Arum Maculatum L.
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ARUM L.

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Arum maculatum L.

F. A. Sowter

A robust, somewhat fleshy perennial, 15–40 cm., with 4–6 radical leaves springing from a stout whitish corm. Leaf lamina hastate, with deflexed lobes, shining, with irregular black to purple blotches or uniformly green; veins pinnately branched, sometimes whitish; petiole channelled above, 10–20 cm. Flowers monoecious, protandrous, crowded on a

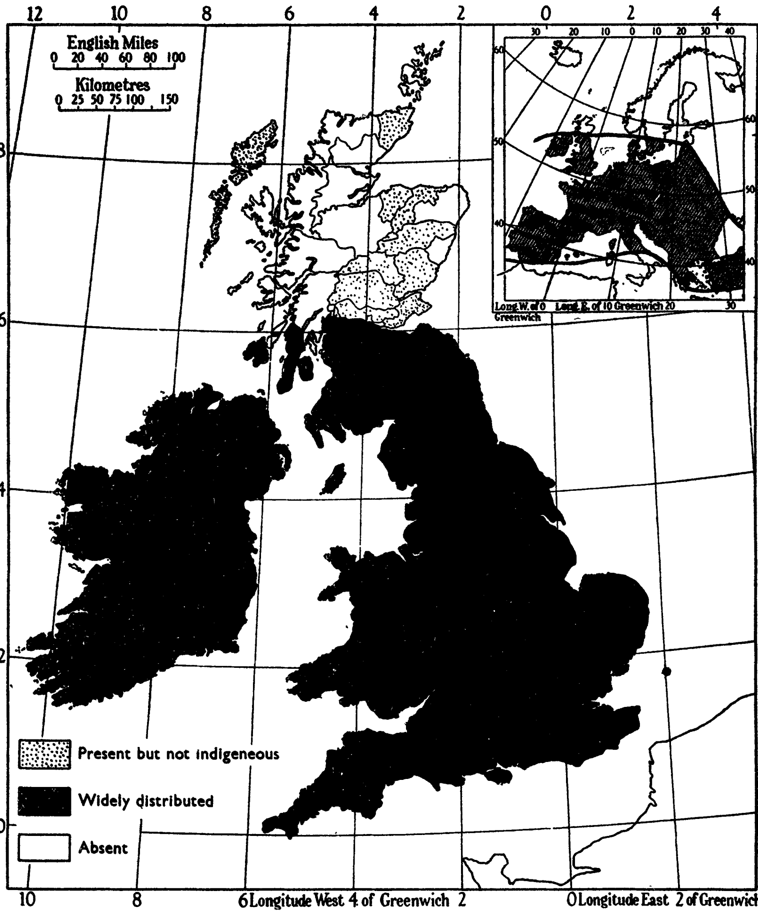

Fig. 1. *Arum maculatum* L. Vice-comital distribution in British Isles and (inset) distribution in Europe.

vertical axis prolonged as the purplish or yellowish club-shaped spadix (5–6 × 0·5–0·7 cm.). Spathe cowl-shaped, tapering, convolute with overlapping edges at the base, open at the base of the spadix, shrivelling after flowering, spotted or uniformly green, 10–25 cm. long. Inflorescence axis bearing (in order from the base of the spadix downwards): (*a*) a zone of 30–40 deflexed hairs, 4–5 mm. long; (*b*) a zone of *c*. 100 sessile purplish red to yellow anthers, 1–1·5 mm. long, dehiscing longitudinally, mostly arranged in pairs; (*c*) 30–50 pale yellow syncarpous unilocular ovaries, 3 mm. long, with short style and entire stigma; the highest row are sterile and have terminal filamentous processes. Perianth and nectaries none. Infructescence a bare spike of berries, scarlet when ripe, containing 1–4 reticulated, globose seeds (6 × 5 mm.).

Plants with spotted leaves (f. *maculatum*) and those with unspotted leaves (f. *immaculatum*) grow together in similar habitats. The variety *tetrelii* Corb. has a yellow spadix, but plants may be found showing intermediate spadix colours. The dark patches on the leaves of the spotted form are due to a purple anthocyanin (Wheldale, 1916). Stahl (1896) suggested that the anthocyanin of this and other shade plants increases the absorption of heat by the leaves and thus promotes transpiration. Often the marking corresponds with a prominent elevation or depression and both may be found on the same leaf.

The frequency and distribution of spotted and unspotted plants in Britain is extremely variable, but Pethybridge (1903) concluded that in England, as in Ireland, spotted plants are much more uncommon than unspotted. A count made by Phillips (1903) at Graignmanagh, Ireland, showed a proportion of spotted to unspotted plants of 1:500, but counts by the present writer in the Midlands gave a proportion of 1:4·88. Bromfield (1856) states that the unspotted plant is rarer in the north.

A lowland species of woods, hedgebanks and shady places widely distributed throughout England, Wales, Ireland and southern Scotland.

