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Nuclear DNA variation in the genus *Allium* L. (Liliaceae)

R. M. Labani and
T. T. Elkington

Department of Botany, The University, Sheffield S10 2TN, U.K.

4C nuclear DNA contents were determined for 42 *Allium* species, selected from all major taxonomic sections in the genus. Estimates of nuclear volumes were also made. A range of 4C DNA values from 41·19 pg to 142·78 pg was found, largely unrelated to basic chromosome number, polyploidy or taxonomic group, but correlated with flowering time. The results are discussed in relation to distribution of DNA values in the genus, proportions of chromosome C-banding, breeding systems and climatic adaptation.

INTRODUCTION

The genus *Allium* has been studied cytologically over many years, commencing with the studies of Levan (1931, 1932, 1933, 1935, 1936). The c. 400 perennial species encompass considerable morphological variation and have been divided into a number of subgenera and sections (see Vvedenskii, 1935; Stearn, 1978, 1980; Wendelbo, 1969, 1971) distributed, mainly in temperate regions of Europe, North Africa, Asia and North America, and with outlying species in Ceylon and South Africa (Stearn, 1978). The genus includes series of basic chromosome numbers from $x = 7$ to $x = 10$ and a number of polyploids. Previous determinations of nuclear DNA in *Allium* species have been made by several authors (see table 3). In common with a range of other Angiosperm genera (see Bennett and Smith, 1976; Bennett, Smith and Heslop-Harrison, 1982) these results indicate that there is substantial interspecific variation in DNA amounts within *Allium*, but they only cover a total of 32 taxa in the genus. On the basis of the results of Jones and Rees (1968) for 25 taxa Narayan (1983) has suggested that, in common with several other genera *viz Clarkia*, *Nicotiana* and *Lathyrus*, the nuclear DNA amounts of *Allium* species are dicontinuously distributed, species forming groups in this respect, between which there are regular increases in DNA amounts. The small sample of species in *Allium* for which DNA determinations are so far available make it difficult to comment adequately on any possible quantitative relationships between species, with taxonomic groupings or indeed on other aspects of the genus' biology. We have therefore, as part of a larger study on variation of the genus *Allium*, determined nuclear DNA values for 42 species-chosen to include representatives of all the major morphological groups in the genus.

MATERIALS AND METHODS

Materials

Roots were obtained from seedlings or bulbs obtained from a variety of sources (table 1). Identifications of the majority of accessions were checked by reference to appropriate keys and reference material in the British Museum (Natural History). Seeds of *A. cepa var. Ailsa Craig* were grown on filter paper at the same time and used as a standard.

Methods

Root tips were collected from the samples and *A. cepa* at the same time, fixed directly in 3 : 1 alcohol acetic acid and stored overnight. Fixed root tips were washed in distilled water and hydrolysed in 1N HCl at 60°C for 10 minutes; they were then stained in leuco-basic fuchsin for 2 hours at room temperature, washed in running tap water and placed in distilled water. Squash preparations were

Table 1 Origins of *Allium* species used with initial flowering time and self compatibility type

