Studies on Gloucestershire populations of *Allium paradoxum* (Bieb.) G. Don

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ABSTRACT

Populations of *Allium paradoxum* in woodland, headland and grass road-verges near Bartonbury, Cirencester, have been studied since 1948. The seasonal development of the plant is outlined, and data are given on bulbil production, floral abnormalities, stature, leaf-dimensions, and the density of established plants and young plants produced from bulbils.

Of a sample of 250 plants, 72% showed floral abnormalities. Only five mature seeds were found in the course of extensive searching. Reproduction is predominantly vegetative, mainly by bulbils.

INTRODUCTION

Allium paradoxum (Bieb.) G. Don is a perennial species of shady woods in the Caucasus, north Persia and neighbouring parts of central Asia (Vvedenskii 1935). It has been naturalised for over a century in northern Britain, especially in mid-Scotland. In recent years many new localities have been reported in the south of England where the plant appears to be spreading rapidly. It has been recorded in Gloucestershire by Riddelsdell *et alia* (1948) and the object of the present work is to study populations near the junction of the Stroud and Tetbury roads, Cirencester, particularly at Bartonbury House.

It is probable that the original centre of establishment was Bartonbury gardens, where the species might have been introduced for decorative purposes or naturalising in rockeries. At present, dense populations are found in the woodlands of the grounds and also on road-verges nearby, though they cover only small areas. The associated flora of the woodland and verges is presented in Table 1. The sites overlie the Great Oolite limestone and the soil pH at six sites (woodland, road-verges, headland) lies between 6·8 and 7·3. A number of sites have been studied since 1948 and in most subsequent years new small populations have been recorded; two are about 1 mile away, near Chesterton bridge and along the Fosse Way.

The spread of the species has been influenced by several factors. First, the movement of waste material and formation of leaf-mould dumps have provided ideal means of spreading the numerous bulbils that lie on the soil surface. Secondly, the mowing of road-verges and the sweeping of the hay has moved and shaken off bulbils. Thirdly, the species is frequently picked for its appearance in springtime and eventually thrown away because of its overwhelming odour. In this way bulbils are dispersed over wider areas than is normal and this may be the cause of establishment at Chesterton. The net result has been a gradual movement along the Stroud and Tetbury roads.

TABLE 1. ASSOCIATES OF *ALLIUM PARADOXUM*

	Bartonbury Wood	Bartonbury (Verges)	Fosse Way (Verge)
Bromus ramosus	o		
Dactylis glomerata		a	o
Festuca rubra		a	o
Poa trivialis		f	
Poa angustifolia		f	o
Arrhenatherum elatius		f	o
Brachypodium pinnatum		o	a–d
Brachypodium sylvaticum	o		
Geranium robertianum	f		
Geranium lucidum		o	
Saponaria officinalis			o
Eranthis hyemalis	o		
Rubus sp.	r		
Hedera helix	a–d		
Allium vineale			o

d *dominant*, a *abundant*, f *frequent*, o *occasional*, r *rare*

POPULATION DENSITY AND SIZE

The population density of the Bartonbury centre is remarkable and during late winter a thick carpet of established plants and newly germinated bulbils is found. There are in the main wood approximately one million plants and the density may be as high as 100/sq. ft but this varies (Table 2). If bulbil development is impeded in the previous year by early cutting then the plant density is not high. The number of plants which are capable of flowering is much lower and they can easily be detected by their broader leaves and deeper bulbs. The mortality rate amongst the bulbils is high.