I. *Geographical and altitudinal distribution.* Recorded for all English vice-counties. Much planting has occurred in Scotland, but it extends northwards as a native species to a line approximating the River Forth to Argyle. North of this limit it is generally considered naturalized. It is doubtfully recorded for west Perth with Clackmannan (87), mid-Perth (88), south Aberdeen (92), Banff (94), Moray (95) and Caithness (109). There are also records from east Perth (89) and Angus (90). In the latter vice-county it grows in a shrubbery at Parkhill near Arbroath, where it has probably been planted (U. K. Duncan). Campbell (1936) records it for North Uist (110) 'under wall, outside a garden'. It is abundant at Finlarig Castle, Killin, Perthshire (88), but not native (White, 1898). Although noted as 'doubtful' from Fife with Kinross (85) (*Comit. Fl.*), it is recorded from eleven localities in this vice-county (Young, 1936). Recorded for all Irish vice-counties, but it is generally rarer in the west than in the east (*Ir. Top. Bot.*), its north-western limit being reached in the Donegal Bay area (*Bot. Irl.*). In the Channel Islands it occurs in Jersey (Babington, 1839), Guernsey, Sark and Jethou. Absent from Alderney, Herm, Lihou and Crevichon (Marquand, 1901). Widely spread over southern and central Europe, northwards to southern Sweden (lat. 58° N.) (absent from Norway), and eastwards to Poland, the Carpathians and the Caucasus, where it is replaced by *Arum orientale*. It is cited for Turkey (*Cyb. Brit.* Compendium); the Balkan Peninsula southwards to Peloponnesus; in Italy to the centre of the peninsula. Also in Spain and, according to Watson, crossing to Algeria (lat. 35° N.), but Battandier & Trabut (1902) do not record it for Algeria and Tunis and say that *A. italicum* has been recorded in the past as *A. maculatum*. Jahandiez & Maire (1931, 1934) say it is absent from Morocco, but mention that it has been recorded in error. Thus it seems absent from North Africa. Its frequency is variable. In central and western France it is common, widespread in Belgium and Holland, whilst in certain parts of Germany it is quite absent (e.g. East Mecklenburg and Prussia) (*Lebensg.* **1**, iii, p. 33).

In England ascends to 1350 ft. (411 m.) on Thornthwaite Scar, above Brough (Wilson, 1938); 1200 ft. (365 m.) on Leck Fell, west Lancs; 1050 ft. (320 m.) in Derbyshire (West); 980 ft. (298 m.) in Teesdale; 750 ft. (228 m.) Buckden, Craven-in-Wharfedale (Lees, 1937). 1500 ft. above Llanthony, Black Mountains, Monmouthshire (E. W. Jones). In Wales 1000 ft. (304 m.) or higher on Llansannan, Denbigh (A. A. Dallman). In Ireland to 1000 ft. (304 m.) in the Mournes (*Alt. Range Br. Pl.*). In Europe it ascends to about 1000 m. (Switzerland to 1050 m.) (Hegi, *Fl.* **2**, 133). In the Swiss Jura it is recorded at 710 m. at La Clochatte and 810 m. at Vers-chez-les Blanc (Bonner, 1940). In Canton Graubünden (Switzerland) it occurs only in the beech region at 500–600 m. (Braun-Blanquet & Rübel, 1932).

II. *Habitat.* (*a*) *Climatic and topographical limitations.* In deciduous woods, coppices, fox coverts, plantations, hedgerows, hedgebanks, scrubs, thickets, orchards, gardens, on wooded cliffs, and occasionally amongst the ground vegetation of marsh formations (alder-willow association). In dense woods it becomes marginal. For optimum growth it requires a moist, loose soil, well supplied with humus. It seems to be equally abundant in woodland of long standing as in woods which are only 100–140 years old. Light intensity determinations (actinometer) were made in Selsdon Wood, Surrey, by C. T. Prime (1943) during the period of its active growth (March), and they showed that on a fine sunny day, the average intensity inside the wood was 50 % of the light outside the wood, but on an overcast day the average intensity inside the wood was 95 % of the light outside the wood. The humidity was determined at the same time and showed the relative humidity to be 73 % in the wood, and 61 % outside the wood.

(*b*) *Substratum.* It is found on a wide variety of soils of high base status including sand, loam and calcareous soils but is absent from acid peaty ground. It tolerates considerable moisture but also grows on very porous highly drained soils. Soil samples were examined from the following localities:

(i) Ravensdale, Derbyshire, on very stony limestone slopes amongst scrub with a humus layer ½–1 in.

(ii) In Leicestershire on a heavy clay soil mixed with the 'Brand' series of slates the corms were found 3 in. down. There was a sparse layer of dead leaves.

(iii) In a mixed coppice (oak-ash) on a dark clay for 5½ in. (corms) and then becoming lighter:

	(i)	(ii)	(iii)
Water content (%)	46·3	16·8	22·5
Humus content (%)	23·6	6·74	6·64
Nitrates	+	–	–
Base deficiency (Comber)	–	–	–
Carbonates (HCl test)	+	–	–
pH (elecrometric)	6·1	6·1	5·7

Its tolerance of wet conditions is shown in Bishop Wood, near Selby, Yorks (alder-ash-elm) on Warp Clay. Soil a grey clay, with winter water-table at about 4 in. from surface. Summer water-table absent. Very high exchangeable calcium content but very low K and PO_4, pH of surface soil, 4·68; pH at 24 in., 6·58. The following figures (E. W. Jones) illustrate the limitations in soil: In Dorset on chalk it is recorded in 16 out of 133 stands; of these 6 out of 16 occurrences are on shallow chalk soils, and none on flint gravels or deep clay-with-flints. On Tertiary strata it is present in 1 out of 54 stands; this was in a planted stand of relatively recent origin on former arable soil and was associated with other calcicoles. In the Chilterns (Watlington) it is recorded in 2 out of 44 stands on clay-with-flints on the plateau, and in 8 out of 9 stands on chalk soils of steep slopes. At