Subgenera and Sections	Taxon	Initial month of flowering	Compatibility type*	Source
Subgenus Rhizirideum				
Section Rhizirideum	*A. cernuum* Roth.	June	i	Royal Horticultural Society (RHS) Gardens, Wisley, UK
	A. angulosum L.	August	c	Botanical Garden, Vacratot, Hungary
	A. barsczewskii Lipsky	August	—	RHS Gardens, Wisley UK
	A. farreri Stearn	May	c	RHS Gardens, Wisley, UK. (ex Iran)
	A. mairei H. Lev.	August	c	Amsterdam, Free University Botanical Garden, Holland
	A. ochroleucum W. et Kit.	August	i	Copenhagen Botanical Garden, Denmark
	A. obliquum L.	July	c	Botanical Garden, Goteborg, Sweden
	A. saxatile Bieb.	July	c	Botanical Garden, Goteborg, Sweden
Section Schoenoprasum	*A. schoenoprasum* L.	July	c	University of Louis Pasteur, Strasbourg, France
	A. lineare L.	June	c	Botanical Garden, Karl Marx University, E. Germany
Section Cepa	*A. cepa* L. cv. Ailsa Craig	June	c	Suttons Seeds Ltd
	A. altaicum Pall.	July	—	Botanical Garden, Sheffield University, UK
	A. fistulosum L.	July	c	RHS Garden, Wisley, UK
	A. galanthum Kar. and Kir.	August	c	Botanical Garden, Sheffield University, UK
	A. pskemense B. Fedtsch.	July	—	R. Dadd
	A. roylei Stearn	July	—	R. Dadd
Section Anguinum	*A. victorialis* L.	July	—	Botanical Garden, Sheffield University, UK
Subgenus Allium				
Section Molium	*A. geyeri* Wats.	June	—	Royal Botanic Garden, Kew, UK
	A. moly L.	June	i	Van Tubergen, Holland
	A. oreophilum C. A. Meyer	June	c	Van Tubergen, Holland
	A. scorzonerifolium Desf. ex DC.	June	—	R. Dadd
	A. trifoliatum Cyr	May	i	R. Dadd
	A. wallichii Kunth.	May	—	R. Dadd
Section Briseis	*A. triquetrum* L.	May	c	Van Tubergen, Holland
Section Ophioscorodon	*A. ursinum* L.	April	—	Grindleford, Derbyshire, UK
Section Scorodon	*A. parciflorum* Viv.	July	—	Botanical Garden, Sheffield University, UK
Section Codonoprasum	*A. flavum* L.	July	c	Botanical Garden, Copenhagen, Denmark
	A. carinatum subsp. *pulchellum* Bonnier and Layens	July	c	Botanical Garden, Copenhagen, Denmark
	A. carinatum L. subsp. *carinatum*	July	c	Botanical Garden, Copenhagen, Denmark
	A. oleraceum L.	July	i	Botanical Garden, Copenhagen, Denmark
Section Allium	*A. heldreichii* Boiss.	May	—	Royal Botanic Garden, Kew, UK
	A. sphaerocephalon L.	August	—	Botanical Garden, Copenhagen, Denmark
	A. ampeloprasum L.	August	—	Royal Botanic Garden, Kew, UK
	A. porrum L. cv. Musselburgh	June	—	Suttons Seeds Ltd
Subgenus Melanocrommyum				
Section Melanocrommyum	*A. atropurpureum* Waldst. and Kit.	June	c	Van Tubergen, Holland
	A. aflatunense B. Fedtsch.	May	i	Van Tubergen, Holland
	A. cristophii Trautv.	June	c	Van Tubergen, Holland
	A. giganteum Rgl.	July	i	Van Tubergen, Holland

Table 1 continued

Subgenera and Sections	Taxon	Initial month of flowering	Compatibility type*	Source
	A. macleanii Baker	June	—	Van Tubergen, Holland
	A. stipitatum Rgl.	June	i	Van Tubergen, Holland
	A. karataviense Rgl.	July	i	Van Tubergen, Holland
	A. rosenbachianum Rgl.	June	i	Van Tubergen, Holland
	A. schubertii Zucc.	June	c	Van Tubergen, Holland

* c, self compatible; i, incompatible (Data from Al-Sheikh Hussain, 1977; Badr, 1977; El-Gadi, 1976; El-Maghbub, 1982; Labani, 1984).

made in a drop of distilled water and made permanent by freezing in liquid carbon dioxide and mounting in Euparal. Measurements of DNA were made within two days using a Vickers M86 scanning microdensitometer at λ_{max} (approximately 570 nm). Nuclei in early or mid-prophase (4C) were selected for scanning. Two readings of absorption were made on each nucleus and the background.

From these figures the nuclear DNA amounts for each sample was calculated using the formula:

$$4C \text{ nuclear DNA} = \frac{A}{B} \times C$$

where $A = 4C$ nuclear DNA value of *A. cepa* var. *Ailsa Craig* i.e., 76·00 pg from the determinations of Van't Hof (1965) and Bennet and Smith (1976). $B =$ mean absorption figure measured for the *A. cepa* sample. $C =$ mean of the absorption figures measured for the sample nucleus minus those of the background readings.

DNA values reported are means and standard errors of 10 nuclei per root tip for each of three root tips taken from a different seedling or bulb. The errors inherent in microdensitometry are discussed in detail by Bennett and Smith (1976) and D. J. Goldstein (1981).

