic Conditions in Withering Plants.

		<i>Fresh.</i> %	<i>After one week's</i> <i>withering.</i> %
<i>Tradescantia fluminensis</i>	Young parts	22-24	30-32
	Adult „	10-12	20
<i>Sempervivum tectorum</i>	Young „	28-30	34
	Adult „	20-22	30

However, the most striking example of turgor-regulation was seen in the case of storage organs for food reserves, such as tubers. In the potato the osmotic pressure of the growing shoot was always greater than that of the tuber itself, but fell off from day to day as the reserve was gradually depleted, and in this way only as much starch would be utilized as would be needed for growth. The mechanism of turgor-regulation as conceived by Pringsheim consists in the manufacture of osmotically active substances in the actively growing regions, thus setting up a diffusion stream upwards which, however, can last only as long as the turgidity of the cells concerned is not wholly lost.

It is probable that there may be some such regulatory mechanism within the plant, but this difficult question can hardly be regarded as wholly solved. As regards the question of the rate of transpiration of attached and detached leaves, whilst Pringsheim's figures seem indisputable for transpiration measurements reckoned on fresh weight, yet, in experiments

which I have made, the loss per unit area of the detached leaves was undoubtedly greater than that of attached similar leaves taken at the same time, under the same conditions. My experiments, however, were generally for much shorter periods of time, lasting from one to eight hours instead of several days, as did Pringsheim's. In the case of *Mesembryanthemum edule* a shoot and an adult detached leaf, both sealed at the cut end, were weighed at intervals for three weeks. Throughout that time the loss in water per unit area of the detached adult leaf was much greater than that of the shoot with which it was compared. In the other cases examined by me, where the same is true, pairs of similar shoots were chosen and the transpiration per sq. dm. of a whole shoot compared with that of the lowest leaf of the control shoot detached from its stem. In every case loss from evaporation at the cut surface was prevented by sealing over with an adhesive wax mixture. In every case the transpiration of the detached leaf per unit area was greater than that of the attached ones.

Whatever be the explanation, however, of this conservation of water in the plant, there is no doubt that it may be of great oecological value, as Pringsheim points out, not only in enabling the plant to withstand long periods of drought without injury to the growing point, but also in providing a means of vegetative reproduction; for in many cases the exhaustion of the water supply of older parts causes the death of the lower parts; the apex then continues its growth, and often roots freely, and becomes independent in some more favourable spot. This is seen in many species of *Sedum*, *Mesembryanthemum*, *Crassula*, *Rhipsalis*, *Cassytha*, and many others. The ease with which adventitious roots form in these examples, however, varies greatly. In *Sedum* one or more adventitious rootlets regularly form, even in very dry air, just above the axil of the leaf, when each leaf is about half depleted. In *M. edule* roots are formed, but much less readily, and in *M. crystallinum* often not until many weeks have passed. In mesophytic plants the advantage is less obvious, for they have less power of storing water and often none of rooting from the apex; but the greater transpiration of the younger, less protected leaves may be, at least in part, compensated by the water supply from the older ones.

(γ) The Conducting System.

There is no doubt that the means of water conduction in a plant stands in close relation to the rate of transpiration. In general, the greater the amount of transpiration the larger will be the number and size of the conducting elements in the stem and root. Jost found that by cutting off the leaves and buds of seedlings of *Phaseolus multiflorus* and other plants, the vascular bundles, and especially the water-conducting elements, remained in a rudimentary condition. He interpreted this as

a kind of self-regulation, keeping the nature of the conducting tract in relation to the particular need of the plant.¹

In the case of succulent plants we have little information as to the conducting tissue. Volkens, in his observations on plants of the Egyptian-Arabian desert, found that the conducting tissue of the shrubs and trees there was but poorly developed, and many of these would be succulent or semi-succulent plants either in stem or leaf.

The experimental observations of Cannon,² however, at the desert laboratory at Tucson, do not bear out Volkens's statement. A number of plants, including *Fouquieria splendens*, *Covillea*, and *Zizyphus*, were grown in the desert region, but were kept constantly irrigated with water for from two to four years. At the end of that time a careful comparison was made between the structure of the wood in irrigated and non-irrigated plants. It was found that in every case the irrigated plants grew much more luxuriantly and organized more woody tissue than the non-irrigated; but they formed a relatively large number of non-conducting parenchymatous elements; whereas in branches of the same diameter of the unwatered plants larger and more numerous tracheal elements were found. Cannon concluded that the desert flora in these cases is a reaction to a minimum water supply, the relative transpiration being greater in the non-irrigated plants, although the total water loss would be less.

