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Contrasting patterns of genetic structure in the South African species *Androcymbium bellum*, *A. guttatum* and *A. pulchrum* (Colchicaceae)

Juli Caujapé-Castells*[,a,1], Joan Pedrola-Monfort[b], Núria Membrives[b]

[a]*Department of Botany and Institute of Cellular and Molecular Biology, University of Texas at Austin, Austin, Texas 78713-7640, USA*

[b]*Estació Internacional de Biología Mediterrània-Jardí Botànic Marimurtra, Ap. de correus 112, 17300 Blanes Girona, Spain*

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Abstract

Spatial autocorrelation analyses on genetic variability from three isozymic loci was used to explore the presence of possible patterns of genetic structure in four populations representing the South African species *Androcymbium bellum*, *A. guttatum* and *A. pulchrum*. Consistent profiles of short-distance genetic structure are only detected in patchy populations (*A. bellum* and *A. guttatum*), regardless of the sharp ecological differences between them. In the absence of microhabitat heterogeneity, our result strongly suggests that the predominant action of assortive mating (in *A. bellum*) and of vegetative reproduction (in *A. guttatum*) fostered the creation and enhancement of physical clumps that correspond to genetically related plants. A much lower incidence of both clonal propagation and outcrossing in the two continuous populations of *A. pulchrum* examined explains why isozymic variability is not spatially structured in this species.

Keywords: *Androcymbium*; Colchicaceae; South Africa; Isozymes; Genetic structure; Spatial autocorrelation

1. Introduction

Androcymbium bellum Schltr. et K. Krause, *A. pulchrum* Schltr. et K. Krause and *A. guttatum* Schltr. et K. Krause are morphologically distinct species ascribed to the

*Corresponding author. Tel.: 0034 93 2318 534; e-mail: caujape@lix.intercom.es

[1]present address: C. de la Marina 170 3-3, 08013 Barcelona, Spain.

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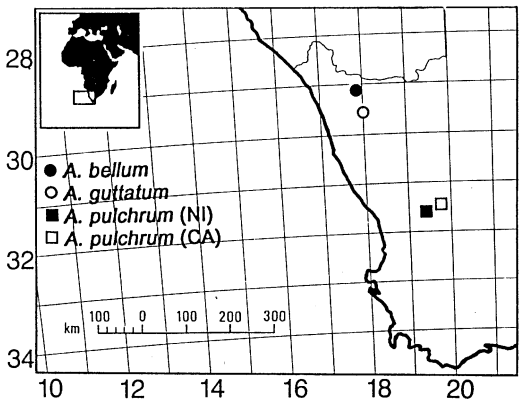

Fig. 1. Geographic site map of the four accessions considered.

sections *Erythrostictus* Bentham (*A. bellum*) and *Androcymbium* (Margelí et al., 1998) of the genus *Androcymbium* Willd. These plants are hermaphroditic cormose monocots whose populations occur in substantially different ecological conditions along the Atlantic fringe of South Africa (Fig. 1). The genus *Androcymbium* has economical importance because these plants produce the alkaloid Colchicine.

At present, the morphological descriptions of South African *Androcymbium* species available in the literature (Baker, 1874, 1880; Krause, 1920) are only cursory and frequently misleading. Until recently, they had never been surveyed for molecular variation. These facts have stood in the way of a proper understanding of their populational and reproductive biology.

High levels of isozymic variability for all the species of *Androcymbium* distributing in north Africa have been reported recently (Caujapé-Castells and Pedrola-Monfort, 1994, 1996). A detailed survey of the north African *A. gramineum* for spatial autocorrelation (Caujapé-Castells and Pedrola-Monfort, 1997) demonstrated that considerable amounts of variability were maintained in that endemic species by a combined action of vegetative reproduction and outcrossing. No information regarding either the amounts or the strategies of maintenance of variability exists for any of the southern African species. This kind of knowledge would be crucial to shed light on the poorly understood relationship between species richness and narrow endemism (Cody, 1986; Gentry, 1986; Myers and Giller, 1988; Cowling et al., 1992) that is suggested by the general increase in species richness with decreasing latitude (Pianka, 1966; Brown, 1988). *Androcymbium* is a conspicuous example of this pattern: only six species are described in northern Africa, versus about 35 in southern Africa (Krause, 1920; Müller-Doblies and Müller-Doblies 1984, 1990).

Recent evidence from chloroplast restriction site changes (Caujapé-Castells et al., in mss.) and isozyme variation patterns (Membrives et al., in prep.) for a thorough

representation of the genus including *A. bellum*, *A. guttatum* and *A. pulchrum* hint at high levels of variability in these three species coupled with substantial differences both within and among populations.

In this paper, we survey two patchy (*A. bellum* and *A. guttatum*) and two continuous (*A. pulchrum*) South African stands using the information provided by isozymic markers. Our main objective is to assess possible patterns of genetic structuring in space. Particularly in the present environment of restricted knowledge, we believe that our research will provide basic insights to understand the influence of different ecological conditions on the distribution of genetic variability in southern African *Androcymbium*.

2. Materials and methods

2.1. Ecological context

The three species considered occur in very different environments. *A. bellum* is found in the vegetational zone named Bloomkoolganna Veld (a calcareous variation of the arid Karoo), and can attain high numbers after good rains, which fall mostly in autumn following an extremely erratic regime. This is by nature a region where grasses are the only perennial plants (Acocks, 1988). The sampled specimens occurred in sandy, well-drained soils.