Photographs were taken of interphase nuclei from each *Allium* species, using a Zeiss Ultraphot microscope with phase contrast optics. Prints were made at a final magnification of ×3500. Nuclear volumes were determined using a Graphics tablet and Apple II micro-computer together with a program for computing volumes from readings of nuclear circumference; this assumed nuclei to be spherical, following Sparrow and Nauman (1974).

RESULTS AND DISCUSSION

Nuclear DNA values

The results (table 2) show that there is considerable variation in 4C nuclear DNA contents in the 42 *Allium* species for which determinations were made. Each DNA value represents a single sample of the species; a comparison with other published values (mostly also listed in Bennett and Smith 1976; Bennett, Smith and Heslop-Harrison, 1982) is given in table 3. Some of the results show some similarity to previously published values but generally lie outside their 95 per cent confidence limits (table 3). Only in *A. porrum* is a previously published figure (117·0 pg; Murin 1976) near to the 95 per cent confidence limit. The other previously published figure for this species (48·2 pg; Ranjekar, Pallota and Lafontaine (1978)), is very discrepant. The high correlation between the nuclear DNA content and nuclear volume (fig. 3) determined in the present investigation supports strongly the value recorded here. It is therefore difficult to explain the difference unless Ranjekar *et al.* (1978) were wrong in their DNA determination or species identification. In *A. schoenoprasum* our value is almost double that recorded by Jones and Rees (1968) for the diploid *A. sibiricum* which Stearn (1978) includes within *A. schoenoprasum.*

In addition to the species listed in table 3 a 4C DNA value of 151·6 pg is given for *A. globosum* Bieb. by Jones and Rees (1968); this value, the highest to be recorded in the genus, should be compared with the value of 44·59 pg for *A. saxatile* determined here, since Stearn (1978) has shown *A. globosum* to be included within *A. saxatile.* Jones (personal communication) has stated that independent identifications of plants grown by Jones and Rees (1968) were not made, so this and some other values given by them may not be attributable to listed species.

Distribution of nuclear DNA values

Narayan (1983) has proposed that in *Allium*, as in several other genera, the distribution of DNA amounts between species is discontinuous with species group 2C DNA means at intervals of

Table 2 Chromosome number, polyploid level, 4C nuclear DNA value ± S.E., ($n = 30$) 4C DNA amounts per genome and chromosome, mean chromosome length ± S.E. and mean nuclear volume for all species studied

Subgenera and Sections	Taxon	Chromosome number	Polyploid level	4C DNA value (pg) ±S.E.	4C DNA genome (pg)	4C DNA/ chromosome	Mean chromosome length ±S.E. (μm)	Nuclear volume (μm^3)
Subgenus Rhizirideum								
Section Rhizirideum	*A. cernuum*	14	2×	91·24 ± 0·91	45·62	6·52	13·22 ± 0·53	1426·84
	A. angulosum	16	2×	64·54 ± 0·53	32·27	4·03	7·51 ± 0·30	1092·12
	A. barsczewski	16	2×	71·78 ± 1·57	35·89	4·49	N/A	1463·22
	A. farreri	16	2×	120·71 ± 1·47	60·36	7·54	11·15 ± 0·91	1687·80
	A. mairei	16	2×	69·47 ± 0·94	34·74	4·34	7·80 ± 0·28	1011·80
	A. ochroleucum	16	2×	72·82 ± 0·48	36·41	4·55	6·91 ± 0·17	1196·30
	A. obliquum	16	2×	41·19 ± 0·28	20·60	2·57	6·00 ± 0·15	759·42
	A. saxatile	16	2×	44·59 ± 0·65	22·30	2·79	6·73 ± 033	771·36
Section Schoenoprasum	*A. schoenoprasum*	32	4×	60·66 ± 0·55	15·16	1·90	5·38 ± 0·12	1079·84
	A. lineare	48	6×	102·74 ± 0·93	17·12	2·14	4·80 ± 0·13	1722·24
Section Cepa	*A. altaicum*	16	2×	54·21 ± 0·99	27·10	3·39	N/A	1211·62
	A. fistulosum	16	2×	56·20 ± 0·60	28·10	3·51	8·73 ± 0·38	740·99
	A. galanthum	16	2×	69·53 ± 0·73	34·76	4·35	8·98 ± 0·56	1256·18
	A. pskemense	16	2×	74·81 ± 0·52	37·41	4·68	N/A	1236·67
	A. roylei	16	2×	70·03 ± 0·68	35·02	4·38	N/A	1178·98
Section Anguinum	*A. victorialis*	16	2×	86·42 ± 1·41	43·21	5·40	12·95 ± 0·31	1379·28
Subgenus Allium								
Section Molium	*A. geyeri*	14	2×	108·14 ± 0·64	54·07	7·72	N/A	1522·90
	A. moly	14	2×	101·98 ± 0·85	50·99	7·28	12·28 ± 0·43	1781·44
	A. oreophilum	14	2×	72·36 ± 0·65	36·18	5·17	10·26 ± 0·14	1419·90
	A. scorzonerifolium	14	2×	87·26 ± 1·13	43.63	6·23	12.00 ± 0·37	1233·86
	A. trifoliatum	21	3×	73·85 ± 1·48	24·62	3·52	8·55 ± 0·43	1219·22
	A. wallichii	28	4×	119·13 ± 0·96	29·78	4·26	N/A	1921·02