In some epiphytes and many halophytes the aqueous tissue is provided with storage tracheides. These may be developed in connexion with the bundle system, and these usually occur as a group of isodiametric elements at the ends of the finest veins of the leaf. Often, however, storage tracheides are developed from the parenchymatous cells of the ground tissue, either singly as idioblasts, or as small groups of cells; but in each case independent of the bundle system. These storage tracheides seem to play an important part in the distribution of the water in fleshy stems and leaves. They occur always near a source of water, and are usually also in connexion with the assimilating cells, which they probably keep supplied with water. There appears to be no direct evidence that these tracheides can exercise a distributive function, but in the case of many species of *Salicornia*, Dr. E. de Fraine³ tells me that their disposition in the stem would lend support to this view. They appear to be most numerous near the periphery of the fleshiest region of each internode, and they are more numerous in the flowering than in the vegetative shoot. In *Salicornia* the storage tracheides are unligified, but they are spirally thickened with cellulose, and, according to this observer, retain their shape even when empty of water;

¹ Haberlandt, Dr. G.: *Physiologische Pflanzenanatomie*, 1896, p. 296.

² Cannon: *Water-conducting Systems of Desert Plants*. *Bot. Gaz.*, 1905.

³ Moss, de Fraine, and Salisbury: On the genus *Salicornia* (anatomical section). *Linn. Soc. Trans.* (in the press).

moreover, in some species of *Salicornia* there appears to be every transition between lignified stereides and spirally thickened unligified storage tracheides.

II. TRANSPIRATION IN RELATION TO HABITAT.

Probably the factors in the environment which most affect the transpiration of a plant are the water supply and the atmospheric conditions, although undoubtedly other climatic and edaphic influences are also concerned. We have now to consider the effect of the chief physical factors on the principal types of succulent plants.

In the truly xerophilous succulents of desert regions we have a reaction to extreme scarcity of water, to strong illumination, and to the desiccating effects of warm, dry air; adaptations are, therefore, found connected with both absorption and retention of water. The former process is facilitated by the development of deeply penetrating and often much branched root systems, and in many cases there is little doubt that the plants are for this reason almost independent of rainfall. Volken, indeed, describes shrubs in the deserts of Northern Africa which seem to thrive where there is absolutely no rainfall for eight months of the year. In some cases the root absorption seems to be supplemented in an important way by absorption of dew by means of glands on the leaves, as in the Tamaricineae, also described by this author for the same region.

It is, perhaps, on account of the efficiency of the extensive root systems, that in spite of the very limited water supply the desert plants examined by Cannon developed more conducting tissue when grown in a dry than in an irrigated place. The same explanation may apply to the statements of Prof. F. E. Lloyd that *Fouquieria splendens* and *Verbena ciliata* are characteristic of truly desert regions and yet form leaves which in structure resemble those of a slightly succulent mesophyte; here, however, there is the additional explanation that the leaves are annual and are shed just before the hottest season.

The retention of water within the plant is accomplished partly by the formation of protective structures in the epidermis, and partly by the accumulation of mucilaginous substances and salts of organic acids within the aqueous tissue.

The most frequent protective adaptations are the development of a thick cuticle, which is often covered with a coating of wax, or with finely divided wax particles, the formation of relatively few stomata, which may also be sunken below the level of the neighbouring epidermal cells, protected with depositions of wax particles or surrounded by a raised wax collar as in *Euphorbia Tirukalli*.¹ Less often the stomata are protected by hairs. In all these cases there is a certain amount of reduction of

¹ Figured in Haberlandt's *Physiologische Pflanzenanatomie*, 1896, p. 397.

transpiring surface, consequent on the adoption of the succulent habit, and in the epiphytic Bromeliaceae Linsbauer has recently found that the protective means and surface reduction seem to ensure the minimum of transpiration which could be consistent with sufficient aeration.

The experimental work of Aubert shows clearly how important is the presence of organic acids and of mucilaginous substances in the aqueous tissue of all succulent plants. There is little doubt that, owing to the high osmotic activity of these substances, the retention of water in the aqueous tissue is greatly facilitated.