A. guttatum's stand was on a rocky hill top in the Great Karoo, a Veld type characterised by stony plains almost completely denuded of soil, where succulents are relatively scarce. The vegetation is in general very sparse, with stunted shrubs (especially in rocky locations).

The sampled *A. pulchrum* stands occur only some 20 km apart from each other in the area of Calvinia, in the overlap between the succulent Karoo and the arid Karoo. This is the vegetational type of the low altitude, hot, arid areas with a winter-concentrated or through the year sparse rainfall. It is dominated by shrubs, with few trees (Acocks, 1988).

According to Boucher and Moll (1981) edaphic conditions are also different for the four stands. *A. bellum* grows in very shallow calcareous sands and loams, *A. guttatum* in weakly developed alluvial soils with lime acummulations in bottom lands, *A. pulchrum* from Nievoudtville (NI) in mainly acid arenosols, and *A. pulchrum* from Calvinia (CA) in lithosols and bare rocks.

2.2. Plant material

The physical distribution of plants in the populations of *A. bellum* and *A. guttatum* was patchy, with clear-cut, easily identifiable clumps. These were more readily appreciable in *A. guttatum*, due to its growing exclusively within narrow clefts in plaques of stone. By contrast, both populations of *A. pulchrum* formed characteristically continuous (but not very dense) prairies in a muddy soil. Crossing experiments reveal that *A. guttatum* is an obligate outcrosser, while *A. pulchrum* and *A. bellum* are

preferential outcrossers that display only very low levels of self-fertilization in the greenhouse. Capsules are dehiscent in the three species.

2.3. Sampling

Because these species are narrow endemics, sampling had to be restricted to a maximum of two populations per species. Intra-populational sampling in the two patchy stands was executed along all clumps, whereas in the two populations of *A. pulchrum* a representative collection of points was selected from the continuum of plants. In all cases, individual plants were assigned a code and a pair of map coordinates before being unearthed. Subsequently, they were put into paper bags, carried to the Marimurtra Botanical Garden and planted in a greenhouse using a homogeneous substrate.

2.4. Electrophoretic assays

Tips of fresh leaves were cut for horizontal starch-gel electrophoretic assays, which were carried out using the same protocols as with the north African *Androcymbium* species (Pedrola-Monfort and Caujapé-Castells, 1994). We assayed protocols for 17 isozymic loci. In this work, we use data from the only three loci where we detected intra-populational variability: phosphoglucomutase (PGM) E.C. 5.4.2.2, phosphoglucose isomerase (GPI) E.C. 5.3.1.9 and phosphogluconic dehydrogenase (6PGD) E.C.1.1.1.44. Loci GPI and PGM were interpreted following the hypothesis of codominance. The allele corresponding to the fastest migrating isozyme was assigned number 1, and each successively slower isozyme was given a sequentially higher number. Enzyme mobilities were ascertained through side-by-side comparisons of allelic variants on the same gel. In all cases, isozymes had banding patterns consistent with their expected quaternary structure. We interpreted PGM as containing two monomeric loci corresponding to the faster (PGM-1) and to the slower (PGM-2) bands towards the anode. Only one band was visible for PGM in the intra-populational localities labelled 6 in *A. bellum*, and 1–4 and 10 in *A. pulchrum* from NI (Fig. 2). In these cases, we interpreted two alleles (one corresponding to PGM-1 and one to PGM-2) with identical mobility based on the higher intensity of these bands. Locus GPI was interpreted as a dimer.

We did not carry out a program of crosses to check the inheritance of the alleles because of the long time taken (3–4 yr) for plants grown from seed to develop leaves suitable for electrophoresis. Allelic data were recoded so that each mapped plant was assigned a value of 0.0, 0.5 or 1.0 depending on the absence, presence in heterozygosity or presence in alternative homozygosity of every submitted allele at every locus, respectively.

Since banding patterns associated with 6PGD were not immediately interpretable in terms of genotypic frequencies (see Fig. 2), we coded the presence (1) or absence (0) of all the observed bands. For this locus, the fastest anodally migrating band was assigned the number one and each subsequently slower band, the corresponding number in the numerical sequence.