Symonds Yat, Monmouthshire (High Meadow Woods) it is recorded in 75 out of 147 stands on Carboniferous Limestone, in 17 % of the stands on Old Red Sandstone (when it is local and confined to moist valley bottoms), and in 4 out of 100 stands on Coal Measure loams. In Wales and the Lake District, on Silurian and Ordovician shales, it is a very local plant and in general is present in less than 1 % of the stands. In the beech woods of the Cranham Common-Painswick district (Cotswolds, Jurassic limestone) it is present in 43 % of the stands. It invades abandoned arable land as shown by its presence in the interior of the oak-hazel wood succession in 1914 on the Broadbalk Wilderness at Rothamstead (Herts), abandoned in 1882 (Tansley, *Br. Isl.*). In ashwoods on limestone pavement it is an occasional species. B. L. T. de Silva (1934) examined thirteen soil samples from various woodlands in Kent where *A. maculatum* is present. These showed that it grows in soils rich in exchangeable calcium even when calcium carbonate is absent. His observations gave a range of exchangeable calcium from 4·5 to 19·9 m.equiv. with an average value of 12·3, whilst the pH values ranged from 5·9 to 7·0 with an average value of 6·4.

III. *Communities.* (*a*) Deciduous woodlands. In Britain in pedunculate damp oak-woods on heavy soils, it is a common associate of *Mercurialis perennis* provided that the Mercury shoots are not too dense (Tansley, *Br. Isl.*). Swamping by these shoots is suggested by the description (Jones, 1944) of the ground flora of a 30-year-old hardwood plantation on calcareous grit near Oxford where the dominant *M. perennis* forms a 20–100 % cover and *Arum maculatum* is recorded as 'rare'. Other important associates of this species are: *Corylus avellana, Scilla non-scripta, Oxalis acetosella, Ranunculus ficaria, Anemone nemorosa, Ajuga reptans, Galeobdolon luteum, Primula vulgaris, Sanicula europaea, Asperula odorata, Potentilla sterilis.* In an oak (pedunculate) and *Fraxinus* wood in Ireland where the limestone lies practically bare, it occurs with *Quercus* and *Corylus avellana* (co-dominants), *Anemone nemorosa, Viola reichenbachiana, Oxalis acetosella, Geum urbanum, Circaea lutetiana, Viburnum opulus, Veronica chamaedrys, Prunella vulgaris, Neottia nidus-avis, Epipactis atropurpurea, Scilla non-scripta, Carex sylvatica, Polystichum setiferum, Dryopteris filix-mas* (*Bot. Irl.*). In sessile oakwoods on damp soil with mild humus with an undergrowth of *Rubus* spp., *Rosa* spp., *Crataegus oxycanthoides, Hedera helix, Lonicera periclymenum,* the field layer contains *Mercuralis perennis, Ranunculus ficaria, Anemone nemorosa, Deschampsia caespitosa, Holcus mollis, Digitalis purpurea, Melandrium dioicum, Stellaria holostea, Teucrium scorodonia, Pteridium aquilinum, Glecoma hederacea, Ajuga reptans* and *Rumex acetosella.*

At Carrickreagh, Ireland, ridges of bare limestone rise from the shore of Lough Erne and are covered with scrub which is continually cut. *Quercus sessiliflora* is sometimes dominant, sometimes *Betula pubescens*, and sometimes *Corylus* with much *Fraxinus, Viburnum opulus* and *Prunus spinosa. Arum maculatum* is present in the field layer with *Aquilegia vulgaris, Rubus saxatilis, Lysimachia nemorum, Prunella vulgaris, Epipactis helleborine, Scilla non-scripta* and *Pteridium aquilinum* (*Bot. Irl.*). It is less frequent in *Quercus sessiliflora* woods than in pure *Quercus robur* or *Fraxinus-Quercus robur* woods.

(*b*) Composition of communities in oak woods. (see Table 1).

(1) Malvernian and Uriconian formation: light clayed loams, occasionally fairly stiff clays; low humus content and water content may be low in dry weather.

(2) Woods of May Hill Sandstone on a loamy clay, generally acidic.

(3) Wenlock limestone: Rock has high percentage of calcium carbonate but surface soil leached (lime content less than 1 %).

(4) Aymestry limestone: Limestone nodules interbedded with shales. Lower lime content than the Wenlock limestone. Leaching of surface layers reduces lime content to usually less than 1%.

(5) In oak-hornbeam woods of Hertfordshire (Salisbury, 1916, 1918) it is included amongst the commonest species of the shade flora in a mixed society, occupying the transition region between a damp society dominated by *Mercurialis perennis* and a dry society dominated by *Anemone nemorosa.*

