

On damp surfaces in cabin, 82° 27' N. lat. Sporidia globose, .00032 inch in diameter. In the British plant .0005; but in other respects the two are identical. "This fungus grew abundantly on damp surfaces in the cabin next to the berth-deck of the 'Alert' during the winter of 1875-76. The atmosphere during the winter was replete with sporules. Some of them must have entered the ship." Some species of *Mucor* seem also occasionally to have accompanied the *Chaetomium*.

22. *VENTURIA MYRTILLI*, Cooke, *Journ. of Bot.* Aug. 1866, tab. 50. fig. 4.

On semiputrid leaves, Discovery Bay (J. C. Hart). Probably the same thing occurred at Pnoven on *Cassiopeia tetragona*.

23. *SPHÆRELLA LINEOLATA*, De Not.—*Sphæria lineolata*, Desm. *Pl. Crypt.* no. 1263; Cooke, *l. c.* tab. 51. fig. 31.

On grass with the last. The perithecia are scattered; but the leaf is very small. Sporidia at first hyaline, uniseptate, gradually acquiring a brown tinge, at length triseptate, the articulations slightly constricted, .0013 inch long.

24. *DOTHIDEA BULLULATA*, B.

Discis parvis bullulatis ostiolis punctiformibus notatis, e basi filamentosa oriundis; sporidiis uniseptatis uniserialibus utrinque leviter attenuatis.

On leaves, Disco (H. C. Hart). Sporidia .0006 inch long, about half as much wide.

Experiments on the Nutrition of *Drosera rotundifolia*.

By FRANCIS DARWIN, M.B., F.L.S.

[Read January 17, 1878.]

THE mass of observation and experiment contained in my father's book on Insectivorous Plants is all brought to bear on the central theory of the book—the belief that the power of catching and digesting insects is advantageous to the plants, and plays an important part in their economy. If this explanation of the facts be not accepted, we find ourselves in the presence of a number of elaborate, but quite meaningless, structures and properties:—structures such as the trap of a *Dionæa* or *Utricularia*; delicate powers of discriminating between different kinds of stimuli, as in *Drosera*; and properties of forming a peptic secretion, such as that

in *Pinguicula*, *Dionæa*, *Drosera*, &c. Many observers have acceded to my father's views on this subject; but since he has given no direct proof of advantage accruing to the plant from the capture and digestion of insects, a provisional acceptance of his theory may fairly be followed by a request that such direct proof should be furnished. It was to supply this want that an experiment was set on foot several years ago by my father. Plants of *Drosera* were cultivated in plates, each of which was divided into halves by a strip of zinc plate. The plants on one side of the partition were to have been fed, the other half being kept without food, their growth &c. being compared. Unfortunately both the fed and the starved plants died, either poisoned by the zinc, or injured in some other way: in consequence of this accident the experiment failed.

The experiments here described are of precisely the same nature as those begun by my father; but profiting by his experience, I have used wooden instead of metal partitions.

It may not be without interest to show, by reference to the recent literature of the subject, that the want of some such experiments has been rather widely felt.

E. Morren, of Liège, although he considers* it beyond doubt that the leaves can absorb animal matter from the captured insects, remarks† that it ought to be experimentally established that the absorption really contributes to the nourishment of the plant.

Cramer, of Zurich, goes carefully into the question‡, and points out (p. 33) that many experienced cultivators and naturalists, such as Kurz, Munk, Regel, Schenk, Veitch, and Williams, find that *Dionæa* §, *Nepenthes*, *Sarracenia*, *Cephalotus*, and *Aldrovanda* thrive as well when starved as when supplied with insects. Cramer remarks that the question ought to be experimentally decided.

* 'La Digestion végétale,' 1876.

† 'La Théorie des Plantes carnivores,' Liège, 1876.

‡ 'Insectfressenden Pflanzen,' 1876.

§ I have found it a difficult task to starve *Dionæa*-plants properly. I have at the present time 30 plants growing under a closely-gauzed case. 15 are being starved, the others fed. On looking over the plants I have frequently found woodlice caught by the *starved* leaves. I suppose they got in with the moss used to pack the pots, or in some other way. An unpractised eye would easily mistake a closed leaf containing a small insect for a young unopened leaf.