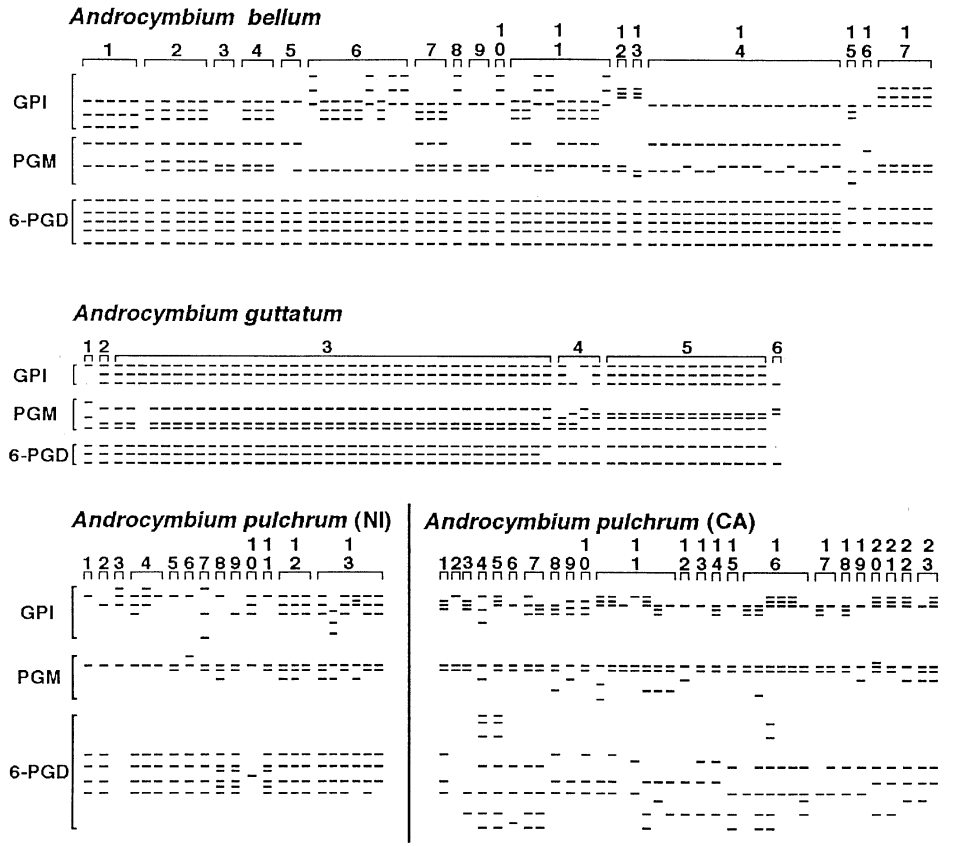

Fig. 2. Schematisation of the banding patterns obtained for all the sampled individuals in the populations of *A. bellum*, *A. guttatum* and *A. pulchrum* from Nievoudtville (NI) and Calvinia (CA). Sample sizes are, respectively, 68, 59, 22 and 37 individuals. The three considered loci are represented. Integer numbers label intra-populational localities from where plants were drawn. Blank spaces for 6PGD at the third lane in NI and at the second lane in CA correspond to individuals whose patterns for this locus could not be reliably ascertained and were thus left uninterpreted. The empty lane for PGM in *A. guttatum* corresponds to an individual whose banding pattern was not visible.

2.5. Spatial autocorrelation analyses

For each of the four considered populations, the resulting data matrix and a location matrix containing the individual intra-populational coordinates were entered in SAAP version 4.3 (Wartenberg, 1989) and subjected to spatial autocorrelation analyses. This is a statistical methodology that tests whether the observed value of a nominal, ordinal or interval variable at one locality is independent of the variable values at neighboring localities. When dependence exists, the variable is said to exhibit spatial autocorrelation (Sokal, 1979). We used Moran's I as the coefficient of spatial

autocorrelation (Cliff and Ord, 1973), which was calculated by SAAP. Moran's I varies from -1 to $+1$, and its expected value is given by the expression $E(I) = -1/(n-1)$, where n is the total number of individuals in the sample (Sokal and Oden, 1978; Oden 1984). Departures from the expected value of Moran's I for each distance class, as well as overall correlogram significances were also tested for every band/allele in SAAP. Correlograms (which plot the change in Moran's *I* through distance classes) were drawn considering five distance classes.

We assayed two codings of isozymic variability. First (as explained above), we coded GPI and PGM according to allele presence in homozygosis, presence in heterozygosis or absence, and 6PGD for band presence or absence. Secondly, we coded the three loci for band presence or absence. Since no appreciable differences were detected among the two coding methods, we used the second approach for the sake of uniformity.

2.6. Soil analyses

We collected about 2 kg of soil from each population. These samples were dried and subjected to chemical and texture analyses. Chemical analyses followed the protocols in Page et al. (1982). Evaluation of sand grain percentages was done through sieving. The values of the 14 variables analysed (Table 1) were standardised. Subsequently, we calculated an ecological distance for every pairwise combination of populations (Table 2) using the distance option for interval data in NTSYS version 4.2 (Rohlf, 1988).

Table 1
Summary of the ecological parameters measured through soil samples from the four stands considered. Units of measurement are given in parentheses

Ecological parameters	Populations			
	A. bellum	*A. guttatum*	*A. pulchrum* (CA)	*A. pulchrum* (NI)
pH	8.11	6.68	7.19	6.57
Water retention capacity (%)	8.58	5.12	9.08	36.71
Salinity (mm hos/cm at 25°C)	0.56	0.27	0.48	0.32
Total carbonates (%)	1.83	0.68	1.15	1.04
Organic matter (%)	0.56	1.21	1.08	1.08
Extractable N (mg N/100 g)	0.54	0.08	0.10	1.89
Extractable P (mg/100 g)	2.94	1.82	2.07	2.86
Extractable K (meq/100 g)	0.46	1.37	0.19	0.40
Cationic exchange capacity (meq/100 g)	3.28	5.33	10.21	18.03
Silt (%)	15.37	9.56	14.11	27.27
Clay (%)	4.32	5.83	16.08	31.75
Sand coarse grained (%)	28.79	21.87	34.87	4.26
medium grained (%)	36.45	54.42	27.02	15.39
tiny grained (%)	15.07	8.32	7.92	21.33

Table 2
Ecological distances between pairwise combinations of the four *Androcymbium* stands considered

	A. bellum	*A. guttatum*	*A. pulchrum* (*CA*)
A. guttatum	1.415		
A. pulchrum (CA)	0.975	1.046	
A. pulchrum (NI)	1.608	1.796	1.463

3. Results and discussion

As shown in Tables 3 and 4, respectively, 58 and 53% of the total variables scored in the populations of *A. bellum* and *A. guttatum* resulted in significant short-distance spatial autocorrelation. Only in the first distance class, 81% and 56% of points are significantly positively autocorrelated (mean $I = 0.19$ and 0.38, respectively). The average multiband correlograms of these populations (Figs. 3 and 4) display a regular monotonic decline in the values of Moran's I through the five distance classes, with a slump between the first and the second of 0.17 units in *A. bellum* and of 0.36 units in *A. guttatum*.