TABLE 2. DENSITY OF *ALLIUM PARADOXUM*

Site	Plants / sq.ft	Mature plants / sq.ft
Bartonbury 1	104·2 ± 4·2	8·3
Bartonbury 2	96·2 ± 4·2	6·5
Road-verge 1	89·3 ± 3·4	4·5
Road-verge 2	120·0 ± 4·7	9·0

SEASONAL DEVELOPMENT

Mature plants of *A. paradoxum* have small spherical bulbs about 1–2 cm in diameter lying at soil depths of up to 13 cm. There is a long dormant period between June and October when hardly any trace of the populations can be found above ground. However, bulbils are easily located in the surface litter. Germination of the fleshly bulbs usually begins in October with the production of fine adventitious roots. A blunt shoot emerges and on dissection is seen to consist of an outer modified leaf with a small bud in its axil, a large leaf with another axillary bud and a triquetrous stem with the inflorescence enclosed in a spathe. The modified leaf appears above ground and then the large linear leaf elongates. During early January the buds are suitable for the study of PMC meiosis. During February inflorescence buds are easily found and dissected out and both bulbils and flowers can be found within the spathe. In March the leaves are longer, the apex unrolls to reveal a linear blade and the closed inflorescences are just beginning to appear on the strong triquetrous scapes.

During late March and April the inflorescences are fully emerged, the pedicels and bulbils clustered at the base being subtended by the spathe.

The form of the inflorescence in the Bartonbury populations is very irregular. It usually consists of a spathe subtending several bulbils and a single white flower (occasionally two) on a slender pedicel. Variations recorded consist of the following:

a. Bulbils only.
b. Pedicel bearing bulbils and no flowers.
c. Pedicel bearing bulbils with another pedicel extending from these bearing a flower.
d. Wing-like expansions of the pedicels.

The many-flowered umbel as described by Vvedenskii (1935) has not been found in the Bartonbury populations.

Various Diptera have been observed on the flowers; seed-setting is however poor. The aerial parts gradually wither and the bulbils are scattered over the adjacent area; the plants eventually die back completely during late May and June.

The small plants developed from recently dispersed bulbils are different from those already described. They have very small bulbs that lie on or just beneath the soil surface and occasionally produce a short scape with a few bulbils. They occur in very high densities, have a high mortality rate and rarely flower.

When established plants begin to die back in the autumn the following development occurs. The base of the linear leaf swells and its axillary bud develops to perpetuate growth and produce the bud containing the aerial parts of the following year. The axillary bud of the modified leaf dies or develops into a small offset on the outside of the swollen linear leaf-base.

PLANT CHARACTERS

The other characters studied were those of flower-structure, leaf-length and width, stem-height, bulbil and seed production in established plants (Tables 3 and 5) and cytology.

The normal structure of the hypogynous flower is a perianth of six white segments, six stamens adnate to these, and a trilobed ovary with trilobed stigma. The following variations are common:

a. Deficiencies of one unit in all parts giving P 2+2, A 2+2, $\underline{G}$ (2) with a bilobed stigma.
b. Deficiency in perianth and androecium, with stigmas and style imperfect or absent.
c. Proliferation to give additional stamens and ovary.
d. Perianth segments with one or two of the anthers adnate to the apical margin.
e. Bulbils within the flowers.

The abnormalities of individual parts were scored and the percentage of abnormal flowers calculated; the results are presented in Table 3.

It can be seen that abnormalities occur in all the floral parts and in 72% of the flowering plants examined. A non-random selection of 10 two-flowered plants was scored for inflorescence and floral variation (Table 4).

TABLE 3. PERCENTAGE ABNORMALITY OF INDIVIDUAL FLOWER PARTS

Flower Part		Number abnormal	% abnormal
Gynoecium (whole)		119	47·60
Stigmas		97	38·76
Style		2	0·81
Carpels		45	17·89
Androecium		146	58·64
Perianth		129	51·82
Total normal plants	70		
Total abnormal plants	180		72·00
Total plants sampled	250		

TABLE 4. THE INFLORESCENCE CHARACTERS OF TWO-FLOWERED PLANTS

	Plant no.									
Character	1	2	3	4	5	6	7	8	9	10
No. of pedicels	5	2	2	2	3	2	2	2	2	2
No. of bulbil groups	4	2	2	2	3	2	2	2	2	2
No. of bulbils/ group	14:4: 2:5	10:2	12:1	7:1	7:3:2	9:1	7:1	7:2	9:1	8:1
No. of perianth parts	6:5	6:5	6:4	6:3	6:5	6:4	6:5	6:4	6:6	6:4
No. of carpels	3:2	3:2	3:2	3:2	3:2	3:2	3:2	3:2	3:3	3:2
No. of styles	1:1	1:1	1:1	1:1	1:1	1:1	1:1	1:1	1:1	1:1
No. of stigmas	3:2	3:2	3:2	3:1	3:2	3:1	3:2	3:2	3:3	3:2
No. of stamens	6:4	6:5	6:2	6:3	6:5	6:4	6:5	6:4	6:6	6:2