Munk (as quoted by Cramer) remarks that the catching and driving away of insects may be of service to the plant; but in the digestion he can only see an injury. He suggests that the peculiarity of the digestive process being both pathological and physiological, seems to agree with the fact that in spite of a highly differentiated organism, *Dionæa* appears to be approaching extinction.

Cramer quotes (p. 34) Schenk, who, like Munk, finds it impossible to believe that a digestive process that kills the functioning organ can be serviceable to its possessor. As Cramer remarks, these pathological results are no doubt in some cases the result of overfeeding. Schenk (quoted by Cramer, p. 34) appears to doubt the digestive powers of *Aldrovanda*, because he found it flourish for a long time in Knop's nutritive solution. Cohn* remarks that Schenk's results only prove that the leaves of *Aldrovanda* can absorb nitrogenous (though not animalized) fluids; and he adds that his own experiments prove that these plants do not flourish in pure water with no insects.

Duval Jouve† observes that the fact of digestion causing the death of *Dionæa* (Canby), and the results of Lawson Tait's experiments (Nature, July 29, 1875), make him extremely doubtful as to the process being any advantage to the plant.

Casimir de Candolle‡ made a comparative experiment on four *Dionæa* plants, two of which were fed and two starved. They were carefully watched for six weeks, and no difference was noticed between the two sets. M. de Candolle concludes that animal food is not necessary to the plants. He is careful to point out that the number of plants experimented on is too few to draw any certain conclusions therefrom.

Göppert§ remarks that "the so-called carnivorous plants do not absolutely require animal food for their support, and can well dispense with it."

Ch. Cavallier addressed the question to a number of distinguished observers as to their opinion on the subject of vegetable digestion. A few of the published replies are here given||.

* Thätigkeit der botan. Section der schles. Gesellsch. für vaterl. Cultur, 1876, p. 113.

† Causerie Botanique, Aug. 1876.

‡ Archives des Sciences phys. et nat. Genève, April 1876, p. 3.

§ Thätigkeit der botan. Section der schles. Gesellsch. 1876, p. 101.

|| Annales de la Soc. d'Horticulture de l'Hérault, March and April 1876, p. 56.

Faivre, of Lyons, points out that the problem is at present rather stated than solved.

Ch. Naudin considers that there is far from being any proof that the substances dissolved by the secretion of the leaves are absorbed or assimilated. He states that digestion is assumed to occur without proof; and it is a matter of doubt whether this proof will ever be obtained.

P. Duchartre finds it impossible to admit that the capture of insects serves directly for the nourishment of the plant, because it is contrary to our present knowledge that leaves should be able to absorb liquids. He points out that no one has demonstrated that animal food supplied to the leaves produces any appreciable effect on the plant.

Parlatore, of Florence, admits that the captured insects are dissolved but not absorbed; he remarks that such absorption has not been proved to take place.

Béchamp, who goes into the question from the point of view of a chemist, considers that "scientifiquement c'est faire un épouvantable cercle vicieux que de supposer des végétaux carnivores." Because animals depend ultimately on vegetables for food, therefore no vegetables can be supported by animals. M. Béchamp concludes: "L'idée de plantes carnivores est donc le produit d'une illusion le renversement des démonstrations les mieux fondées de la science."

The most recent remarks which I have been able to find on this subject are in a highly interesting memoir by W. Pfeffer, of Basel*. He considers it to be doubtful whether the capture of insects is any definite advantage to the plants in a state of nature. He remarks that he has himself observed the thriving growth from winter-buds of *Drosera*-plants to which no animal food is given.

In the periodical above quoted (p. 112) are some valuable remarks by Cohn. He points out that insectivorous plants are often cultivated in rich soil, whereas in nature they grow in poor peaty land. Therefore under culture they obtain the nitrogen by their roots, for which in a state of nature they depend on their leaves. Pfeffer, *loc. cit.* p. 988, insists that the smallness of the roots of many insect-catching plants is not a fair argument in favour of the view that the chief nitrogenous supply comes from

* Landwirthschaftliche Jahrbücher, 1877, p. 986.

the leaves, because many ordinary marsh-plants have equally small roots. Cohn concludes that the fact of *Dionæa*, *Sarracenia*, or *Nepenthes* thriving under culture when deprived of animal food is in no way contradictory to the belief that the leaves can digest nitrogenous materials.