Section Briseis	*A. triquetrum*	18	2×	89·15 ± 0·94	44·58	4·95	8·66 ± 0·55	1346·68
Section Ophioscorodon	*A. ursinum*	14	2×	142·78 ± 1·01	71·39	10·20	24·65 ± 0·63	2226·28
Section Scorodon	*A. parciflorum*	16	2×	91·59 ± 0·78	45·80	5·72	12·01 ± 0·41	1496·08
Section Codonoprasum	*A. flavum*	16	2×	84·90 ± 2·18	42·45	5·31	7·03 ± 0·16	1309·20
	A. carinatum subsp. *pulchellum*	16	2×	70·60 ± 1·00	35·30	4·41	8·40 ± 0·30	1112·16
	A. carinatum subsp *carinatum*	24	3×	100·56 ± 1·55	33·52	4·19	9·30 ± 0·20	1520·70
	A. oleraceum	40	5×	105·56 ± 1·12	21·11	2·64	7·92 ± 0·17	1487·74
Section Allium	*A. heldreichii*	16	2×	88·67 ± 1·26	44·34	5·54	9·30 ± 0·23	1479·40
	A. sphaerocephalon	16	2×	49·65 ± 0·86	24·83	3·10	8·46 ± 0·23	1148·58
	A. ampeloprasum	32	4×	119·64 ± 1·16	29·91	3·74	8·93 ± 0·25	1641·62
	A. porrum	32	4×	121·15 ± 1·96	30·29	3·79	10·23 ± 0·35	1643·24
Subgenus Melanocrommyum								
Section Melanocrommyum	*A. atropurpureum*	16	2×	113·66 ± 1·33	56·83	7·10	12·56 ± 0·39	1693·08
	A. aflatunense	16	2×	124·59 ± 1·01	62·29	7·79	11·07 ± 0·27	1784·44
	A. cristophii	16	2×	96·41 ± 0·90	48·20	6·03	12·64 ± 0·35	1391·98
	A. giganteum	16	2×	82·39 ± 1·24	41·20	5·15	11·31 ± 0·32	1358·32
	A. macleanii	16	2×	117·38 ± 0·68	58·69	7·34	10·48 ± 0·32	1665·94
	A. stipitatum	16	2×	109·12 ± 1·94	54·56	6·82	10·62 ± 0·28	1490·80
	A. karataviense	18	2×	96·18 ± 1·07	48·09	5·34	9·82 ± 0·44	1567·49
	A. rosenbachianum	16	2×	115·84 ± 1·32	57·92	7·24	10·65 ± 0·27	1641·96
	A. schubertii	16	2×	111·65 ± 0·96	55·83	6·98	16·71 ± 0·46	1542·20

* Data from Al-Sheikh Hussain, 1977; Badr, 1977; El-Gadi, 1976; El-Maghbub, 1982; Labani, 1984 and S. White (personal communication)

Table 3 Comparison between *Allium* nuclear DNA values determined and their 95% confidence limits and other published values

