On the Development of Arum maculatum from the Seed.

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RINA SCOTT AND ETHEL SARGANT.

With Plate XXV.

plants anywhere in the neighbourhood. Instow, in Devonshire. Most of the plants had but one small ovate-shaped leaf above ground. There were no mature N April, 1895, a large patch of Arum maculatum was noticed by one of us growing on an open common at

dead tubers of previous years in most cases, though the distinct from its fellows. One could trace at least two seedlings, though not very young, but each plant was quite plants as yet had not produced the characteristic sagittate On digging some of these up, it was clear that they were

under what conditions the plant is reproduced by seeds and to study the germination of the seed and generally to test Arum-leaf It seemed worth while to collect some Arum-fruits, in order

a large number of plantlets with ovate leaves are always under what by vegetative budding. found. If a clump be dug up, most of these will be found Fig. 10 A), while a few are true seedlings. to arise by vegetative budding from the mature tuber (see Amongst the clumps of mature plants with sagittate leaves

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maculatum from the germination of the seed onward. forms which suggested the study of the life-history of Arum It was the contrast between the young and the mature

presence of raphides 2 (see p. 404). the berries. The disagreeable taste is principally due to the taste, there seems no reason why birds should not also eat and as the tuber is equally pungent and disagreeable to the scratches out and eats the tubers of Arums from dry banks, his Natural History of Selborne¹, mentions that the thrush that birds do not touch them. However, Gilbert White, in these berries is much needed, as many country people say two of these in half an hour. Further evidence of birds eating a pair of chaffinches were seen to clear off the berries from spadices of ripe fruits were watched, and on one occasion In July of the same year the mature plants with their

common at a long distance from the parent plants. the seeds could have been deposited on the gorse-covered If birds often eat these berries, it will be easy to see how

preserved in spirit. and young seedlings in their various stages of germination germinated readily. The earth was disturbed at intervals, seeds sown in flower-pots, as soon as ripe in July. They Fruits were collected from several ripe spadices, and the

of a young plant produced by vegetative budding from the itself, which at this stage is difficult to distinguish from a leaf seasons' growth, and in the third only one ovate leaf shows as nothing is to be seen above ground during the first two is no wonder that the seedling plants have been little noticed, The growth of the young plants is extraordinarily slow; it

length of the underground part of the petiole, which in a The easiest way of distinguishing them is, perhaps, by the

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vegetatively produced plant is as long as the distance from petiole is very material. deep, the difference in length between this and the seedling as the tuber of the mature plant is situated from ro-16 cms. the upper part of the tuber to the surface of the ground, and

extent independent of reproducing itself by seeds. produced vegetatively, for the Arum is a plant in which the individual becomes very well established, and is to a great In a favourable habitat the majority of the new plants are

of the germination of the seed. It will now be necessary to give a more detailed account

intervals of a month or less for four seasons. slow and laborious, as the material had to be collected at The work in this part of the subject has been necessarily

and radicle (see Fig. 1). Even at this stage, reached in emerges from the seed-coats, carrying with it the plumule form the tuber, and is packed with food-material. January, the hypocotyl below the plumule is enlarged to The seed first swells considerably, then the cotyledon

quite rudimentary, and a growing point. the hollow cylindrical cotyledon, consists of two leaves, one The stem-bud, which is situated on the tuber and within

appeared, and the bud now contains all the leaves, which will reach maturity during the third season. doubled its diameter; within the stem-bud a new leaf has radicle and cotyledon have elongated, and the tuber has In the next stage, represented in Fig. 3, April, 1896, both

will not be fully developed until the fourth season, appears. In Fig. 4, May, 1896, a rudiment of a fourth leaf, which

seed-coats with it, has been detached from the tuber, leaving disappears. Shortly before this the cotyledon, carrying the the formation of periderm 1. the stem-bud exposed. This process is brought about by In Fig. 5, June, 1896, the radicle shrivels and soon entirely

Up to the stage shown in Fig 4 the tuber is covered by

² Stahl, Pflanzen und Schnecken, Jena, 1888, p. 85,
³ The 'second season' in this paper corresponds to the first season of Rimbach.
In England the seeds ripen in July, and germinate in the autumn; whereas in the do not germinate till the spring. colder climate of Germany the seeds do not ripen till September, and consequently