Table 3
Values of Moran's I for the bands that provided non-redundant information in the *A. bellum* population. Bounds associated with each of the five distance classes are 1, 3, 4, 6 and 54 meters.

Band	Distance class					Mean frequency
	1	2	3	4	5	
GPI-1	0.15**	− 0.20**	0.05*	− 0.06	− 0.01	0.132
GPI-2	0.19**	0.08**	− 0.08*	0.00	− 0.26**	0.103
GPI-3	0.02	0.00	− 0.03	− 0.03	0.01	0.029
GPI-4	0.38**	0.22**	0.03	− 0.45**	− 0.26**	0.412
GPI-5	0.30**	0.17**	0.03	− 0.33**	− 0.24**	0.559
GPI-6	0.13**	0.11**	0.04	− 0.16**	− 0.19**	0.338
GPI-7	0.33**	0.11**	0.08**	0.08**	− 0.67**	0.074
PGM1-1	0.32**	− 0.27**	− 0.23**	0.14**	− 0.03	0.632
PGM1-2	− 0.03	− 0.02	− 0.01	− 0.02	− 0.01	0.015
PGM2-1	0.33**	− 0.09*	0.01	− 0.24**	− 0.09**	0.074
PGM2-2	0.23**	− 0.05	− 0.26**	0.11**	− 0.10**	0.588
PGM2-3	0.22**	0.05*	− 0.18**	− 0.15**	− 0.01	0.691
PGM2-4	− 0.05*	0.00	− 0.01	− 0.02	0.00	0.015
PGM2-5	− 0.03	− 0.01	− 0.01	− 0.02	0.00	0.015
6PGD-1	0.21**	0.06*	− 0.07	0.00	− 0.28**	0.897
6PGD-5	0.23**	0.05*	− 0.06	− 0.01	− 0.28**	0.897
Average	0.19	0.02	− 0.05	− 0.07	− 0.17	

*$p < 0.05$; **$p < 0.01$.

Table 4
Values of Moran's I for the bands that provided non-redundant information in the *A. guttatum* population. Bounds associated with each of the five distance classes are 0.25, 0.50, 0.75, 1 and 2 m.

Band	Distance class					Mean frequency
	1	2	3	4	5	
GPI-1	− 0.06	0.04	− 0.02	− 0.04	− 0.01	0.966
GPI-2	− 0.05	0.01	0.00	0.00	− 0.05	0.966
PGM-1	0.01	0.01*	0.02	0.02	− 0.14*	0.017
PGM-2	0.59**	0.15**	− 0.13**	− 0.49**	− 0.20**	0.690
PGM-3	0.80**	0.01	− 0.15**	− 0.51**	− 0.24**	0.293
PGM-4	0.79**	0.01	− 0.15**	− 0.53**	− 0.20**	0.328
PGM-5	0.94**	− 0.12**	− 0.15	− 0.53**	− 0.22**	0.672
6PGD-1	− 0.04	− 0.01	− 0.01	− 0.02	− 0.01	0.983
6PGD-2	0.89**	0.11*	− 0.21**	− 0.63**	− 0.25**	0.661
Average	0.38	0.02	− 0.08	− 0.28	− 0.13	

*$p < 0.05$; **$p < 0.01$.

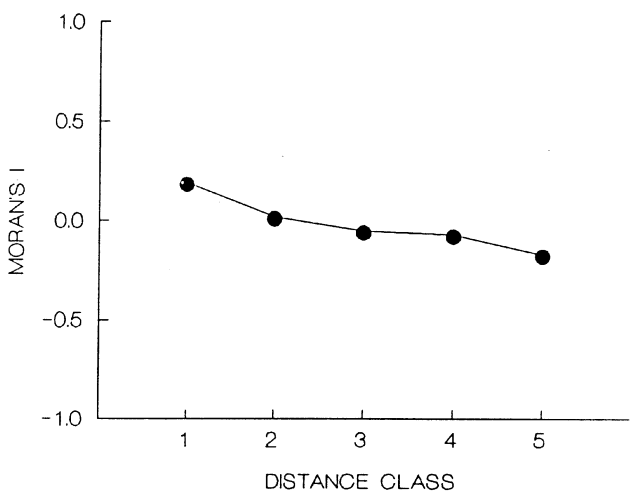

Fig. 3. Average multiband correlogram through the five distance classes in *A. bellum*. The size of homogeneous areas, as estimated from the intersection with the abscissa, is of 3.3 m.