My experiments were conducted in the following manner. The *Drosera* plants were obtained from a neighbouring common on June 11, 1877, and were planted in moss in six ordinary soup-plates. The plates were placed in two rows on a wood tray having a raised border all round, and were covered by a wooden frame 1 foot (about 30 centims.) in height, over which gauze netting (with a mesh of 1·4 millim. diameter) was stretched. This gauze was similar to that used by my father in his crossing experiments, and known to be effective in excluding insects. The frame lifted off and on like a bell-glass, and fitted close within the rim of the tray. Hardly any insects penetrated into the case; but I did not particularly attend to this point, because any insects caught by the starved plants could only render my results less striking, but could introduce no error. The whole apparatus stood near the light in a grape-house where no artificial heat was applied. The shade produced by the vine-branches and by the gauze, appeared to suit the plants, as they thrived wonderfully. The plants and the moss in which they grew were kept very moist; and by frequently pouring out the water in the plates and adding a fresh supply, the water was constantly renewed.

Owing to a delay in beginning the experiment, the plants were well grown when collected. The results might have been more striking if the experiment could have been commenced with younger plants; but as it was, I had at least the advantage of knowing that the plants were perfectly healthy. Each plate was divided by eye into two halves separated from each other by a thin piece of wood hardly reaching above the surface of the moss. That half of each plate which appeared *least* flourishing was selected to be the "fed" side, the opposite side being labelled "starved"*. The plants grew so close together that it was difficult to count them accurately; but the following Table gives the numbers as counted roughly.

* For the sake of clearness in my notes &c., I used the word "starved" in place of the more correct "unfed."

TABLE I.

Distinguishing label on plate.	Number of plants.	
	Starved.	Fed.
I.	16	14
II.	12	13
III.	19	14
IV.	17	13
V.	13	15
VI.	14	17
Total.....	91	86

The number of plants on the fed side could not have differed from that on the starved side materially; for on Sept. 3 the contents of three of plates (I., III., and VI.) were floated in water and the plants carefully picked out and counted, and the starved plants were 82, the fed 84 in number, including a number of minute dwarf-like offsets.

The plants were arranged with the partition-line of each pointing to the light, so that neither side received more light than the other; and the arrangement of the plates was systematically varied, so as to prevent any one profiting from light or air more than its fellows. The plates were placed under the net on June 12th, and the leaves fed on that and the following day. Owing to my absence, they were not again fed till July 5th, after which date the following Table gives the days of feeding.

TABLE II.

Days on which plates I., II., and III. were fed.	Days on which plates IV., V., and VI. were fed.
July 9	July 13
„ 14	„ 18
„ 22	„ 21
„ 25	„ 27
„ 31	Aug. 3
Aug. 4	„ 13
„ 17	„ 25
„ 25	

II., IV., and V. were fed Aug. 8; I., III., and VI. Aug. 9.

The feeding was carried out as follows:—Roast meat was cut into thin slices across the grain, and the fibre teased and cut into fragments so minute that fifteen weighed, when damp, only 2 centigrams: each is therefore 1.3 milligram, or $\frac{1}{75}$ grain; and sometimes smaller pieces were used. These small pieces of meat were, on the fed side of the plates, placed on every leaf which had secretion on the glands. I found it best to place two or three of the smallest pieces each on a separate tentacle. On several occasions I attempted to increase the size of the morsels, but was forced to return to the smaller size on finding the meat covered with mould instead of being digested. When such mouldy leaves were noticed, they were usually removed, lest the meat should be washed off and putrefy among the roots of the plants, thus vitiating the experiments. In the tedious process of feeding a number of plants I occasionally dropped a morsel of meat among the moss; the infinitesimal error arising from these accidents would be counteracted by the frequent renewal of the water in the plates.

The first difference noticed between the fed and starved halves of the plates was on July 17th, when the fed side, viewed as a whole, was clearly greener than the starved half. The difference was quite distinct in all six plates, as both my father and myself observed. The tentacles on the starved side were also of a redder colour than those of the fed plants.