The storage of water which is thus rendered possible may be of the greatest importance to desert plants, enabling them to endure long periods of drought without any evil consequences to the assimilating cells. In extreme cases, like that of *Sauromatum*, the so-called 'Monarch of the East', so much water is stored in a fleshy corm until the beginning of the dry season that the whole inflorescence and, later, the single leaf, are produced entirely at its expense. In the majority of succulent plants there is a definite displacement of water, in time of need, from the older to younger parts, and Pringsheim has shown that this is of value not only in prolonging the life of the more important tissues, but in providing a means of vegetative reproduction. In this way new shoots and buds are for long supplied with sufficient water for growth even when detached from the parent plant; and, in habitats in which germination is attended by great danger from drought, the reproduction is commonly effected by the rooting of such buds and shoots.

Much discussion has been raised over the question of the transpiration of plants of the warm, damp forest regions of the tropics, many of which are either epiphytic, as in the case of the Orchidaceae, or halophytic, as in the case of the genera collectively known as 'Mangroves'.¹

The experiments of Haberlandt² led to the conclusion that transpiration of plants in these regions is less active than in most mesophytes of middle Europe, both in rate and in total amount. The observations of Stahl, Wiesner, Burgerstein, and Giltay, however, pointed to an exactly opposite state of affairs. The explanation of these conflicting results was finally given by Holtermann, who proved that although for hours together the transpiration of these plants may be wholly suspended owing to heavy dews at night and nearly saturated misty air by day, yet for a few hours near midday, under the influence of a tropical sun, the rate of transpiration might become enormous. The plants which are exposed to these alternating extremes are provided with aqueous tissue, although to a less extent than

¹ Schimper noted the similarity in habit between epiphytes and Mangroves; in the case of *Ficus diversifolia* the same species is found growing equally well as either an epiphyte or halophyte. Holtermann: *Der Einfluss des Klimas, &c.*, p. 125.

² Quoted by Burgerstein in *Die Transpiration der Pflanzen*, 1904.

in many succulent desert types, and during the periods of rapid transpiration the aqueous tissue may become so depleted of its water that the leaf becomes perceptibly flaccid. This, indeed, frequently happens after a hot day, according to Holtermann, in the plants of the Mangrove swamps. The following morning, however, the leaves may be found erect and turgid again after a night of heavy dew, so that Holtermann suggests that an appreciable surface absorption of the dew must have taken place. On the other hand, it is possible, in the light of the experimental researches of Wille¹ and others, that root absorption persisting all through the hours of suspended transpiration would alone account for the change. A similar phenomenon may easily be seen in our British halophytes, and probably the same explanation may be found true.

The experiments of Haberlandt and Holtermann on Mangrove plants indicate that here, as in true xerophytes, there is some power of water displacement, but to a somewhat less extent than in typical desert and rock plants. I have noticed a distinct power of water displacement from old to young leaves during withering, in shoots of *Salsola Kali* and in *Mesembryanthemum edule*, and to a less extent in *Suaeda maritima*; the same power may exist in *Salicornia*, but if so it is not sufficient to prevent the young parts from withering in drought, before the older internodes appear to suffer. The displacement of water from old to younger parts in time of need is by no means limited to succulent plants; it is often to be seen in mesophytes, although here it is less obvious, and probably of little biological importance.

In the majority of halophilous and in many epiphytic plants, the transpiring surface is little protected from water loss, being usually glabrous, with little cuticle or none, and with often numerous unsunken active stomata; relative to the surface area the transpiration may often be far greater than obtains in the majority of mesophytes under the same conditions.

The question of the relation of the halophytic plant to its environment is one of much difficulty. There is no doubt, as Schimper, Lesage, Holtermann, and others have shown, that it is intimately related to the presence of chlorides in the habitat. Probably the conclusion of Warming comes nearest the truth: that, whereas some maritime plants are true halophytes and cannot thrive in the absence of chlorides, others are only halophilous and, whilst showing greater succulence in the presence of chlorides, can thrive almost equally well in their absence; such are *Aster Tripolium* and *Plantago maritima*, and numerous other examples might be given. Moreover, owing to concentration by atmospheric evaporation and to dilution by rainfall, the salt content of the soil water must always be a very variable factor, and the halophyte must, therefore, possess in an unusual degree the power of accommodation to such changes. Further evidence on this