Taxon	Chromosome number ($2n$)	4C DNA value determined (pg)	Confidence limits	Published 4C DNA values (pg)
A. cernuum	14	91·24	89·45–93·03	66·4 (Jones and Rees, 1968)
A. angulosum	16, 32	64·54 ($2n = 16$)	63·50–65·58	82·4 ($2n = 32$; Jones and Rees, 1968)
A. schoenoprasum	16, 32	60·66 ($2n = 32$)	59·57–61·74	30·4 ($2n = 16$; *A. sibiricum*; Jones and Rees, 1968)
				31·2 ($2n = 16$; Ranjekar *et al.*, 1978)
				33·8 ($2n = 16$; Jones and Rees, 1968)
A. fistulosum	16	56·20	55·02–57·38	50·1 (Van't Hof, 1965)
				52·6 (Jones and Rees, 1968)
A. galanthum	16	69·53	68·10–70·96	48·8 (Jones and Rees, 1968)
A. moly	14	101·98	100·31–103·64	90·4 (Ranjekar *et al.*, 1978)
A. oreophilum	14	72·36	71·10–73·63	89·2 (*A. ostrowskianum*; Ranjekar *et al.*, 1978)
A. triquetrum	18	89·15	87·31–90·99	72·6 (Jones and Rees, 1968)
A. carinatum subsp. *carinatum*	16, 24	100·56 ($2n = 24$)	97·53–103·60	44·8 ($2n = 16$; Bösen and Nagl, 1978)
				65·3 ($2n = 24$; Nagl and Fusenig, 1979)
A. porrum	32	121·15	117·31–124·99	48·2 (Ranjekar *et al.*, 1978)
				117·0 (Murin, 1976)
A. karataviense	18	96·18	94·08–98·29	90·8 (Jones and Rees, 1968)

4·25 pg. Since his data were restricted to 25 taxa studied by Jones and Rees (1968) it was thought worthwhile to plot the distributions of the 75 DNA values available for the genus (see table 2; Bennett and Smith 1976; Ranjekar *et al.* 1978; Bennett, Smith and Heslop-Harrison, 1982). Figure 1 plots the distribution as DNA 4C values and shows that although some discontinuities exist, there are no regular groups with means separated at 8·5 pg and alternating discontinuities. Comparison of the values of Jones and Rees (1968) with subsequent determinations (fig. 1) shows that the apparent discontinuities recognised by Narayan (1983) are the result of inadequate sampling in this large genus. It is possible that some of the discontinuous DNA distributions suggested for other genera (Rees and Narayan, 1981; Narayan, 1982, 1983) may also result from a similar sampling error, particularly in *Lathyrus* where determinations of only 24 North temperate species are available from a world total of 130 species (Willis, 1966).

DNA contents in relation to basic chromosome number, polyploid levels and genomes

The species sampled vary in ploidy level from 2 to 6× and have basic chromosome members of $n = 7$, 8 and 9 (table 2). The 4C nuclear content per nucleus ranges from 41·19 pg in *A. obliquum* ($2n = 16$) to 142·78 pg in *A. ursinum* ($2n = 14$) showing that there are significant differences in nuclear DNA content, amounting to a 4 fold variation, which are unrelated to ploidy level. Also there is no correlation between variation in basic number and DNA content; an analysis of variance of mean 4C DNA amounts of the species studied, grouped by base number ($x = 7$, 8 species; $x = 8$, 32 species; $x = 9$, 2 species) shows that there is no significant variation (Table 4). These findings confirm those of Jones and Rees (1968).

4C nuclear DNA values per genome have been calculated (table 2) and show a wide variation between species. In the closely related *A. carinatum*

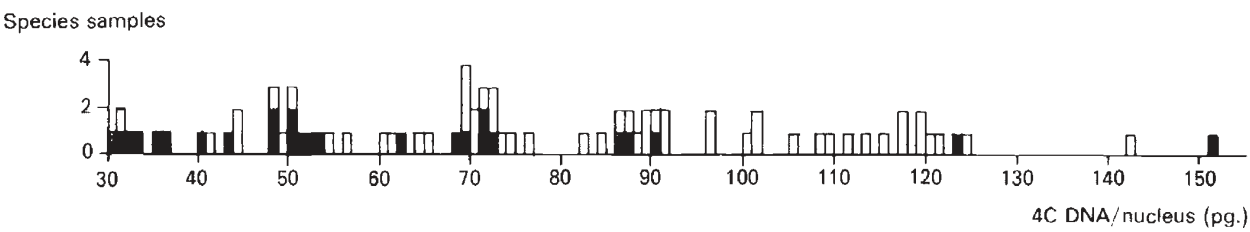

Figure 1 Histogram showing distribution of all *Allium* nuclear DNA values determined, published figures recalculated as 4C values where necessary; those of Jones and Rees (1968), as used by Narayan (1983) are shaded.