The increase in the amount of chlorophyll in the fed plants thus indicated is an interesting fact; and it agrees with the result of the final comparison of dry weights, which proves that a much greater quantity of cellulose is manufactured by the fed than by the starved plants. An increase of chlorophyll is associated with an increased assimilation of carbonic acid; and this permits the production of a larger quantity of cellulose. An average leaf from the fed and from the starved side were examined on July 18th*, when the difference was most marked, the fed leaves being clearly distinguishable outwardly by their dark purple hue, and microscopically by large and numerous chlorophyll grains crowded with starch.

Unfortunately no more leaves were examined at this date.

* The chlorophyll was removed by alcohol, and the sections then treated with dilute acetic acid, washed, treated with iodine solution, washed again, and mounted in glycerine.

When, on Aug. 16, 17 and 21, leaves were examined in the same way, they did not show any striking difference in the amount of starch. This may be accounted for by migration of starch to the root-stocks and flower-stems having begun. Since, however, the starch represents the surplus of assimilated matter which has not been converted into cellulose, is it not possible that in spite of great activity of the chlorophyll-function there might be no accumulation of starch because of great formation of cellulose? The final results of the experiment prove conclusively that far more carbohydrates were formed by the fed plants; therefore it is almost certain that the first results obtained (July 18th) represent the true state of the case. The body of the chlorophyll grain being protoplasmic, it is obvious that an increased supply of nitrogen will favour the multiplication of chlorophyll and increase the starch-producing power of the plant. Hence the well-known effect of manure in increasing the yield of starch in many seeds, roots, &c. Fraustadt* states that the starch in *Dionæa* "diminishes with absorption of organic matter by the leaves." This result may be perhaps attributed to over-feeding.

The following Table shows that absorption of nitrogenous food had by Aug. 7 produced a most decided effect.

TABLE III.

Number of Flower-stems on each side in the six plates (Aug. 7).

Plate.	Starved.	Fed.
I.	16	22
II.	17	28
III.	26	32
IV.	19	25
V.	20	30
VI.	18	36
Total	116	173

or in the proportion of 100 : 149·1.

It will be seen that in every plate there are more flower-stems on the fed side. The above stems bore mostly ripening capsules; but as the fed plants seemed to have more actual flower-bearing stems, the following Table was made on August 8.

* 'Anatomie der vegetativen Organe von *Dionæa muscipula*,' Inaugural Dissertation, Breslau, 1876, p. 33.

TABLE IV.

Number of Stems which bear at least one flower (Aug. 8).

Plate.	Starved.	Fed.
I.	0	5
II.	2	10
III.	7	1
IV.	4	7
V.	4	4
VI.	2	7
Total	19	34

or in the proportion of 100:178.9.

Here the difference does not run quite uniformly through the six plates.

The following Table gives the number of healthy leaves on the starved and fed sides of three of the six plates. The healthiness was determined by the presence of secretion on the glands. As it was impossible to disturb the plants, this counting could not be very accurate.

TABLE V.

Number of Healthy Leaves.

Plate.	Starved.	Fed.
IV.	48	67
V.	78	92
VI.	61	97
Total.....	187	256

Or as 100:136.9.

At the same time * the diameter of 45 fed and 45 starved leaves taken at random were measured. As the leaves could not be removed, the measurements were rough; the diameters, exclusive of tentacles, were taken with a pair of compasses and pricked along a line, which was afterwards measured with a millimetre-scale. Forty-five starved leaves gave a total of 301 millims., the corresponding total for 45 fed leaves being 323 millims.; the proportion between the average diameters is therefore 100:108.9.

On Aug. 8th the flower-stems of the fed plants were noticed to be clearly redder than those of the starved plants. This fact

* The dates of these observations and of those in Table V. were omitted. They were all made about the middle of August.

tallies with an unrecorded impression that the fed flower-stems were previously much greener than the starved plants.