¹ Cf. Parkin, On some points in the Histology of Monocotyledons, Ann. of Pot.

cells which cut right across the parenchymatous tissues of seedlings no doubt a greater number of cell-layers is formed. formations are connected by one or two layers of peridermof the zone in which the cotyledon is inserted. These two near the middle of the tuber, and two or three on either side the cotyledon, just where it is inserted on the tuber. In older drawn in Fig. 4 show five or six layers of periderm-cells the layer of cells immediately below the epidermis of both of the first leaf. The formation of periderm begins in of the inner cotyledonary surface and with the epidermis and the epidermis which covers it is continuous with that part of the tuber is enclosed within the cylindrical cotyledon, ceases abruptly where the primary root begins. The upper is continuous with the outer epidermis of the cotyledon, and a smooth white epidermis. It must be remembered that the into two regions. The epidermis covering the lower part insertion of the cotyledon divides the surface of the tuber Transverse sections through such a tuber as that

discarded cotyledon and seed-coats, which are left to rot into the ground, and in this way is at last freed from its measurements show that the tuber actually sinks deeper of the roots up, rather than to pull down the tuber. But ment the effect of the contraction would be to draw the tip in the ground. It is clear that without some point of attachroots at this stage, by which, no doubt, they are firmly fixed generally two, are contractile 1 (see Fig. 8). We found rootthe upper surface of the tuber (Fig. 6). new roots are sent out (from four to six in number) from hairs produced in clusters near the tips of the contractile to dig them up without shifting them. In the summer some time, though organically separated. It is often possible The two parts often remain in contact with one another for Some of these,

The tubers when last examined in May (Fig. 4) were only The result of the contraction of the rootlets is very startling.

Oliver, Journal of the Royal Horticultural Soc., April, 1898, p. 493. 1 Rimbach, Berichte der Deutsch. Bot. Gesell., April, 1897; and Prof. F. W

> about 2 cms. below the surface. On turning up the soil in October for new specimens, none were to be found, and that the missing tubers were discovered (Fig. 6). Probably it was not until the soil had been turned up almost 7 cms. and in a week will regain its normal depth. planted near the surface, it will send out new contractile roots, to increase the effect of the pull. If a young tuber be reunder natural conditions, and this may perhaps have tended the soil in the flower-pot was looser than it would have been

at the various times of year. by learning the exact depth at which they are to be found stage in nature, even when in the winter resting-condition, With practice it is quite easy to find seedlings in any

process has up to this time been carried on underground, and no chlorophyll has been formed. This is the end of the second season's growth; the whole

to grow in size until June, when next year's tuber is formed. scale-leaves, appears above ground (Fig. 7); the tuber continues In the following spring the first ovate leaf, with its two

to horizontal. ground, this time shifting its position as a rule from vertical leaf withers and the tuber is drawn still deeper into the New roots now arise, some of which are contractile. The

sheathing petiole of the innermost leaf (Fig. 9). and two scale-leaves, the inflorescence being enclosed in the flowering plant (Fig. 10) generally bears three sagittate leaves later, that the first sagittate leaves are found. The mature It is not, at any rate, until the fourth season, and generally

in addition to the advantage of procuring its food-stuff ready does, from the lower surface of the mature tuber (Fig. 10 A). that a vegetatively produced plant arising, as it generally eaten up by thrushes or scratched up by animals, and also in the ground. In this way it eliminates the risk of being duced from seed, in starting from the first at its normal depth made, has a further very great advantage over the plant prosaves itself a large amount of unnecessary expenditure of It will be seen from this description of the seedling-plant,

rarely flowers before the seventh year. flowers much younger than that produced from seed, which purposes. The result is that the vegetatively produced plant energy in the yearly production of contractile roots for burying