subsp. *carinatum* (4C DNA/genome 33·52 pg) and subsp. *pulchellum* (4C DNA/genome 35·30 pg) the similar DNA amounts/genome suggest that *A. carinatum* subsp. *carinatum* is an autopolyploid based on *A. carinatum* subsp. *pulchellum*; this has previously been proposed on cytological grounds (Levan, 1937; Al-Sheikh-Hussain, 1977; Vosa, 1976). Constancy in DNA content/genome has also been shown in an autopolyploid series in *Ranunculus ficaria* (Smith and Bennett, 1975). In *A. schoenoprasum* the DNA content/genome in the tetraploid studied (15·16 pg) is consistent with the values for diploid samples determined by other authors (15·2–16·9 pg) (see table 3).

DNA content and chromosome length

There is a significant relationship (correlation coefficient 0·812; $p < 0·001$; $n = 36$) between the mean 4C nuclear DNA value per chromosome and the mean chromosome length in the complement of all taxa studied (table 2, fig. 2). This indicates that DNA amount increases proportionately with increasing mean chromosome length and that the amount of DNA per unit chromosome length in *Allium* species remains uniform. A similar relationship has been shown by Nagl and Ehrendorfer (1974) in the *Anthemideae* (Asteraceae) and in *Allium* between DNA content and chromosome volume (Jones and Rees, 1968).

DNA content and Nuclear Volume

Mean nuclear volumes have been estimated for all taxa, for which DNA determinations were made (table 2). These results show that there is a significant variation in nuclear volume between the *Allium* species studied, with a range of 741·0 μm^3 for *A. fistulosum* ($2n = 16$) to 2226·3 μm^3 for *A. ursinum* ($2n = 14$); there is a close association (correlation coefficient 0·814; $p < 0·001$; $n = 42$) between the amount of DNA per nucleus and its volume (fig. 3), indicating that the DNA concentration per unit volume is constant in all *Allium* species studied. This relationship was first proposed by Sparrow and Miksche (1961) and Van't Hof and Sparrow (1963) and has been confirmed in a range of angiosperms e.g., *Phaseolus* (Ayonadhu, 1974), *Lathyrus*, *Vicia* (Rees, Cameron, Hazarika and Jones 1966), *Anthemideae* (Nagl and Ehrendorfer, 1974) and Gramineae (Sparrow and Nauman, 1974). In *Eu-Sorghums*, however, Paroda and Rees (1971) reported a significantly different correlation in this respect between the wild and cultivated species, indicating that there is a sharp distinction between these two species groups in terms of DNA density.

DNA content and C-banding

It has been shown (cf. Flavell, 1982) that much increase in DNA is due to sequence amplification. An association between highly repetitive sequences and heterochromatin has been demonstrated in both animals (John and Miklos, 1979) and plants (Appels, Driscoll and Peacock, 1978; Bedbrook *et al.*, 1980; Deumling and Greilhuher, 1982). Furthermore positive correlations between the percentage of C-banded heterochromatin in the karyotype and DNA content have now been shown for a