At the end of August the capsules were mostly ripe; and as there was the danger of loss of seeds by the bursting of capsules, the flower-stems from all six plates were cut on August 31 and September 1st. Thirty capsules were taken by chance from the fed and the same number from the starved stems. When dry, the capsules were opened and their seeds carefully counted under a dissecting-microscope. The stems were set aside to dry, and were then measured, weighed, &c., as shown in the following Tables.

TABLE VI.

A.		B.
The numbers, heights, and weights of the starved and fed plants.		Proportion between the numbers in the starved and fed columns of A; "starved" being taken = 100.
Number of plants in plates I., III., and VI., <i>roughly</i> counted (June 12th).		Starved. Fed.
Starved. 49	Fed. 45	100 : 91.6
Number of plants (including minute offsets) accurately counted, Sept. 3rd.		
82	84	100 : 101.2
Total weight of 81 fed and 83 starved plants without flower-stems. Dried at 80°-90° C.		
gram. 1.176	gram. 1.429	100 : 121.5
After gathering and washing the plants, they were preserved in spirit with a view to examining the root-stocks to compare the amount of starch; this was, however, found impracticable. The alcohol which had contained the fed plants was much more discoloured, showing that they contained more chlorophyll. I intended to evaporate the alcohol and add the weight of the residue to the dry weight of the plants. This, however, failed, owing to an accident with the water-bath.		

TABLE VII.

A.		B.	
Total number of stems (including those bearing flowers as well as those bearing capsules) gathered from all the plates.		Proportion between the two columns of A; starved being taken = 100.	
Starved. 117 (including 2 flowers).	Fed. 193 (including 9 flowers).	Starved. 100	Fed. : 164.9
Sum of the heights of 115 starved and 184 fed stems (excluding flower-bearing stems).			
millims. 16835	millims. 26918	100	: 159.9
Average height of the above 115 starved and 184 fed stems.			
millims. 146.4	millims. 146.3	100	: 99.9
Total weight of 116 starved and 191 fed stems (including both those bearing flowers and those bearing capsules).*			
gram. 1.91	gram. 4.43	100	: 231.9
Average weight per stem.			
gram. .01646	gram. .023193	100	: 141.3
<i>Note.</i>—The stems which bore only flowers were not included in the measuring because they were not full-grown; they were included in the weighing because it was not worth while going over the whole set of stems to exclude them. * The numbers in the first compartment are 117, 193, because 2 plants used for microscopic examination are here counted.			

TABLE VIII.

A.		B.	
Total number of capsules borne by 115 starved and 184 fed stems (from all the plates).		Proportion between the two columns of A; starved being taken =100.	
Starved. 756	Fed. 1471	Starved. 100	Fed. 194.4
Average number of capsules per stem.			
6.57	7.99	100	: 121.6
Total weight of 30 starved and 30 fed capsules.			
gram. .10	gram. .13	100	: 130
Total number of seeds contained by 29 starved and 29 fed capsules.			
2640	3239	100	: 122.7
Average number of seeds per capsule.			
91	111.7	100	: 122.7

Among the starved capsules the minimum number of seeds was 44, maximum 129; the minimum for fed capsules was 52, the maximum 168. One starved capsule contained only 20 seeds, and was therefore not included; one fed capsule was lost; so that the seeds of same number of capsules of each kind were counted.

In calculating the average weight of a seed &c. in the following Table the produce of only 20 fed capsules could be employed, as the counted seeds of 9 fed capsules were thrown away before it occurred to me to weigh them.

It will be seen from the Tables that the difference between the fed and starved plants was investigated in a variety of ways, and that in every particular the fed show a marked

TABLE IX.

A.		B.	
Weight of 2640 starved and 1578 fed seeds.		Proportion between two columns of A; starved being taken = 100.	
Starved. mgrs. 25.5	Fed. mgrs. 24.0	Starved.	Fed.
Average weight of each seed.			
mgr. .00966	mgr. .0152	100	: 157.36
Total calculated number of seeds yielded by the plants in all the plates.			
68,040	164,296	100	: 241.5
Total calculated weight of seeds yielded by the plants in all the plates.			
gm. .6572	grms. 2.4956	100	: 379.7

advantage. It is true that the *average* height of the stems is almost exactly equal (starved : fed :: 100 : 99.9). But if the average height of stem *per plant* had been calculated, it would have been about 100 : 159.9, which is the proportion between the sum of the heights of all the starved and all the fed plants. Another interesting fact is that, although the number and height of the stems and the number of the seeds of the fed plants considerably exceed the corresponding numbers in the "starved" column, yet the *weights* of the stems and the *weights* of the seeds on the fed side exceed the corresponding weights in the starved columns in a still higher ratio. This is important, because increased weight is a better proof than an increase in numbers or size of increased assimilation.