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below the insertion of the cotyledon. bend inwards to join the central cylinder for some distance axis of the plumule, for the cotyledonary traces do not to the stem. Moreover, the greater part of it represents the and it may therefore be considered as belonging entirely not show complete root-structure until we reach its base, so far anticipate our results as to say that the tuber does of the bundles in the tuber has been worked out, but we may is no external mark to divide the plumule from the hypocotyl. stem alone has been enlarged or part of the root as well These questions will of course be settled when the course And in that part of the tuber which represents the stem there main axis, but we cannot tell from inspection whether the however, be true of a seedling which has just germinated represents the stem-axis of the previous year. This cannot describing the mature plant, has rightly stated that its tuber of the tuber, or the way in which the cotyledon is detached maculatum would be incomplete without some examination The tuber of that drawn in Fig. 2 clearly forms part of the from it at the proper age (cf. Figs. 4 and 5). Irmisch 1, in for instance, are insufficient to determine either the homology phology must otherwise remain obscure. External characters, of their anatomy. Certain points in their external mor-Any account of the curious second-year seedlings of Arum

of the tuber. The cells which contain them are larger than the are abundant in cotyledon, stem-leaves, and in the periphery The raphides which give the juice of Arum its acrid quality²

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panying the vascular bundles. presence of tannin. We have not found tannin sacs accomwith salts of iron their contents become black, showing the needle-shaped crystals. Thick-walled secretory sacs are also surrounding cells, and are nearly filled by dense masses of Occasionally they even occur in the epidermis. On treatment found in the tissues of the cotyledon and of the older leaves

of third or fourth year plants show these peculiarities most much crushed and strained 1. Sections from the ribbed roots of the whole root, but the cells of the outer cortex are very plainly. section is in no way distorted by the consequent contraction cortex. The appearance of the central cylinder in transverse mention a third point in which the anatomical characters of for the radial elongation of the cells belonging to the inner contractile roots of older specimens (Fig. 8) are remarkable these seedlings throw light on their external form. The Before passing on to another part of the subject, we may

from two points of view, which we will consider separately. study of this system is interesting in itself, and of importance referred briefly to their vascular system. But the detailed anatomy of Arum seedlings which serve to complete our knowledge of their external form. For this purpose we have Hitherto we have dealt only with those points in the

girdle at each node. This peculiarity is found in many complications render the task impossible in this case. All which possesses internodes of moderate length. Two other through the cortex to enter the central cylinder at one of the case even with the leaf-traces which are passing downwards the tuber anastomose freely with each other. This is the genera of the Aroideae 2. But besides this, all the bundles in the bundles of the central cylinder form a continuous vascular follow the vascular system in a shortened stem than in one cannot be deciphered. It is always much more difficult to The course of the bundles in the mature tuber of Arum

Berlin, 1850, p. 164. ¹ Irmisch, Zur Morphologie der monokot. Knollen- und Zwiebelgewächse,

² Stahl, Pflanzen und Schnecken, Jena, 1888, p. 85.

² De Bary, Comp. Anat, Eng. ed., pp. 268-269.

lower nodes. Thus a complicated network is formed in which no ground plan can be recognized.

The formation of a vascular girdle at each node is indicated even in the youngest seedlings we possess (Fig. 1). But the bundles which unite these are not completely fused with each other, and can be distinguished throughout their course. The tendency to anastomose is also shown very early. We have found an irregular lateral anastomosis in a seedling no older than that drawn in Fig. 4. No great complications have yet arisen from this cause however, and therefore the course of the leaf-traces can be clearly followed from their entrance into the tuber until they join the central cylinder, as well as the disposition of the bundles in the cylinder itself.

The transition from stem to root in the hypocotyl has been described in very few Monocotyledons. In these plants it takes place as a rule with great abruptness, and it is hardly possible to prepare a series of transverse sections from which the course of the bundles in so short a region can be accurately determined, without the aid of a microtome. In his elaborate researches on the anatomy of this region in Vascular Plants, M. Gérard states that his choice of Monocotyledonous species was much limited by the necessity of using those only which possess a moderately long hypocotyl. In fact, he described but nine species, nor has much been done in this direction since the publication of his paper in 1881. The anatomy of the hypocotyl in any Monocotyledon is therefore worth investigation.