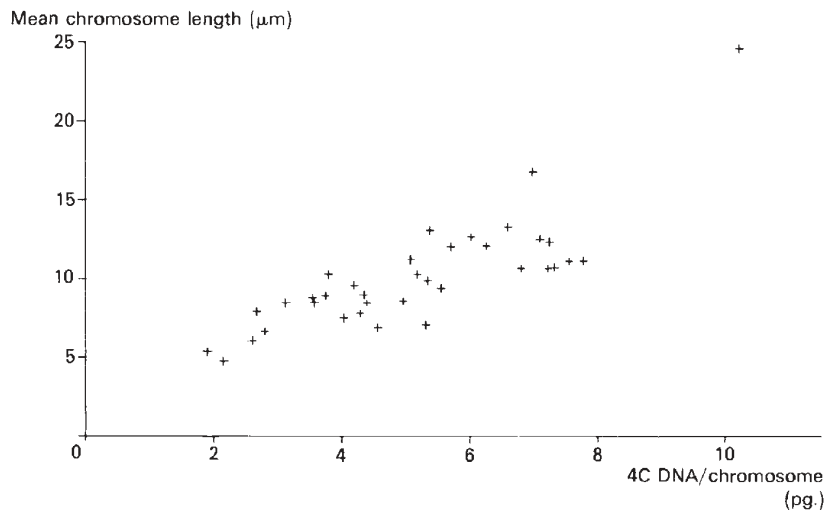

Figure 2 Relation of mean 4C DNA values per chromosome for all *Allium* species studied and the mean chromosome lengths, obtained from mitotic metaphase root tip cells, pretreated with 0·05% colchicine for 4 hours and stained with leuco-basic fuchsin.

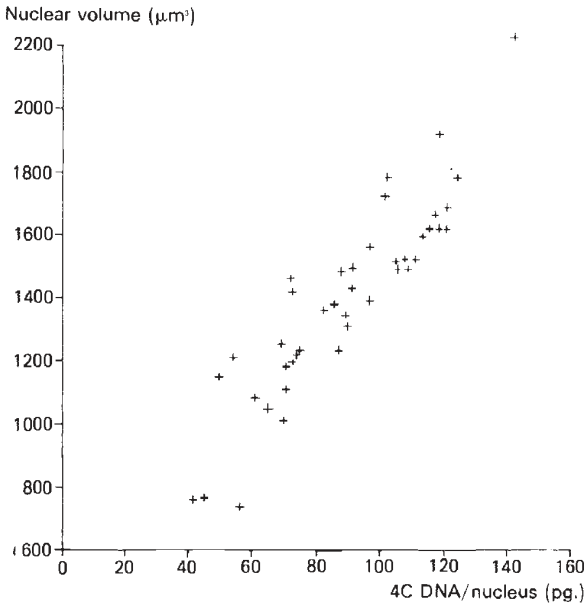

Figure 3 Relation of mean 4C DNA values per nucleus and mean nuclear volumes of interphase cells determined from 30 nuclei

range of flowering plants including *Lolium* (Thomas, 1981), *Secale* (Bennett, Gustafson and Smith, 1977), *Gibasis karwinskyana* (Kenton, 1983) and *Zea mays* (Rayburn, Price, Smith and Gold, 1985). *In Allium*, however, there is no correlation between increase in DNA nuclear content and proportion of C-banded material in the karyotype. Indeed *A. ursinum* with the largest DNA content (71·39 pg 4C DNA/genome) has one of the lowest proportions of C-banded chromosome material in the genus (0·4 per cent) (Labani, 1984), while *Allium* species with the highest proportions, in section *Codonoprasum* (Vosa, 1976; Al-Sheikh-Hussain, 1977), have 10–30 per cent of C-banded material, but only moderate DNA amounts (21·11–42·45 4C DNA/genome). If therefore there is any relationship between nuclear DNA and repetitive DNA it would appear to be unrelated to the proportion of C-banded heterochromatin.

Table 4 Analysis of variance of species 4C DNA amounts partitioned by basic chromosome number

ANOVA source	df	S.S.	M.S.	F
Basic number	2	1148·6	574·3	0·95 ($P > 0·05$)
Residual	39	23484·9	4602·2	

DNA content and taxonomic groups

To investigate possible correlations between taxonomic groups and DNA nuclear content in *Allium* an analysis of variance (Table 5) was carried out on DNA amounts using subgenera to partition the between section variance according to the taxonomic classification of Stearn (1978) given in table 2. The variance ratio is not significant showing that there is no correlation between DNA nuclear content and subgenera for this sample of species.