The correlogram corresponding to the *A. bellum* stand intercepts the *x*-axis at 3.3 m, and that of *A. guttatum* at about 0.5 m. Sokal (1979) demonstrates that the first *x*-axis intercept is an operational estimate of the average length of the shortest side of true patches that are irregular in shape or variable in size. According to this interpretation, homogeneous areas are smaller in the population of *A. guttatum*. However, we construe the magnitude of this estimate as numerically biased, given that genetic drift

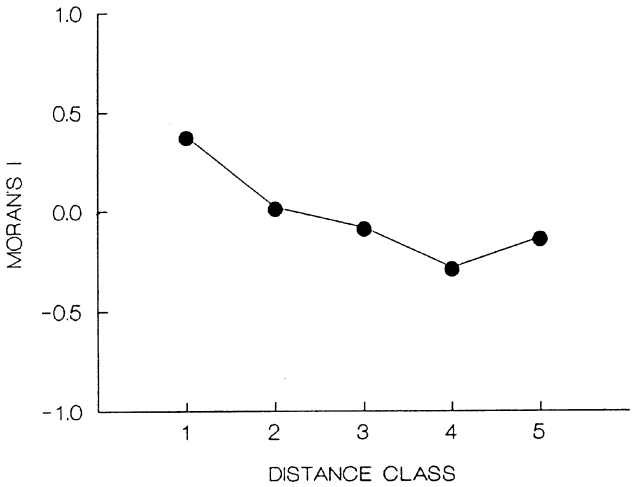

Fig. 4. Average multiband correlogram through the five distance classes in *A. guttatum*. The size of homogeneous areas, as estimated from the intersection with the abscissa, is of 0.5 m.

is likely to have produced the scarce inter-plant variability observed (*A. guttatum*'s stand was by far that with the lowest number of individuals).

In contrast, the corresponding estimate of the size of homogeneous areas in *A. bellum* is more reliable because the higher isozymic variability within its stand allows a ready detection of differences among sampling localities. A clear qualitative perception of these contrasts can be gained from the observation of Fig. 2. Particularly, the distribution of variability in locus GPI allows a fairly accurate circumscription of individuals to each of the sampled clumps in the population of *A. bellum*.

Why have these analogous structures of genetic variability occurred in populations displaying such different ecological traits? A number of studies in plant populations have elicited patterns of genetic organisation over short distances (Epperson and Clegg, 1986; Schoen and Latta, 1989; Schnabel et al., 1991; Perry and Knowles, 1991; Wagner et al., 1991; Shapcott, 1995). In *Androcymbium*, this pattern was found for a population of the endangered northern African *A. gramineum* (Caujapé-Castells and Pedrola-Monfort, 1997), where the short-distance structuring of genetic variability was explained as the primary consequence of capsule indehiscence overlaid with vegetative reproduction. Quite obviously, this cannot be the whole case for these two southern African species, because the capsules are dehiscent in both of them. However, the incidence of vegetative reproduction may have been an important factor in generating the observed patterns. In this aspect, *A. guttatum* (the only obligate outcrosser according to our experiments) displays the lowest levels of inter-individual isozymic variability and the highest levels of observed heterozygosity at loci GPI and PGM. In the absence of evidence for heterozygote advantage, this observation is most important in supporting a high incidence of clonal propagation. Reports on the role of this reproductive asset in population regeneration and in the development of genetic

structure are not unprecedented (Shapcott, 1995). Ongoing experiments concerning reproductive biology of South African *Androcymbium* (Membrives et al., in prep.) are expected to provide definitive data to substantiate this interpretation. According to current knowledge, patterns of short distance genetic structure in *A. bellum* and *A. guttatum* are best explained by a high incidence of assortive mating and vegetative reproduction, respectively. Both reproductive features foster the creation and enhancement of family clumps.

What does our data reveal about the continuously distributed plants in the two stands of *A. pulchrum*? The picture that emerges shows that neither of these stands furnish proof of short distance spatial autocorrelation (Tables 5 and 6 and Fig. 5). Qualitative consistency for this result is that both of them display considerable isozymic variability at the three loci considered, which should have allowed us to detect related individuals in case these populations had been spatially structured for these kinds of genetic characters. Quantitatively, only 22 and 18% of the total bands displayed significant spatial autocorrelation in the populations labelled NI and CA, respectively (mean I values 0.05 and 0.07). The correlograms intercept the x-axis only once at about 3 m in NI and at 0.5 m in CA. A possible explanation for this difference between the magnitudes of the interception points is that population NI might be older, and therefore more likely to have developed larger homogeneous areas. Although the recent phylogeny for the genus based on chloroplast restriction sites (Caujapé-Castells et al., in press.) is not informative in this regard, results from computer simulations do support this hypothesis. Progressive increases of the average x-intercept and the rapid generation of very large patches are predicted due solely to

Table 5
Values of Moran's I for the bands that provided non-redundant information in population of *A. pulchrum* in Nievoudtville. Bounds associated with each of the five distance classes are 1, 6, 9, 12 and 19 m, respectively

Band	Distance class					Mean frequency
	1	2	3	4	5	
GPI-1	0.03	0.11	− 0.02	− 0.12	− 0.24*	0.136
GPI-2	− 0.04	0.07	− 0.04	0.03	− 0.24*	0.818
GPI-3	− 0.13	0.05	− 0.02	− 0.11	− 0.02	0.045
GPI-4	0.01	0.15*	0.07	0.03	− 0.48**	0.591
GPI-5	− 0.13	0.02	− 0.02	− 0.02	− 0.09	0.045
GPI-6	0.28**	− 0.06	0.39**	− 0.42**	− 0.42**	0.500
GPI-8	0.05	− 0.18	0.00	− 0.16*	0.05	0.045
PGM-1	0.02	− 0.13	− 0.02	− 0.16	0.05	0.045
PGM-3	0.17*	0.04	0.12	0.01	− 0.58**	0.545
PGM-4	0.28**	− 0.04	0.22*	− 0.26*	− 0.41**	0.273
6PGD-2	0.05	− 0.20	− 0.16	0.00	0.05	0.955
6PGD-6	0.17*	− 0.02	− 0.44**	− 0.04	0.11	0.136
6PGD-7	0.07	− 0.11	0.14	− 0.19	− 0.02	0.857
Average	0.05	− 0.05	− 0.04	− 0.08	− 0.12	

*$p < 0.05$; **$p < 0.01$.