Course of the Bundles in the Stem

At the end of the first year, the three leaves which will come to maturity in the following season are fairly well differentiated in the stem-bud. But to understand the vascular system of the tuber we must choose a seedling in which the cotyledon is still present—such a specimen, for

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example, as that drawn in Fig. 4. A transverse section passing through the cotyledon and the stem-bud just above the insertion of the latter on the axis, shows the cotyledon as a ring of tissue studded with five vascular bundles. Within it are three concentric rings which represent the three leaves already mentioned. A fourth rudimentary leaf is indeed present, but as it will not come to maturity in the following year, we are not now concerned with its structure.

node, the course of the bundles is indicated by the arrows of the first leaf; a, β , γ , those of the second. The midrib of 3 is the midrib. The circles A, B, C represent the traces donary bundles are numbered 1-5, and of these that marked a section is diagrammatically shown in Fig. 11. The cotylethat of the cotyledon. The position of the bundles in such third shows a single procambial strand representing its midrib. very characteristic of the young node. It is well shown in in a broken crescent fronting the midrib-an arrangement other bundles. The xylem groups of the latter stretch out the midrib always remains quite distinct from that of the tangentially, do not yet unite to form a ring; the xylem of which are the groups of xylem. These, though extended of the four bundles indeed forms a continuous ring, within left, they form an incomplete vascular girdle. The phloem inwards, and with the midrib l, which forks to the right and in the diagram. The inmost circle of traces, a, β , γ , bend the third leaf is called L. In the node next below this interlower down, beneath the insertion of the stem-bud but above We can trace these seven bundles in a section taken rather Fig. 15 which represents the first node of the young stem. Each of the two outer leaves displays three bundles, the

The node just described is the third of the young stem, and from it arises the first whorl of roots. When the roots are fully formed, as in the seedling drawn in Fig. 6, a section through their insertion shows the formation called by M. Van Tieghem the 'réseau radicifère'!' The xylem as well as the

¹ Gérard, Passage de la Racine à la Tige Ann. d. Sci. Nat., Sér. 6, Vol. xi, Bot., 1881.

phloem forms a complete circle. This xylem-girdle is thickened at certain points, and on these the central cylinders of the roots are inserted.

Returning to our younger stem (Fig. 4), we pass downwards from the third node into the second internode. In this the bundle l has disappeared, for one of its branches has fused with β , the other with γ . Throughout the second internode we have, as shown in Fig. 12, three bundles in the central cylinder which are the direct continuation of the traces from the second leaf, a, β, γ . Surrounding these we have the traces of the first leaf, A, B, C, and in a peripheral circle the cotyledonary traces 1–5. In the succeeding node—the second of the young stem—the traces A, B, C bend inwards to the lateral bundles β and γ . a forks to right and left, and we again have an incomplete vascular girdle formed. This time, however, it is the xylem of A which is distinct from the rest.

The two branches of a ultimately fuse with B and C. Thus on entering the first internode there are only three bundles within the ring of cotyledonary traces. Here, however, the series of sections which we have been following breaks off. A diagram (Fig. 13) can easily be constructed from other examples to show what will take place in the coming node. But it will be more convenient to consider its structure in detail when we deal with the transition from stem to root. This transition begins almost before the formation of the first node, and continues throughout the short hypocotyl.

TRANSITION FROM STEM TO ROOT.

The transition from stem to root in the hypocotyl of Arum maculatum can be most satisfactorily followed in very young seedlings. Even at the age shown in Fig. 1, all the bundles of the first internode are clearly differentiated. Fig. 14 is drawn from a section passing through the stem-bud of the youngest seedling in our possession. Only two leaves and a growing point are found within the cotyledon, and the

second leaf is quite rudimentary. Yet not only are the bundles of the cotyledon well developed, but three procambial strands are already indicated in the first leaf. A little lower down in the axis these strands are better defined, and the structure of the first internode is perfectly clear. The five cotyledonary traces form a peripheral circle; within them are the three plumular bundles which correspond in position to the traces of the first leaf. But this, as we have seen, is the typical structure of the first internode in much older tubers.

Complete series of sections can be cut through the axis in seedlings of this age without difficulty, and we possess five such sets of transverse sections. All of them begin near the base of the stem-bud and are continued through the tuber into the primary root. Three series are cut through seedlings of the age shown in Fig. 1; two through rather older specimens, corresponding to Fig. 2. The main features of the transition are the same in all these cases, though no two are alike in every detail. Figs. 14 and 15 are drawn from two sections cut from the same axis.