Table 1. *Communities with* Arum maculatum

(*a*) Oakwoods

Field layer ...	1	2	3	4	5
Arum maculatum	o.	l.c.	f.-c.	l.f.	o.-l.c.
Ajuga reptans	+	+	f.-c.	o.-f.	l.f.-l.c.
Alliaria petiolata (margin)	f.	r.	f.	+	.
Allium ursinum (flushes)	.	l.ab.	l.f.	l.c.	.
Anemone nemorosa	l.c.	c.-l.ab.	c.	l.c.	r.r.-l.c.
Angelica sylvestris (flushes)	+	l.f.	+	o.	.
Anthoxanthum odoratum	f.	o.-f.	?	+	.
Arctium vulgare	c.	+	o.-f.	f.	r.r.
Arenaria trinervia (margin)	f.-c.	+	+	o.	r.
Arrhenatherum elatius (margin)	f.	f.	f.	f.	.
Asperula odorata	+	f.-r.	f -l.ab.	o.-f.c.	r.r.-l.f.
Brachypodium sylvaticum (margin)	o.	f.	f.-c.	f.-c.	.
Bromus ramosus	r.r.	r.	o.-f.	o.	.
Campanula trachelium	r.	r.	o.-f.	+	.
Cardamine flexuosa	o.	o.	+	+	.
Carex sylvatica	+	f.-o.	o.	f.	r.
Chrysosplenium oppositifolium	l.f.	l.c.	r.r.	+	.
Circaea lutetiana (damper places)	o.	f.-l.c.	f.c.	+	r.
Cirsium palustre	o.	l.f.	o.	+	.
C. vulgare	o.	o.	o.	.	.
Clinopodium vulgare	f.	o.-f.	f.-ab.	+	.
Conopodium majus	+	+	+	f.	r.-r.r.
Deschampsia caespitosa (flushes)	l.	l.-o.	r.r.-l.f.	f.	.
Digitalis purpurea	c.-f.	f.c.-c.	r.-o.	f.	.
Dryopteris filix-mas	o.	o.	o.	f.	r.r.-v.r.
Epilobium montanum	f.-l.c.	o.-f.c.	f.	+	o.
Euphorbia amygdaloides	f.-c.	f.-o.	l.ab.	f.-l.c.	r.r.-l.f.
Festuca gigantea (margin)	l.f.	r.	o.-r.	.	.
Filipendula ulmaria (flushes)	.	l.f.c.	l.f.	l.f.	.
Fragaria vesca	f.	f.-ab.	c.-l.ab.	f.-c.	r.r.
Galeobdolon luteum	f.	f.c.-c.	f.-c.	f.	r.r.-f.
Galium aparine	o.	+	+	+	.
Geranium robertianum	f.-f.c.	f.	f.	f.	.
Geum urbanum	f.	+	f.	+	r.r.
Glecoma hederacea	c.-l.ab.	o.	o.-f.c.	l.f.	o.-l.ab.
Holcus lanatus	l.ab.	f.c.	f.c.	+	.
H. mollis	c.-f.	ab.-c.	f.-c.	l.ab.	c.-r.
Hypericum perforatum	o.-f.	r.-l.c.	f.	o.	.
Luzula pilosa	o.-l.f.	c.	r.r.	f.-c.	o.-f.
Lysimachia nemorum	f.	f.-c.	o.-c.	f.	.
Melica uniflora	f.	f.	f.c.	f.c.-f.	.
Mercuralis perennis	c.-l.ab.	l.c.	ab.-c.	c.-ab.	l.ab.-r.r.
Milium effusum	.	r.	l.f.-r.	r.r.	.
Oxalis acetosella	c.	v.c.-c.	o.	f.-v.c.	o.-f.
Poa nemoralis (margin)	c.	c.	f.-f.c.	f.c.-v.c.	.
Potentilla sterilis	+	f.-f.c.	f.	o.	.
Primula vulgaris	o.	o.-c.	f.c.-c.	f.-v.c.	.
Prunella vulgaris	+	f.	c.	f.c.	.
Pteridium aquilinum	l.c.-ab.	l.ab.-f.	r.-c.	o.-r.	v.c.-l.ab.
Ranunculus auricomus	.	f.	o.-f.	l.f.	l.r.
R. ficaria	c.	l.c.-f.c.	l.ab.	l.c.	.
R. repens	r.r.-f.	l.f.	+	f.	.
Sanicula europaea	l.r.	l.	f.c.-ab.	c.	r.r.-f.
Scilla non-scripta	r.r.-c.	c.-l.ab.	f.-c.	f.-l.c	r.r.
Scrophularia nodosa	o.	o.	o.	o.	r.r.

Table 1 (*continued*)

(*a*) Oakwoods (*continued*)

Field layer ...	1	2	3	4	5
Tamus communis	o.-v.r.	o.	f.-c.	r.r.	.
Teucrium scorodonia (margin)	f.-v.c.	f.c.-c.	c.	f.c.-c.	o.-f.
Urtica dioica	f.	+	o.	.	.
Veronica chamaedrys	f.	f.-c.	c.	f.	.
V. montana	+	l.f.	f.	+	r.r.
V. officinalis	l.f.	c.	o.	+	.
Viola reichenbachiana	+	o.	v.c.	v.c.	r.-o.
V. riviniana	+	o.-c.	v.c.	v.c.	r.-f.

(1) Beech woodlands of the South Downs (Watt, 1924, 1925).

(2) A beechwood on chalk, Ditcham Park, Hampshire (Adamson, 1921).

(*a*) Wolver Wood Series. Soil reaction pH 8.

(*b*) The Miscombe Series. Soil reaction pH 8·5.

(*c*) Oakham Bottom. A calcicolous coppice. Soil reaction pH 7.

(3) A beechwood of the Central Cotswolds on Inferior Oolite (Tansley & Adamson, 1913). It is present in the ground vegetation in which there is no generally dominant species.