Table 6
Values of Moran's I for the bands that provided non-redundant information in population of *A. pulchrum* in Calvinia. Bounds associated with each of the five distance classes are 0.3, 0.6, 0.9, 2 and 2.9 m, respectively

Band	Distance class					Mean frequency
	1	2	3	4	5	
GPI-1	0.13	− 0.36**	0.09	− 0.06	− 0.04	0.393
GPI-2	0.00	0.00	− 0.10	0.12	− 0.25	0.143
GPI-3	0.20*	0.07	− 0.09	0.08	− 0.49**	0.301
GPI-4	− 0.03	0.00	− 0.04	− 0.28	0.12	0.071
GPI-5	0.24	0.23*	− 0.51**	− 0.26	0.07	0.321
PGM-2	− 0.20	− 0.08	0.09	− 0.06	0.01	0.857
PGM-3	− 0.09	− 0.14	0.07	0.02	− 0.08	0.107
PGM-4	− 0.09	− 0.07	− 0.07	− 0.02	0.00	0.036
PGM-5	− 0.16	0.01	0.08	− 0.02	− 0.14	0.142
6PGD-1	0.28**	− 0.01	0.11	− 0.15	− 0.45**	0.077
6PGD-4	− 0.10	− 0.07	− 0.10	0.09	− 0.07	0.154
6PGD-5	− 0.01	0.11	− 0.21	0.06	− 0.18	0.115
6PGD-6	0.23*	− 0.14	− 0.22	0.13	− 0.24*	0.423
6PGD-7	0.15	0.09	− 0.05	0.02	− 0.43**	0.462
6PGD-8	0.35**	0.40**	− 0.54**	0.15*	− 0.52**	0.769
6PGD-9	− 0.08**	− 0.08	− 0.07	0.05	− 0.07	0.077
6PGD-10	− 0.03	0.02	0.05	− 0.16	− 0.12	0.538
6PGD-11	0.41**	− 0.09	− 0.53**	− 0.03	0.01	0.038
6PGD-12	− 0.06	− 0.06	− 0.12	− 0.07	0.05	0.308
6PGD-13	− 0.03	0.04	0.01	− 0.08	− 0.18	0.133
Average	0.07	− 0.01	− 0.09	− 0.03	− 0.17	

*$p < 0.05$; **$p < 0.01$.

nearest neighbour pollination and limited seed dispersal (Turner et al., 1982). Nonetheless, simulations reported in that paper leave out the effect of clonal propagation, which is a key reproductive factor in many plants and could also have played a role in the demographic evolution of these two *A. pulchrum* populations.

The similarity between the mean multiallele correlograms of both these stands suggests that the absence of genetic structure is a feature of this taxon. We consider that the possibility of our results being statistical artifacts is unlikely, given that the number of plants sampled (Fig. 2) accounts accurately for the real size of these populations. For the same reason, the possibility of a non-representative sampling seems an unsound explanation for the differences with regard to *A. bellum* and *A. guttatum*.

Is there a cogent explanation that patterns of short distance genetic structure are only associated with patchiness? Based on data for a wealth of plant species Loveless and Hamrick (1984) and Hamrick and Godt (1989) forecast analogous patterns of genetic structure under similar ecological characteristics. A practical example provided in Schnabel et al. (1991) supports this prediction by reporting short-distance genetic structure in the co-occurring trees *Maclura pomifera* and *Gleditsia triacanthos*.

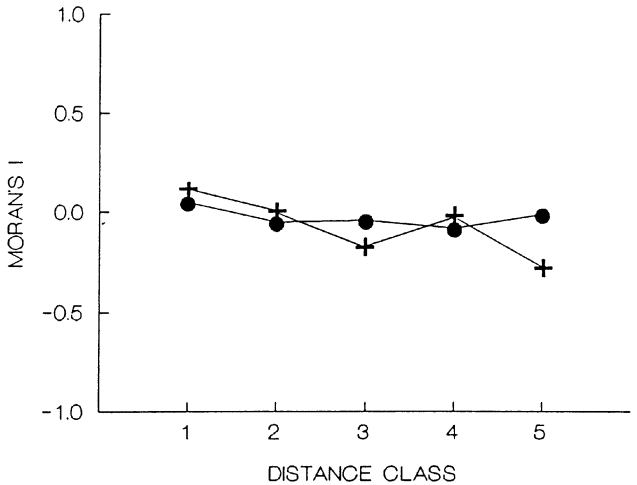

Fig. 5. Average multiband correlogram through the five distance classes in the *A. pulchrum* stands from Nievoudtville (closed circles) and Calvinia (crosses). The size of homogeneous areas, as estimated from the intersection with the abscissa, is of 3 and 0.6 m, respectively.