The diagram (Fig. 13) shows that the eight bundles of the first internode form three groups in the succeeding node. But the process is not nearly so symmetrical here as in the second and third nodes. We have five traces entering the central cylinder in place of three, and the transition to root structure begins in the node itself. No part of the hypocotyl therefore shows the characters of a true stem. It will perhaps be easier to appreciate the difficulty of interpretation if we follow the bundles from the first internode through the succeeding node, and the hypocotyl into the primary root in a single instance. We will choose that seedling from which Figs. 14 and 15 are drawn.

It has already been stated that there are eight bundles in the first internode. The five cotyledonary traces lie near the periphery, while the three plumular bundles form a smaller

¹ In Fig. 14 the cotyledon shows six bundles. The sixth is more slender than the others, and disappears lower down. This is a common anomaly.

circle within them. The lateral bundles of the plumule are merely procambial strands, but the third is the direct continuation of the midrib from the first leaf, and its xylem is partially lignified. This bundle we will call A to distinguish it from the others, numbering the cotyledonary traces as in Fig. 14.

As we move downwards through the first internode, the cotyledonary traces turn inwards, and at the same time I approaches 2 and 5 approaches 4. Near the base of the internode the plumular bundles spread slightly outwards until a section is reached in which all the bundles of the internode lie on the circumference of a single circle. They do not long remain separate from each other. The bundle A forks, one bundle fusing with its right-hand neighbour (5), and the other with that on its left hand (1). The two lateral strands of the plumule fuse with 2 and 4 respectively. We have thus five bundles left, corresponding in position with the five cotyledonary traces.

xylem. In this way the alternate arrangement of xylem and itself among these three groups, leaving none external to the Fig. 15, and it will divide the xylem-crescent into two parts node. But the phloem of the midrib (ph) is clearly branching where, perfectly distinct from the other xylem-groups. These of the midrib. The xylem of the midrib is here, as else-All the phloem of the central cylinder will finally divide A third phloem-group is indicated at the place marked * on already partly formed near the horns of the xylem-crescent. to right and left, and will ultimately join two phloem-groups features, as we have seen, are characteristic of every young gradually assumed the characteristic appearance shown in Fig. 15. The four lateral bundles form a crescent in front close to each other near the centre of the section, have is, the protoxylem is internal. But already the transition to a root-structure has begun. The bundles, which now lie and on the same radius. The xylem itself is centrifugal; that the stem-type, the phloem-groups lying outside the xylcm Up to this time all the bundles in the axis have been of

phlocm characteristic of root-structure is attained. It is clear that the root will be triarch.

case we are considering, this group of xylem has assumed of the midrib shows it clearly enough. In the particular in the shapeless groups forming the crescent. But the xylem xylem, the process by which the protoxylem becomes external plate is formed. nearer the periphery of the section than those which form with reference to the larger one. Gradually, however, it (Fig. 15). This little crescent is at first placed symmetrically centre. Each horn is formed of two or three larger vessels the form of a crescent, with the protoxylem-elements in the remaining elements of the xylem. While this has been going become completely external, and then die out. In this way the right-hand horn. Ultimately the two left-hand vessels which form the left-hand horn of the xylem-crescent are this rotation has already begun; the two larger elements the other directly inwards. It will be seen that in the figure rotates in such a way that one horn at last points outwards, from the conjunctive tissue within them. In this way a xylemtogether, and one or two larger vessels have been differentiated on, all the bundles of the stele have drawn much closes the protoxylem-elements (px, Fig. 15) are left external to the It would be hopeless to try to follow the 'rotation' of the

It is clear from this description that the transition from stem to root structure has taken place according to the third type described by M. Van Tieghem¹. The xylem-groups have remained *in situ*, 'rotating' through 180°, in order that the protoxylem may become external; and the phloem-groups have branched to right and left, the adjacent branches of two groups uniting. The branching of the phloem takes place with great regularity in all the specimens we have examined. But it is merely formal to describe the process by which the protoxylem has become external as a rotation. Sometimes indeed, as in the example just described, a partial