(*b*) Beechwoods

Field layer	1	2(*a*)	2(*b*)	2(*c*)	3
Arum maculatum	o.-l.f.	o.	o.	o.	o.
Ajuga reptans	o.-l.ab.	o.	o.-l.ab.	f.	r.
Arctium minus	o.	o.	o.	.	f.
Arenaria trinervia	r.-l.f.	.	o.	.	o.
Asperula odorata	l.ab.	f.	l.ab.	f.	ab.
Brachypodium sylvaticum	o.-f.	r.	l.	o.	ab.
Carex sylvatica	o.	.	l.	.	f.
Chamaenerion angustifolium	o.-l.d.	l.a.	.	l.ab.	o.
Circaea lutetiana	o.-l.ab.	l.	l.ab.	o.	l.ab.
Cirsium palustre	r.-l.ab.	.	.	r.	o.
C. vulgare	l.-r.	.	.	o.	.
Clinopodium vulgare	o.	.	.	o.-f.	.
Epilobium montanum	o.-l.ab.	.	o.	o.	f.
Euphorbia amygdaloides	o.-f.	l.f.	l.f.	o.	f.
Fragaria vesca	o.-l.ab.	l.f.	l.	ab.	ab.
Galeobdolon luteum	l.f.-l.ab.	l.f.	l.ab.	f.	o.
Geranium robertianum	o.-f.-l.ab.	.	r.	o.	f
Geum urbanum	o.-f.	.	r.-o.	o.	o.
Glecoma hederacea	o.-l.ab.	.	.	.	.
Melica uniflora	o.	.	l.	.	ab.
Mercuralis perennis	o.-l.d.	o.-l.d.	l.d.	l.d.	l.ab.
Myosotis arvensis	o.	.	r.	l.	o.
Primula vulgaris	o.-f.	.	l.f.-l.ab.	o.	o.
Prunella vulgaris	o.-l.ab.	.	.	.	.
Pteridium aquilinum	o.-l.ab.	.	l.	.	l.ab.
Ranunculus ficaria	r.	.	l.ab.	.	.
Sanicula europaea	r.-l.f.	ab.	o.-l.ab.	ab.-f.	ab.
Scilla non-scripta	l.f.-l.ab.	.	l.ab.	.	l.ab.
Scrophularia nodosa	l.	.	o.	o.	.
Urtica dioica	o.-l.d.	.	o.	.	.
Veronica chamaedrys	o.-f.	o.	o.	o.	f.
V. officinalis	r.-l.ab.	.	r.	.	f.

(*c*) Composition of communities in beechwoods. On the Continent of Europe it is an important consituent of the field layer of beechwoods. It is present in the beechwood associes of many countries within its continental area of distribution. It is found with *Hepatica triloba, Ranunculus lanuginosus, Actaea spicata, Cardamine silvatica, Sanicula europaea, Asperula odorata, Lysimachia nemorum, Vinca minor, Veronica montana, Asarum europaeum, Neottia nidus-avis, Cephalanthera* spp., *Epipactis microphylla, Orchis purpurea, Cypripedium calceolus, Melica uniflora, Hordeum europaeum* (*Lebensg.* **1**, iii, p. 34). In the beechwoods of Britain it has an equally important status (Table 1).

In a fox covert of 'mixed' trees on chalky boulder clay in north Lincs *Arum maculatum* is associated with other marginal species, *Viola odorata*, *V. riviniana*, *Geranium robertianum*, *Bryonia dioica*, *Anthriscus sylvestris*, *Torilis anthriscus*, *Chaerophyllum temulum*, *Lapsana communis*, *Glecoma hederacea* and *Stachys sylvatica* (Woodruffe-Peacock, 1918). The author says these plants were probably not on the site when the covert was planted, but have reached it by following the field fences abutting on to the wood. In a *Fraxinus* coppice in Rutland on oolitic limestone *Arum maculatum* grows in large clumps with *Mercurialis perennis* through a deep covering mat of *Porotrichum alopecurum*.

In hedgerows of *Crataegus monogyna* in Leicestershire it occurs with the following herbaceous plants: *Ranunculus auricomus*, *R. ficaria*, *Alliaria petiolata*, *Melandrium dioicum*, *Stellaria media*, *Arenaria trinervia*, *Geum urbanum*, *Anthriscus sylvestris*, *Hedera helix*, *Galium aparine*, *Lamium album*, *Mercurialis perennis* and *Urtica dioica*. In an orchard to which it has spread from an adjoining woodland in north Lancashire, it grows in the shade of the fruit trees with *Ranunculus ficaria*, *Viola riviniana*, *Myrrhis odorata*, *Primula vulgaris*, *Glecoma hederacea*, *Mercurialis perennis*, *Urtica dioica* and *Galanthus nivalis*.

IV. *Response to biotic factors*. Protected from grazing by the raphides contained in the leaves, although on the Continent leaves have been found in the stomach of the Common Crane (*Grus grus grus* (L.)) (Jourdain, 1940). It was observed in a Leicestershire wood in April 1946 that a large number of spathes had been bitten off at the base. Some of them were afterwards found on the branches of trees, and the damage can therefore probably be attributed to birds. This may be analogous to the destruction of other spring flowers such as the primrose and crocus by birds, or they may be torn off by birds seeking the slugs and snails which enter the spathe for shelter. It was noticed that this only occurred to plants growing in the wood; plants growing under hedgerows were untouched.

Whilst coppicing has the effect of reducing the organic content of the surface layer and its correlated acidity, the increase in light intensity does not appear to have a detrimental effect on the plant. After clear felling, however, the plants are scorched and depauperate in the following season. If regeneration is quick the plant will be saved from extinction. The examination of an area of woodlands which was clear-felled (Adamson, 1921) showed that *Arum maculatum* retained its frequency three years later, a flora of tall herbs 3–5 ft. in height providing the shade.

V. (*a*) *Gregariousness*. (*b*) *Performance in various habitats*. Generally grows in 'clumps' or patches of irregular shape. Some clumps show great variation of individual plants, whilst others show similarity. Clumps showing great similarity are probably due to cloning. This has been investigated by C. T. Prime who dug up and mapped the corms of a uniform colony. The direction of the growth of the corms was compatible with asexual reproduction from the original plants. Measurements of leaves of plants growing in clones show less variation in size than the leaves of plants chosen at random.