¹ Quoted by Burgerstein, loc. cit.

point is given by some experiments of Mr. T. G. Hill.¹ Observations of the concentration of the soil water of the salt-marsh at Erquy, before and after heavy rain, showed a concentration of mixed chlorides varying from 3.3 per cent. to 0.7 per cent.; there is thus a definite dilution or 'washing out' of the salts present in the soil. Measurements of the osmotic equivalent of the root-hairs of young plants of *Salicornia* gave an average value equivalent to a 5 per cent. or 6 per cent. solution of sodium chloride when these plants had been growing in soil of which the soil water contained about 3 per cent. of chlorides. After bathing such a sod containing *Salicornia* seedlings with weaker solutions of chloride or with water, the root-hairs were found to have a correspondingly lower osmotic pressure; and, conversely, when seedlings which had acquired a lower osmotic pressure were transferred to successively stronger solutions and re-examined, the root-hairs were found to have regained a higher osmotic equivalent. There is, therefore, a definite accommodation in the cell-sap of these root-hairs to solutions of gradually increasing or gradually decreasing concentration. It would be of great interest to know how far the same property is possessed by 'halophilous' or facultative halophytes like *Aster Tripolium* or *Plantago maritima*, and by mesophytes.

It has long been known that there are some striking parallelisms between the adaptations of some halophytic and alpine plants, especially in the more succulent types. Occasionally exactly the same species are found on mountain-tops and in maritime districts far from each other, as in the case of *Dodonea viscosa*, which, according to Schimper, occurs in Java only in these two positions, and in *Plantago maritima*, which occurs in Europe, either as an alpine or littoral form.

Bonnier² has made a careful physiological analysis of the conditions affecting alpine plants. He found that the strong unshaded light in high altitudes was largely responsible for the modifications in structure found; whilst the intense cold and dry or rocky soil produced the well-known dwarf habit with long, deeply penetrating root system. The typical alpine plant, as well as the typical halophyte, shows much greater fleshiness in the assimilating organs, largely due to an increase in the depth of a palisade parenchyma; but in alpine plants this is accompanied by an actual intensification of pigmentation, so that there is a more rapid assimilation in alpine than in lowland forms, whereas in halophytes the thickening of the leaf is connected with feebler development of chlorophyll and less active assimilation, many of the internal cells of the mesophyll being probably almost entirely given up to the storage of water. In the case of alpine plants Bonnier regards the more intense pigmentation as a direct adaptation

¹ Hill, T. G.: Observations on the Osmotic Properties of the Root-hairs of Certain Salt-marsh Plants. New Phytologist, 1908.

² Bonnier, Gaston: Adaptation des plantes au climat alpin. Ann. des Sc. Nat., Bot., 1894.

which enables the whole plant to achieve its period of growth in the shortest time, the rapid assimilation compensating to some extent for the short summer. A somewhat greater transpiration value was found for alpine than for corresponding lowland forms, both relative to surface and to fresh weight ; and this in spite of the fact that on the whole there was more cuticular and hairy protection afforded to the alpine types. The greater transpiration, however, is probably due to the relatively greater number of stomata which was found to be a characteristic feature of alpine plants, and to the direct effects of increased assimilation and respiration.

Observations of Holtermann¹ on the vegetation of mountain peaks in Ceylon indicate that here also something more than mere altitude must be responsible for the characteristic modifications which were found. According to Holtermann the peculiarities associated with alpine plants only appear in Ceylon on mountain peaks over 5,000 ft. in height, but not at all in the vegetation of plateaus of an even greater altitude. The most obvious source of explanation was stated to be the absence of humus in the rocky districts of the mountain summits, although possibly other climatic factors might be concerned. If this explanation be true for the alpine vegetation of Ceylon, it is, however, scarcely applicable to that of Switzerland, and it is not borne out by the experience of horticulturalists who now succeed in growing even exclusively alpine plants in suitably prepared rockeries, the interstices of which contain usually a rich humic soil.