Table 5 Analysis of variance of mean sectional 4C DNA amounts partitioned by subgenera, according to the taxonomic classifications of Stearn (1978) (see table 2)

ANOVA source	df	S.S.	M.S.	F
Subgenus	2	1294·5	647·2	3·649 ($P > 0·05$)
Residual	8	1419·1	177·4	

DNA content and breeding system

Although there are no direct data on the breeding systems of the species studied, some data are available on self compatibility and incompatibility in some species studied (table 1). Comparison of DNA values for these species shows that self-compatible species have lower DNA amounts, (4C mean of 18 species, 80·27 pg) than self-incompatible species (4C mean of 10 species 97·36 pg); but these differences are not significant (t-value 2·003; df = 26; $P > 0·05$). There is no evidence therefore of an association between nuclear DNA content and breeding system in *Allium* species. Differences in nuclear DNA content related to breeding system have been described in several other genera, some have outbreeding species with higher DNA contents *i.e.*, *Lathyrus* (Rees and Hazarika, 1969; Rees and Jones, 1972) and *Microseris* (Price and Bachmann, 1975; Price, 1976) where the differences are also correlated with the perennial and annual habits of the out- and in-breeding species respectively; by contrast in *Lolium* outbreeding species have lower nuclear DNA contents than inbreeding species (Rees *et al*, 1966; Rees and Jones, 1967, 1972).

DNA content and adaptation

Recent explanations of variation in DNA content between species have often focussed on selective mechanisms. Thus Bennett (1972) and Smith and

Bennett (1975) have suggested minimum generation time and life cycle type as being selective factors. More recently Grime and Mowforth (1982) and Grime (1983) have suggested that the nuclear DNA content of vascular plants has been subject to climatic selection, plants with large nuclear DNA contents being particularly characteristic of certain temperate zone geophytes and grasses in which early growth is achieved by expansion of large cells formed during warmer conditions in the previous autumn. In contrast fast-growing summer species, particularly colonising species, tend to have low DNA values/nucleus.

In *Allium* the species are distributed over a very wide area including Asia, North Africa, Europe and North America, the majority of species being found in temperate, mountain and mediterranean regions with well marked seasons, but with differing environmental conditions. It is possible therefore that DNA amounts in *Allium* may be related to environmental factors such as temperature, day length and humidity; some *Allium* species including almost all species in subgenus *Melanocrommyum* have originated from arid areas in Asia and North Africa, some e.g., many species in section *Molium*, grow in a Mediterranean climate, while other species have originated from more temperate regimes in Europe and North America. Although it has not been possible here to investigate any possible relationship between climatic adaptation and DNA amount, data are available on the flowering time of the *Allium* species studied. The month of initial flowering (table 1) plotted against DNA content is given in fig. 4. The correlation coefficient is highly significant ($p < 0{\cdot}001$); the early flowering species have most DNA and *A. ursinum*, the only species to flower in April at Sheffield, has the highest DNA content. Since time of flowering is related to growth and development, this result is consistent with the suggestions of Grime and Mowforth (1982) and Grime (1983), but considerable knowledge of the natural climatic ranges of the species and their phenologies would be necessary for any further investigation.

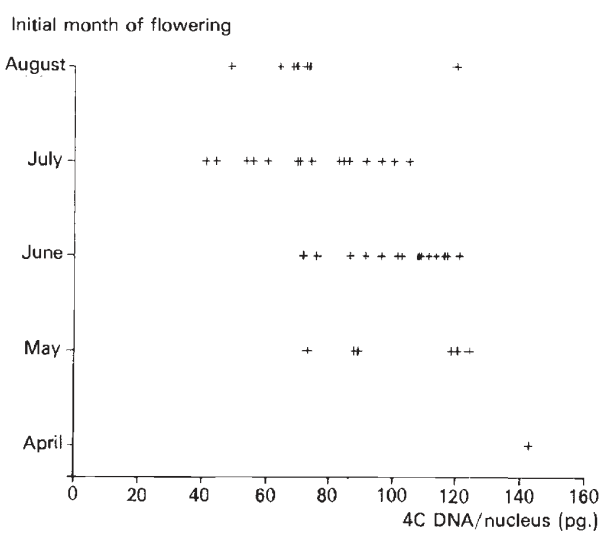

Figure 4 Relation of initial month of flowering of *Allium* species, determined from established plants growing in open ground at Sheffield University Experimental Garden, and mean 4C DNA values; correlation coefficient = −0·61 ($p < 0{\cdot}001$; $n = 43$).

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