(*c*) *Effect of frost, drought, etc*. The young leaves are capable of withstanding frost in spite of their succulent nature. Leaves examined in a spinney in Leicestershire in the morning after a sharp frost were limp but were quite recovered three hours afterwards. The spathes are ruined by cold drying winds and do not unroll (Church, 1908). After the snowfall of 1 May 1945, many spathes were affected and failed to mature. They remained in a shrunken green condition and did not open (E. W. Jones).

VI. (*a*) *Morphology*. The slow-growing tuber is 2 cm. or more in diameter and contains the food reserves accumulated during the summer. It is protected against underground animals by raphides. In autumn a leaf bud is developed for the next season's growth, and behind are one or more corms of the previous years on which there are ring-like leaf scars and root remains. The strongly contractile roots pull the tubers to a depth of 20–30 cm. from the surface. Scott & Sargant (1898) examined tubers which were 2 cm. below surface in May, and by October they were 7 cm. deep. Young tubers replanted near the surface will regain normal depth in a week.

(*b*) *Mycorrhiza.* Endotrophic mycorrhizal association of the arbuscular-vesicular type (Gallaud, 1915). Mycelium at first intracellular, later intercellular is the usual course of events, but the first condition may be quite evanescent (M. C. Rayner).

(*c*) *Perennation.* Stem tuber geophyte. Thick unbranched roots are found on the tuber by September, and then there is a cessation of all growth during the winter. By the end of July the leaves and spathes have withered and only the fleshy axis remains. This dies down after the dispersal of the berries or is killed by the frost, and those berries which are not eaten decay on the surface of the soil. Thus nothing is visible above ground during the winter. Daughter tubers are frequent and are budded off from the under-surface of the mature tuber. The plant produced from seed rarely flowers before the seventh year, whilst plants from daughter tubers flower much younger. Seed is set every year. C. T. Prime made counts of the number of ovules ripening in the fruits of the two forms of this species, and the percentage of ripe seeds of the spotted plants was 39·4, whilst of the unspotted plants was 37·6. The average number of ovules per gynaecium was 2·83 and 3·34 respectively.

(*d*). *Chromosome number.* The basic number is $n=14$. The following values of $2n$ have been reported: $2n=28$, Danish material (Hagerup, 1942, in Löve & Löve, *Scandinavian Flora*); $2n=32$, north German material (Schmucker, 1925) (? error for 28); $2n=56$, British material, near Leeds (H. G. Baker, 1946); $2n=56$, British and German material (*Mert. Cat.* 1939); $2n=84$, British material (*Mert. Cat.* 1940). Maude says this variation can probably be accounted for by polyploidy within the species.

(*e*) *Physiological data.* No information.

VII. *Phenology.* Each spring roots are developed below the leaf bud when the period of maximum growth commences. The leaf bud for the next season's growth is well developed by the autumn, and its base thickens out to form the tuber which will be initiated in the following spring. The leaves expand and uncoil from February to March or earlier in mild winters, e.g. in 1881, at Chelmsford, 26 December, and in 1882 at Saffron Walden, 1 January. The leaves and spathes are coiled 'sinistrally' or 'dextrally', and according to Christy (1914) the leaves on any one plant are always coiled the same way as the flower spathe of that plant. This was further studied and confirmed by Armitage (1921), who also found that there were hardly ever more 'dextrally' coiled than 'sinistrally' coiled spathes, i.e. five 'lefts' to four 'rights'. In the south of Britain it flowers early in April, becoming later in more northerly stations. In Wiltshire, Preston (1888) gives the first flowering 29 March 1882 to 13 May 1879. Average date, 22 April. The flowers are over by the middle of June, and the leaves have mostly gone by the end of July.

VIII. (*a*) *Floral biology.* Pollination is effected by midges of the genus *Psychoda* which are attracted to the flowers by the emission of an odour variously described as 'ammoniacal' 'urinous', 'disagreeable', 'foetid', etc. The colour of the spadix is considered also to be a further attraction to the midges. Dung flies have been observed to alight on the spadix, but they do not enter the spathe. There is a rise in temperature of the tip of the spadix which Church (1908) records as 10–12° C. above the air temperature. The temperature in the floral chamber also rises 1–3° C. above the air temperature, and according to Dutrochet (in Balfour, 1871) the maximum temperature is reached at about 17.30 hr. The starch in the spadix is used up during this active metabolism, and the spadix then becomes limp. The midges enter the chamber through the ring of stiff bristles, which allows them to enter but prevents them from flying out until they have pollinated the female flowers with the foreign pollen which they have carried in on their bodies. The stigmas are receptive on the first day of opening. After pollination the stigmas shrivel and a drop of nectar is exuded. The anthers dehisce and shed pollen on the imprisoned flies up to the 3 days afterwards. The ring of bristles then shrivels and allows the insects to escape. It has often been observed that if a spathe is cut open the imprisoned midges immediately fly to another plant (Knuth, *Poll.* **3**). Owing to the large number of midges found dead in spathes, it was suggested by the earlier botanists that the plant is insectivorous, but there is no evidence to support this (Arcangeli, 1883).