Invoking similar ecological conditions to explain the affinities between patterns of genetic structure in the *Androcymbium* stands with patchy distribution would clearly miss the point. The populations of *A. bellum* and *A. guttatum* live in considerably different edaphic conditions. According to Boucher and Moll (1981), the former occurs in a zone dominated by very shallow calcareous sands and loams, and the latter in weakly developed illuvial soils with lime accumulations in bottom lands. These contrasts are demostrated by Tables 1 and 2. Most remarkably, the minor values of ecological distances are found between *A. pulchrum* form Calvinia and each of the two patchy species (Table 2).

We believe there are three compelling reasons to argue that different ecological contexts have vastly influenced the observed dichotomy in patterns of genetic structure. Firstly, microhabitat heterogeneity was not detected in the patchy stands; therefore, the spatial structuring of isozymic variability cannot be attributed to short distance selection. Secondly, the three species display very similar reproductive capabilities; and thirdly, the capsules are dehiscent for the three species.

Androcymbium guttatum's corms grow in compact clumps by nature, which is undoubtedly an advantage when being compelled to live in small clefts of rocks, as is the present case. Indeed, habitat constraint in this population makes the establishment of seeds comparable to a low probability event, however, facilitated by capsule dehiscence (that makes seed establishment into clefts more likely). For this reason, clump development must have started from a single seed in most of the cases, and this explains why the effects of vegetative reproduction are more conspicuous in this taxon.

In turn, both *A. bellum* and *A. pulchrum* lived in environments that would seem to favour seed settlement. One possibility to account for the contrast between their space

occupancy patterns would be quantitative differences in seed production or germination success. If *A. pulchrum* produced a higher amount of seeds, or if these had a superior rate of germination than those of *A. bellum*, it would be more likely that its population featured a more continuous plant distribution. Alternatively, if *A. bellum's* corms were dormant and *A. pulchrum*'s not, the observed patchy distribution of plants in the former population could be spurious.

Consideration of the characteristics of the soils where these populations occur (Boucher and Moll, 1981) indicates that both possibilities are feasible. *A. bellum's* habitat is sandy and, consequently, with scarce water retention capacity. This would make corm dormancy a good survival strategy during non-auspicious periods, particularly in a zone with such an erratic rain regime. In contrast, both *A. pulchrum* stands lived in muddy soils, in a zone with winter-concentrated or through the year rainfall. A habitat like this enables a ready germination of seeds and guarantees the adult corms will have good conditions to surface and flower each year.

Equivalent reproductive assets under substantially different ecological conditions have been able to produce similar spatial genetic structures in *A. bellum* and *A. pulchrum*. This is an important conclusion, because it shows that establishment of analogous populational structures does not depend exclusively on the similarity of environments. These results do not contradict Loveless and Hamrick's (1984) and Hamrick and Godt's (1989) inference that different species subjected to similar ecological and life history conditions should exhibit analogous patterns of genetic structure. Nonetheless, they indicate that the variety of reproductive quirks that particularly plants can exhibit (not to mention complex genic interactions like those involved in self-incompatibility systems) allow ample room for streamlining the abovementioned hypothesis. The sharp ecological differences between the stands surveyed have prevented us from discussing the influence of the same environments on the spatial genetic structure. A most interesting topic in this regard is the study of spatial genetic structure of co-occurring species. Theory about coexistence splits into two contrasting predictions; while classical postulates predict that the most similar species cannot coexist, recent models support the reverse (Bond et al., 1992). Autocorrelation analyses to be performed with co-occurring populations of different *Androcymbium* species (Caujapé-Castells et al., in prep.) will hopefully add evidence to substantiate whether coexisting south African *Androcymbium* species tend to be more similar than non-coexisting species in terms of isozymic variability and its spatial distribution.

Furthermore, these results impact on reproductive biology studies under way by addressing our attention to two questions. One of them is whether *A. pulchrum's* seeds are endowed with a superior germination success that might explain that its populations are continuous, in contrast to *A. bellum*'s. The other concerns if *A. bellum's* corm has higher dormancy capabilities than *A. pulchrum*'s.

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References

Acocks, J. P. H. 1988. Veld Types of South Africa. 3rd ed. Botanical Research Institute. Praetoria. South Africa.

Baker, J. G., 1874. On the genus *Androcymbium*, with description of seven new species. J. Linnean Soc. Botany 10, 243–246.

Baker, G. J., 1880. A synopsis of Colchicaceae and the aberrant tribes of Liliaceae. J. Linnean Soc. 17, 405–447.

Bond, W. J., Cowling, R. M., Richards, M. B., 1992. Competition and coexistence. In: Cowling, R., (ed). The Ecology of Fynbos: Nutrients, Fire and Diversity. Oxford University Press, Oxford, pp. 206–225.

Boucher, C., Moll, E. J., 1981. South African Mediterranean shrublands. In: di Castri, F., Goodall D. W., Specht, R. L. (eds.), Ecosystems of the World, vol. 11. mediterranean-type Shrublands. Elsevier, Amsterdam, pp. 233–248.

Brown, J. H., 1988. Species diversity. In: Myers, A. A., Giller, P. S. (eds.), Analytical Biogeography. An Integrated Approach to the Study of Plant and Animal Distributions. Chapman & Hall, London, pp. 57–89.

Caujapé-Castells, J., Pedrola-Monfort, J., 1997. Space-time patterns of genetic structure within a stand of *Androcymbium gramineum* (Cav.) McBride (Colchicaceae). Heredity 79, 341–349.