Aubert² attempted to compare by direct measurement the rate of transpiration relative to both the transpiring area, and to the fresh weight in succulent and mesophytic plants. The method employed was, admittedly, rough, and is open to criticism, but the general conclusion is probably trustworthy, that the Cactaceae transpire the least of any succulent plants as yet tested, and that next in order of magnitude come succulent plants of the type of the Crassulaceae and the Mesembryanthaeae, which have, themselves, a greater rate of transpiration than many sclerophytes, such as *Picea* and *Nerium*. In these latter types, however, there may be a very large collective leaf surface, so that the total water loss may be very much greater than in more succulent plants. We have seen that in halophytic, epiphytic, and alpine plants the rate of transpiration may be distinctly greater than in the average mesophyte. Such observations as I have made indicate that in our British Crassulaceae, and in those Mesembryanthaeae which have become acclimatized, the transpiration is greater relative to the surface area than in ordinary mesophytes, although the latter usually possess more numerous stomata. The transpiration relative to the initial fresh weight is, naturally, less in succulent than in mesophytic plants. The explanation of the

¹ Holtermann, Dr. C.: Der Einfluss des Klimas auf den Bau der Pflanzengewebe, 1907.

² Aubert, E.: Turgescence et transpiration des plantes grasses. Ann. des Sci. Nat., Bot., 1892.

greater transpiration in succulents is not altogether clear, but is probably connected with the need for uninterrupted gaseous exchange, by means of the stomata, to compensate for the reduced surface area.

SUMMARY.

In the course of this paper it has been shown that the chief structural peculiarities of succulent plants are connected with (1) the transpiring surface, and (2) the storage of water.

Summing up for the characteristics of the transpiring surface, we see that succulent plants show a varying amount of reduction in leaf surface, and this may or may not be accompanied by arrangements which tend to diminish transpiration. Succulent plants of dry habitat have often either much cuticle or a waxy covering; less frequently protective hairs are found. In many cases water-storing tissue is found, and often the transpiration is considerable relative to the transpiring surface; the stomata are often specially protected in plants of very dry habitats; but in many Crassulaceae, succulent Chenopodiaceae, and halophytes, as well as many epiphytes, the guard cells are unprotected, and lie on a level with the epidermal cells. Many epiphytes absorb water over their whole surface, some also obtain water by means of aerial roots, which are provided with porous water-storing peripheral tissue, forming the so-called velamen. It seems probable that halophytes and desert plants with salt glands absorb water through the hygroscopic nature of the salts excreted; and that other halophytes with a thin cuticle absorb water to a less extent by means of their leaves.

Most succulent plants are characterized by the possession of definite aqueous tissue; others have a great development of mesophyll in the leaves, and then the innermost layers tend to function as storage cells for water. The water stored may be required for long periods of drought as in all truly xerophytic succulent plants. In extreme cases, the whole plant may develop at the expense of the water stored, as in the corms of *Sauromatum*. On the other hand, the water stored may be of value in avoiding the evils of a fluctuating water supply, as in many rock plants; or it may be a provision against temporary rapid transpiration, as in the Mangrove swamps of Ceylon, and perhaps, also, our ordinary British swamp halophytes. How far the aqueous tissue can be replenished from external sources, e. g. rain or dew or standing water, must be regarded at present as an open question; but it is probable that this may at times take place. The formation of aqueous tissue seems intimately related, on the one hand, to the production of organic acids, owing to the influence of limited gaseous exchange on metabolism, and, on the other hand, to the presence of chlorides or sulphates in excess in the soil water. According to Holtermann, however, these influences alone are not sufficient to account for all the peculiari-

ties observed ; for, although many plants, such as *Salicornia*, are modified so far as to be obligate halophytes, and others, such as *Aster Tripolium*, are plastic or facultative, yet there are some plants which can endure a saline or non-saline habitat with little or no change of structure, such as *Suaeda fruticosa* and several species of *Atriplex*. In every case, however, the aqueous tissue appears to be mainly of value as a water-storage tissue, the cells of which are always depleted in time of drought before the assimilating cells lose in turgidity, and filled again when a renewed water supply is available.

Finally, we see that many of the peculiarities of succulent plants must be regarded as adaptations to environment of real importance to the plant. They may be produced during the lifetime of the individual, as in the development of additional mesophyll or storage tissue in a facultative halophyte, or they may appear as permanent characteristics, as in the case of plants which are found exclusively in saline situations. In all cases, however, the presence of aqueous tissue and the power of water storage are probably of the first importance in the economy of the individual, and enable it to support a rate of water loss which is very considerable, relative to the transpiring surface.

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