If we compare Table III. with Table VII., we find that on Aug. 7 the starved flower-stems numbered 116, the fed ones 173; on Sept. 1st the starved stems were 117, while the fed ones numbered 193.

Thus the fed plants had in 24 days produced 20 new flower-stems, while the number of the starved ones was only increased by 1. This fact tallies with the results of Tables III. and IV., which show that the fed plants continue to flower longer—about one fifth of the fed stems having flowers, while one sixth only of the starved ones were in the same state.

It will be seen in Table VI. that on comparing the plants from which the flower-stems had been gathered, no very striking difference is found to exist between the fed and the starved plants; while in all that relates to reproduction of the species the difference is most striking, especially when the corresponding *weights* are compared. Thus, taking the weights of the plants without flower-stems, we find the proportion between starved and fed to be 100:121·5, whereas the weights of the total amounts of seed produced are in the ratio 100:379·7.

It would seem from these results that the great advantage accruing to carnivorous plants from a supply of nitrogenous food to the leaves is the power of producing a vastly superior yield of seeds. This will no doubt partly explain the fact which has been a stumbling-block to many, that insectivorous plants seem to thrive without animal food; although, as I have shown, the fed plants are in reality markedly superior in general appearance. I venture to think that the above experiments prove beyond question that the supply of meat to *Drosera* is of signal advantage to the plants. There can be no doubt that both *Drosera* and other insectivorous plants profit in an analogous manner from the capture of insects in a state of nature.

In conclusion, I may mention that there are three plates of *Drosera* of which the flower-stalks only were gathered, and which are allowed to rest during the winter. It will be very interesting to observe the relative numbers and size of the plants which spring up on the fed and starved sides of the partitions. As the plants are now being forced in the hothouse, I shall probably be able to add an Appendix to the present paper stating their results.

APPENDIX*. April 5th, 1878.

As above stated, three plates were (after the removal of the flower-stalks) allowed to rest during the winter in order to test the relative amounts of reserve material laid up by the starved

* See also an additional memorandum *postea*.

and fed plants. The plates were placed in the hothouse; and by the middle of January, when the fresh leaves began to appear, it was evident that more plants were springing up on the fed side of the partition. The plates were then covered with the gauze netting, and both sets of plants remained without food in the hothouse.

On April 3rd all the plants were carefully picked out from the moss and thoroughly cleansed from adhering fragments; they were then counted, dried in a water-bath, and weighed. The fed and starved plants*, when freshly gathered and before being dried, were pressed together each into a separate handful; the far greater mass of fed plants was very evidently seen in this way. During the processes of counting and cleansing the plants, I was struck by the fact that the fed plants had a decidedly greater amount of root-stock.

The following Table gives the results of counting and weighing the plants.

TABLE X.

	Actual numbers and weights.		Proportion between starved and fed.	
	Starved.	Fed.	Starved.	Fed.
Number of plants	89	105	100	118.0
Total weight	grm. .206	grm. .518	100	251.6
Average weight per plant ...	.0023	.0049	100	213.0

It will be seen that there is only a small difference (18 per cent.) between the *number* of starved and fed plants; a large number of very minute offsets were found on both sides, and were all counted as separate plants. Judging either by the total weight of plants produced or by the average weight per plant, there can be no doubt of the great advantage accruing to the fed plants. It is a striking fact that in spite of the relatively enormous quantity of flower-stalk and seed produced in the summer by the fed plants, they were still able to lay by a far greater store of reserve material than their starved competitors.

Finally, it may be pointed out that this advantage of the fed *Drosera* plants is one which would escape the notice of a casual observer.

* That is, the plants which sprang from the fed and starved sides of the partition.