There is a suggestion that these dead flies have been suffocated by CO_2 from the respiring spadix. The number of midges found in spathes varies considerably and up to 4000 has been recorded (*Lebensg.* **1**, 33–45). *Psychoda phalaenoides* L. is the species most commonly cited by writers. Tonnoir (1940) examined the insects found in spathes in various parts of Britain (Herts, Surrey, Sussex, Devon) and the total number of specimens of *Psychoda* determined were as follows: *P. phalaenoides* L., o ♂, 158 ♀; *P. grisescens* Tonn., 14 ♂, 19 ♀; *P. trinodulosa* Tonn., o ♂, 2 ♀; *P. brevicornis* Tonn., 1 ♂, 2 ♀; *P. setigera* Tonn., o ♂, 1 ♀; *P. severini* Tonn., o ♂, 1 ♀. From these results he suspected *P. phalaenoides* to be parthenogenetic. Further investigations have been made, however, by G. H. Satchell (1944) of the midges in spathes collected over two years near Leeds. His records showed that *P. phalaenoides* was by far the most numerous visitor with 205 ♀ in all and *P. griscescens* second with 38 ♀ and 2 ♂. *P. phalaenoides* was collected from tree trunks near the *Arum* plants at the same time, and both sexes were taken. The females taken from the *Arum* spathes were cultured and gave rise to both male and female offspring. It seems, therefore, that *Arum* is attractive to the female fly only. Other insects such as small beetles, weevils, and aphids are often found in the spathes with slugs, spiders and earwigs, but these stray visitors are probably merely seeking shelter and warmth.

(*b*) *Hybrids*. Colgan (1911) studied the 'unspotted' and 'spotted' forms of *A. maculatum* and suggested that the male parent was heterozygous for 'spotted' character and was fertilized by the 'unspotted' form, but there was no evidence in support beyond the equal proportion of the two forms among the offspring. It has been shown by Schmucker that self-fertilization and parthenogenesis do not occur, and this has been confirmed by the writer who blocked numbers of spathes with cotton-wool and found that no seeds were set. C. T. Prime also 'bagged' plants, and out of 47 plants, only one set seed. He also blocked the spathes of two plants and no seed was set. Crosses were also made by him of the extreme forms, and there did not seem to be any failures. Plants of *A. neglectum* (Towns.) Ridley (*A. italicum* auct. angl.) with spotted leaves are considered by Ridley (1938) to be hybrids with *A. maculatum*. The problem is being investigated by H. G. Baker (1947), whose accumulated evidence so far suggests that *A. maculatum* and *A. italicum* hybridize in this country.

(*c*) *Seed production and dispersal*. Frequency distribution of the number of fruit on 82 plants examined from Hertfordshire, Kent and Pembrokeshire gave $24{\cdot}28 \pm 0{\cdot}34$.

Examination of 175 fruits showed a range in the number of seeds: 1 (150), 2 (16), 3 (6), 4 (3). 86 % contained only one seed. The average seed output is $29{\cdot}4 \pm 1{\cdot}1$ seeds per plant (cf. Fig. 28, p. 176 and Table 89, p. 177, Salisb. *Rep. Capac.*). Colgan (1911) examined 661 ripe fruits and found an average of 1·4 seeds per fruit. Average seed weight in grams = 0·04536 (Guppy, 1912).

Seed dispersal. Ripe berries fall off the spadices or are dispersed by birds. Chaffinches (*Fringilla coelebs gengleri* Kleinschmidt) were observed to eat the berries (Scott & Sargent, 1898). Hulme (1902) says the seeds are eaten by many birds, including pheasants and others.