Leaf-length was determined by measuring the distance from the point of unrolling of the leaf to the apex and this gave a mean length of $31{\cdot}92 \pm 0{\cdot}44$ cm. Leaf-width measurement is greatest near the middle and gave a mean of $1{\cdot}53 \pm 0{\cdot}09$ cm.

Stem-length was taken as that length between the emergence of the scape from the leaf to the point of origin of the spathe. This gave a mean of $21{\cdot}8 \pm 0{\cdot}41$ cm.

As no seed was recorded in the sample plants an extensive search was made for seed-producing plants as it had been observed that ovules were developing in most ovaries. Seed has been found on five plants though only one seed in each case. The seed has a black, rough testa. Offsets have been recorded and

TABLE 5. LEAF-LENGTH AND WIDTH, STEM-LENGTH AND REPRODUCTIVE CAPACITY

Character	Sample size	Mean
Leaf-length	200	30·25 ± 0·60 cm
Leaf-width	2000	1·55 ± 0·09 cm
Stem-length	100	21·80 ± 0·41 cm
Bulbils / plant	177	6·03 ± 0·18
Flowers / plant	177	1·00
Seeds / plant	200	0·0

although no extensive data are available it appears that their contribution to the reproductive capacity is small. The effective reproduction of *A. paradoxum* is therefore by bulbils of which, at Bartonbury, the annual production is in the region of 47·8 bulbils per sq ft.

The chromosome number of the plants was studied in pollen-mother-cells, in pollen-mitosis and in root-tips, all prepared by the Feulgen technique. The chromosome number is $2n = 16$. At meiosis there was abundant evidence for a chromosome inversion as bridges were recorded in the first and second divisions. Fragments were recorded and these were easily seen in pollen grains as well. Data and photographs have been exhibited (Barling 1958).

DISCUSSION

The observations at Bartonbury and adjacent areas show that the species is well established and that bulbils are the main means of reproduction. This has resulted in high plant densities and plants of varying size, only some of which flower. It is likely that the spring-growth reduces shade and aerial competition from its associates in both woodland and road-side swards and contributes to successful colonisation.

The umbel of numerous flowers described by Vvedenskii (1935) has not been found and the poor flowering recorded could be due to bulbil competition during plant development. Gustafsson (1946) considered that in European material the bulbils become more vigorous as flowers are reduced. Bulbil competition probably influences the high percentage of abnormal flowers as the variation found between flowers of the same plant indicates that it is not due to hereditary differences.

Gustafsson (1946, 1947a b) listed three types of embryo-sac degeneration associated with seed sterility in *Allium* and stated that *A. paradoxum* forms slightly developed embryos that never mature. However a small number of fully developed seeds have been found at Bartonbury. The chromosome inversion found will have some effect on fertility but is unlikely to be the main cause of poor seed production. Levan (1937) found that seeds were set if bulbils were removed from bulbiferous *Allium* but no artificial removal has been done in the present study. Gustafsson (1947b p. 296) stated that seed sterility may arise automatically, not owing to any special lethal factor in the gametes or zygote but to bulbil competition for nutrients, and this probably occurs in the Bartonbury populations.

The general importance of bulbils in the Gloucestershire populations contrasts with Vvedenskii's (1935) description "often with bulbils" which suggests that they are usually absent from Russian plants. It is possible that the dominant role of vegetative reproduction and the poor flower production and sexual reproduction in Gloucestershire are responses to changing ecological conditions as the species migrated westward, though more detailed data from its whole range would be needed to clarify this point.

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