¹ Van Tieghem, Traité de Botanique, 2nd ed., Vol. i, p. 783-

and the upper part of the root which we have cut through becomes triarch later on; in the other, the tetrarch structure is first formed. In one of these cases the tetrarch root older seedlings, two show a tetrarch structure when the root three series of sections through the lower part of the tuber, appears from the root-stele, and the phloem-groups on triarch. This variation is probably not uncommon, for in either hand of it unite. Thus the root in the end becomes A. A little lower down, however, this xylem-bundle discorresponding in position to the stem-bundle we have called stele when first formed is tetrarch, the fourth xylem-bundle still more considerable deviation from the type. The rootcase. But in two cases this crescent shows two xylemfour, and in one seven. This last case is remarkable for a groups, in one (besides the example described) it shows more or less completely formed opposite the midrib in every distinct, and is continued into one of the xylem-groups of the triarch root. The characteristic xylem-crescent is also the mode. In all, the xylem-group of the midrib remains series of sections show much variation in the structure of The four other seedlings from which we have cut complete

We are inclined to consider those cases normal in which three distinct groups of xylem are formed in the first node and are continued downwards into the triarch root. These three

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groups would represent three primitive bundles belonging to the cotyledon, two of which branch immediately on entering the first internode. Thus the symmetry of the root-structure would be immediately derived from that of the cotyledon. The anomalies just described show, however, that one of the plumular bundles may occasionally exercise some influence on the root-structure. We hope to obtain some light on this point from the examination of seedlings belonging to allied genera.

EXPLANATION OF FIGURES IN PLATE XXV.

Illustrating Mrs. Scott's and Miss Sargant's paper on Arum maculatum.

Abbreviations: s_i , seed; t_i , tuber; $s_i l_i$, scale-leaf; r_i , root; $c_i r_i$, contractile ot; l_i , bud.

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	ĝ.	:	Arum	maculatum.	Fig. 1. Arum maculatum. Seedling. Jan. 29, 1896.
	Fig. 2.	2.	"	3	" Showing the tuber, radicle, and root-
	1	•			hairs. A little more advanced April 1806.
	Fig. 3.	ယ္	ž	3	" A little more advanced. April, 1890.
	Fig. 4.	4	ï	ય	" Showing tuber much enlarged. May 7,
					1896.
	Fig. 5.	Ćι	÷	77	June 9, 1896. The seed-coats and cotyledon have
					been cut off by periderm.
	Fig. 6.	9	č	3	Oct. 14, 1896. The radicle has shrivelled and new
					roots have been formed.
	Fig. 7.	7	ÿ	3	Young plant third season.
	Fig. S.	ŝ	¥	y	June 9, 1898. Young plant fourth season, showing
					two contractile roots.
	Fig. 9.	9	ä	*	Section through petiole of the innermost leaf of
	4				mature plant (Fig. 10), showing the inflorescence
					enclosed in it and the next year's vegetative
					bud (b).
	Fig. 10	۳ 0	¥	3	Mature plant with vegetatively produced young
	($\operatorname{plant}(A)$ attached, and numerous tubers about to
					form new plants.

Figs. 11, 12, 13. Diagrams illustrating the course of the bundles in the epicotyle donary stem of a seedling about the age shown in Fig. 4.

1-4, Cotyledonary traces.
Λ-C, Traces from first leaf.
α, β, γ, Traces from second leaf.
ℓ, Mid-rib of third leaf.

ph., phloem of midrib which is branching to right and left,

by Miss E. Sargant.

Fig. 14. Transverse section of stem-bud, passing through the growing point. From seedling of age shown in Fig. 1. Six bundles in the cotyledon; one of them—which will disappear inter—is very slender. Three bundles in the first leaf. Fig. 15. Transverse section through central part of hypocotyl, showing transition from stem to root structure. Drawn from same seedling as Fig. 14.

Figs. 1-9 are drawn by Mrs. Scott; Fig. 10 by Mr. C. T. Gwilliam; Figs. 11-15 x, x, x, x, tour groups of xylem forming crescent in front of midrib.

Scott & Sargant.—Arum maculatum.