Caujapé-Castells, J., Jansen, R. K., Pedrola-Monfort, J., Membrives, N., 1999. Chloroplast DNA restriction site phylogeny of the genus *Androcymbium* Willdenow (Colchicaceae). Systematic Botany, in press.

Cliff, A. D., Ord, J. K., 1973. Spatial Autocorrelation. Pion, London.

Cody, M. L., 1986. Diversity, rarity and conservation in mediterranean-climate regions. In: Soulé, M. (Ed.), Conservation Biology. The science of scarcity and diversity Sinauer, Sunderland, pp. 122–152.

Cowling, R. M., Holmes, P. M., Rebelo, A. G., 1992. Plant diversity and endemism. In: Cowling, R. (Ed.), The Ecology of Fynbos: Nutrients, Fire and Diversity. (pp. 62–112. Oxford University Press, Oxford.

Epperson, B. K., Clegg, M. T., 1986. Spatial-autocorrelation analysis of flower color polymorphisms within substructured populations of morning glory (*Ipomoea purpurea*). Amer. Naturalist 128, 840–858.

Gentry, A. H., 1986. Endemism in tropical vs. temperate plant communities. In: Soulé, M. (ed.), Conservation Biology. The science of scarcity and diversity Sinauer, Sunderland, pp. 153–181.

Hamrick, J. L., Godt, M. J. W., 1989. Isozyme diversity in plant species. In: Brown, A. H. D., Clegg, M. T., Kahler, A. L., Weir, B. S. (eds.), Plant population genetics, breeding and genetic resources pp. 43–63. Sinauer, Sunderland.

Krause, K., 1920. Revision der gattung *Androcymbium* Willd. Notizbloch Botanische Garten Berlin 7, 512–526.

Loveless, M. D., Hamrick J. L., 1984. Ecological determinants of genetic structure in plant populations. Ann. Rev. Ecol. Systematics 15, 65–95.

Margelí, M., Pedrola-Monfort, J., Vallés-Xirau, J., 1998. Karyological studies in the genus *Androcymbium* Willd. (Colchicaceae). Australian J. Botany 26(4), in press.

Müller-Doblies, U., Müller-Doblies, D., 1984. Zur Kenntnis der Gattung *Androcymbium* (Colchicaceae) im südlichen Afrika: Zwei Synonima und fünf neue Arten. Willdenowia 14, 179–197.

Müller-Doblies, U., Müller-Doblies, D., 1990. Zur Kenntnis der Gattung *Androcymbium* (Colchicaceae) im südlichen Afrika: 2. *Androcymbium exiguum* hat doch Artwert. Willdenowia 19, 453–470.

Myers, A. A., Giller P. S., 1988. Biogeographic patterns. Introduction. In: Myers, A. A., Giller, P. S., (eds.), Analytical Biogeography. An Integrated Approach to the Study of Plant and Animal distributions, Chapman & Hall, London, pp. 15–21.

Oden, N. L., 1984. Assessing the significance of a spatial correlogram. Geography Ann. 16, 1–16.

Page, A. L., Miller, R. H., Keeney, D. R., 1982. Methods of Soil Analysis. American Society of Agronomy Inc., Madison.

Pedrola-Monfort, J., Caujapé-Castells, J., 1994. Isozymic and morphological relationships among *Androcymbium gramineum*, *A. europaeum* and *A. psammophilum* (Colchicaceae). Plant Systematics and Evol. 191, 111–126.

Perry, D. J., Knowles, P., 1991. Spatial genetic structure within three sugar maple (*Acer saccharum* Marsh.) stands. Heredity 66, 137–142.

Pianka, E. R., 1966. Latitudinal gradients in species diversity: a review of concepts. Amer. Naturalist 100, 33–46.

Rohlf, F. J., 1988. NTSYS-pc. Numerical Tanonomy and Multivariate Analysis version 1.50. Setauket: Exeter software.

Schnabel, A., Laushman, R. H., Hamrick, J. R., 1991. Comparative genetic structure of two co-occurring tree species, *Maclura pomifera* and *Gleditsia triacanthos* (Leguminosae). Heredity 67, 357–364.

Shapcott, A., 1995. The spatial genetic structure in natural populations of the Australian temperate rainforest tree *Atherosperma moschatum* (Labill.) (Monimiaceae). Heredity 74, 28–38.

Schoen, D. J., Latta, R. G., 1989. Spatial autocorrelation of genotypes in populations of *Impatiens pallida* and *Impatiens capensis*. Heredity 63, 181–189.

Sokal, R. R., 1979. Testing statistical significance of geographical variation patterns. Systematic Zoology 8, 227–232.

Sokal, R. R., Oden, N. L., 1978. Spatial autocorrelation in biology 1. Methodology. Biol. J. Linnean Soc. 10, 199–228.

Turner, M., Stephens, J. C., Anderson, W. W., 1982. Homozygosity and patch structure in plant populations as a result of nearest neighbor pollination. Proc. National Academy of Sciences USA 79, pp. 203–207.

Wagner, D. B., Sun, Z. X., Govidarju, D. R., Dancik, B. P., 1991. Spatial patterns of chloroplast DNA and cone morphology variation within populations of a *Pinus banksiana-Pinus contorta* sympatric region. Amer. Naturalist 138, 156–170.

Wartenberg, D., 1989. SAAP version 4.3. Spatial Autocorrelation Analysis Program. Distributed by the author.