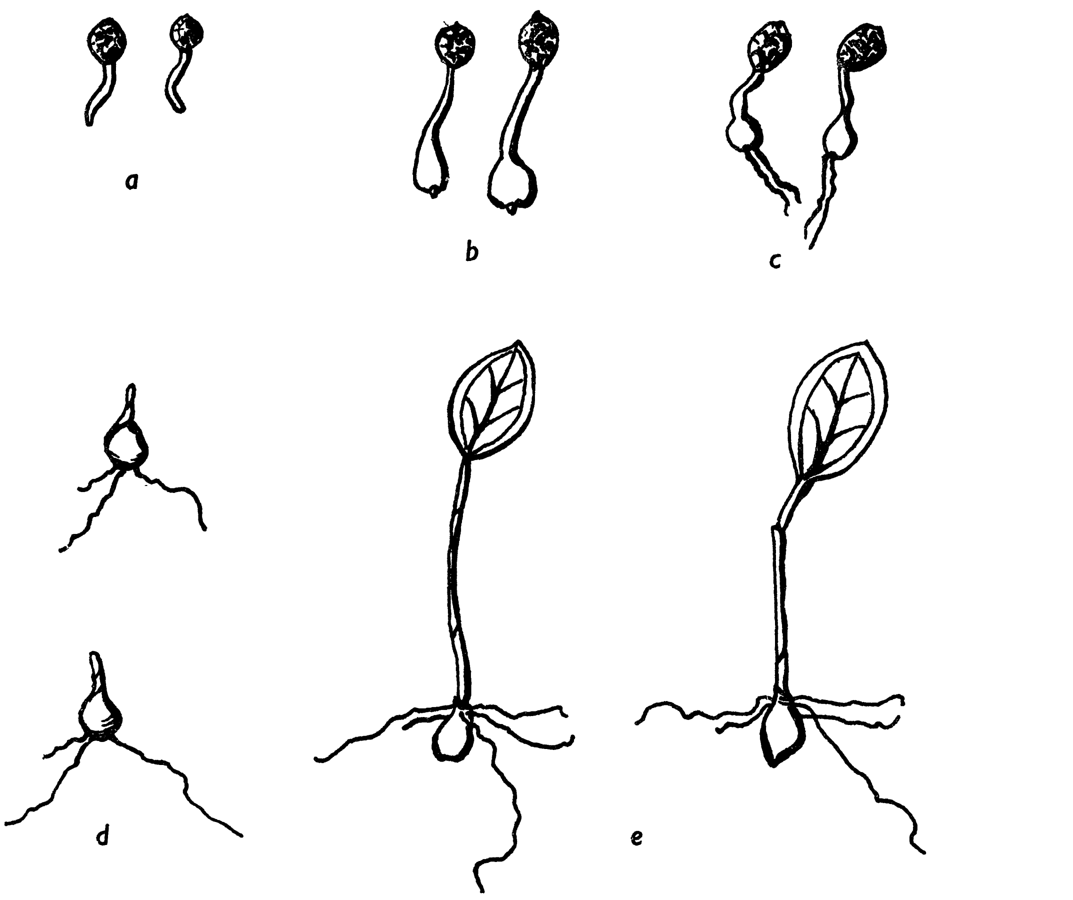

Fig. 2. *Arum maculatum* L. *a–c*, stages of germination: *a*, 9 days, the cotyledon has emerged from the seed coat; *b*, 23 days, the tuber has been formed by the thickening of the hypocotyl; *c*, 44 days, contractile roots have appeared. All grown on filter paper. $\times \frac{5}{6}$. *d*, seedling at the end of the second year. The stem bud is exposed. Grown in soil in pots. $\times \frac{5}{6}$. *e*, third year, the first (ovate) leaf. Grown in soil in pots. $\times \frac{5}{6}$.

(*d*) *Viability of seeds and special conditions affecting germination.* Sets of seeds were kept in Petri dishes at room temperature in daylight and in darkness. Germination in daylight, nil. Germination in the dark, 20 %. Sets of seeds taken from 'unspotted' and 'spotted' leaved plants were planted in soil in pots out of doors and were examined for germination in the second year. The soil was frozen during the first winter. The following results were recorded: 'spotted' seed 85·71 % germination, 'unspotted' seed 91·66 % germination

(Sowter, 1945). The result of a germination test made by Salisbury (*Rep. Capac.* p. 177) was under 6%. Wattam (1938) planted 40 seeds in pots in the spring, and the contents of the pots were frozen during the winter. Germination was 100%.

(*e*) *Seedling morphology.* In Britain, as on the Continent, the seeds germinate in the early spring. First the seed swells and the cotyledon emerges from the seed coat (Fig. 2*a*). Then the hypocotyl thickens out to form the tuber from which grow two or three contractile roots (Fig. 2*b,c*). In the second season the seed coat is detached and the stem bud is exposed (Fig. 2*d*). According to Scott & Sargant (1898) no chlorophyll is formed and nothing is seen above ground. In the germination experiments made by the writer in soil, a large percentage of the seedlings showed a green leaf tip just above soil level. New roots (4–6) are sent out during the summer. As a rule it is not until the third year (Fig. 2*e*) that the first leaf appears above the surface, although Irmisch (1850) and Colgan (1911) report the first leaf in the autumn of the second year as an exception. The first leaf is ovate. Below ground the tuber increases in size until June, when next year's tuber is initiated. The tuber is pulled deeper in the ground each season by the contractile roots which are produced at the end of the summer. It also moves its position from vertical to horizontal. In the fourth or fifth year the first hastate leaf is formed, and flowering rarely occurs before the seventh year.

(*f*) *Effective reproduction.* Examination of clumps suggests that reproduction by vegetative means is more important than multiplication by seed. In addition to having a ready-made supply of foodstuff the tubers start at their normal depth in the ground and the risk of being eaten is therefore almost eliminated.

IX. (*a*) *Animal feeders or parasites.* Several thrips have been taken but are considered to be casual visitors probably not feeding (G. D. Morrison). No Cecidomyids are known to be associated with it (H. F. Barnes). The oil beetle (*Meloë proscarabacus*) sometimes feeds on this plant (Briggs, 1880).

(*b*) *Plant parasites.* The alga *Phyllosiphon arisari* Kühn (Siphonales) which is occasionally parasitic on the leaves in Italy and the south of France (West & Fritsch, 1927) has been found on plants in Scotland at Tillietudlem Castle near Lanark. It causes yellow spots on the leaves (J. Caldwell).

The following fungi are recorded:

BASIDIOMYCETES

UREDINALES: *Caeoma ari-italici* (Req.) Rud., near Salisbury, 1897 (*Br. Rust. F.* p. 388); also found in France and Germany. *Puccinia phalaridis* Plowr. Aecida on *Arum maculatum* May-July (*Br. Rust. F.* p. 269).

FUNGI IMPERFECTI

HYPHOMYCETES: *Macrosporium ignobile* Karst Ayrshire, A. L. Smith & Ramsbottom, 1913 (*Trans. Brit. Mycol. Soc.* **4**, 183); *Ramularia ari* Fautr. at Chipping Campden (*List Hyphomyc.* p. 94).

COELOMYCETES: *Ascochyta ari* Died. (Syn. *A. aricola* A. L. Smith & Ramsbottom) (*Br. Stem and Leaf F.* **1**, 321).

X. *History.* There are no geological records.

XI. *General.* The starch obtained from the rhizomes has in the past been used for several purposes. In the Isle of Portland the starch extracted was sold as 'Portland Sago' (Henslow, 1905). In Elizabethan times it was used to starch the lawn ruffs worn during that period. In Switzerland the rhizomes have been used as a substitute for soap. Medicinally the action of a small dose of the powdered root is diaphoretic. Fatal effects have been recorded from large doses. Children have died from eating the berries. The toxic principle is believed to be saponin. Animals exceptionally eat the plant (Long, 1924). Observations made in Leicestershire near Badger 'setts' suggest that this animal grubs for the roots in winter. Pigs eat the roots (Cornevin, 1887). Gilbert White (1789) says the roots are scratched out from hedgebanks and eaten by birds in winter.

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