ILLiad TN: 406881

Lending String: *FQG,GUA,VXG,VXG,OLM

Patron: terHorst, Casey

Journal Title: South African journal of botany ; official journal of the South African Association of Botanists = Suid-Afrikaanse tydskrif vir plantkunde ; amptelike

Volume: 62 **Issue:** 6
Month/Year: 1996**Pages:** 342-345

Article Author:

Article Title: Oosthuizen, MA and vanRooyen, MW and Theron, GK; A replacement-series evaluation of competition between three Namaqualand ephemeral plant species

NOTICE: These materials may be protected by copyright law (Title 17 U.S. Code)

ILL Number: 38902111

Call #: QK396 .S67 v.62 (1996)

Location: Richter Bound Journals
AVAILABLE

Borrower: FDA

Shipping Address:
Florida State University
ILL Technical Services BORROWING
711 West Madison Street
Tallahassee, FL 32306-1005

Fax: 850-644-3329
Ariel: 146.201.65.31

Date printed: 1/24/2008

Notes: SHARES

S. Afr. J. Bot. 1996, 62(6): 342–345

Short Communications

A replacement-series evaluation of competition between three Namaqualand ephemeral plant species

M.A. Oosthuizen, M.W. van Rooyen* and G.K. Theron

Department of Botany, University of Pretoria, Pretoria, 0002 Republic of South Africa

Received 25 August 1995; revised 23 March 1996

The objective of the study was to determine whether the species could be arranged in a competitive hierarchy and to establish whether the interactions were symmetrical or asymmetrical. Indices of competitive ability indicated a hierarchy, namely *Senecio arenarius* > *Dimorphotheca sinuata* > *Ursinia cakilefolia*. The stronger competitors (*S. arenarius* and *D. sinuata*) were characterized by intraspecific competition having a stronger effect than interspecific competition from *U. cakilefolia*. The weakest competitor (*U. cakilefolia*) was characterized by interspecific competition from *D. sinuata* and *S. arenarius* having a greater effect than intraspecific competition. Total above-ground dry mass per plant of the stronger competitors was enhanced in a mixture, especially when grown with *U. cakilefolia*. However, *U. cakilefolia* performed just as well or better in a monoculture than in a mixture. Results indicated that some degree of niche differentiation exists, which may allow coexistence between the stronger competitors (*S. arenarius* and *D. sinuata*) and the weakest competitor (*U. cakilefolia*). Long-term coexistence between *S. arenarius* and *D. sinuata*, with similar competitive abilities, may be brought about by temporal or spatial refuges. The constantly changing conditions in Namaqualand promote coexistence, as no species is able to retain a competitive advantage long enough to exclude the others. In general, biomass allocation patterns showed no specific trend in response to competitive stress.

Keywords: Coexistence, competitive ability, *Dimorphotheca sinuata*, refuges, replacement-series, *Senecio arenarius*, *Ursinia cakilefolia*.

*To whom correspondence should be addressed.

The question of what permits so many plant competitors to coexist in a community has long interested plant ecologists. Although many theories have been proposed, the debate continues largely unresolved (Aarssen 1983; Shmida & Ellner 1984; Keddy 1989; Goldberg & Barton 1992; Silvertown & Lovett Doust 1993). The niche concept or 'ecological combining ability' (Aarssen 1983) can only satisfactorily explain the coexistence of species that demonstrably differ in the way they make use of resources. However, ecologically similar species share the same niche and their coexistence has to be explained by alternative mechanisms, e.g. 'competitive combining ability' (Aarssen 1983), spatial or temporal refuges (Silvertown & Lovett Doust 1993) or lottery coexistence models (Lauri & Cowling 1994). In multispecies assemblages more than one of these mechanisms is probably operating.

Plants interfere with each other's activities when their density is high enough for individuals to enter into and modify the environment of each other (Mack & Harper 1977). The degree of suppression of one plant of its neighbours depends on (a) the effectiveness of each species in competing for limiting resources; (b) the responsiveness of each species to resource supply; and (c) the effect of different species proportions in the mixture on the preceding factors (Beneke *et al.* 1992).

The interactions between two species can be symmetrical or asymmetrical and the network of interactions between species can either be arranged in a transitive hierarchy or intransitive loops are produced (Shipley & Keddy 1994). The dynamics and structure of multispecies assemblages are profoundly affected by the proportions of these types of interactions between the species.

The three species used in this study, *Dimorphotheca sinuata* DC., *Senecio arenarius* Thunb. and *Ursinia cakilefolia* DC. are abundant in Namaqualand, an arid zone in the north-western corner of South Africa, and occur aggregated or in mixtures. Under favourable conditions, all three species will produce mass floral displays which attract thousands of tourists to the area during the flowering season. The objective of this study was to determine whether the species could be arranged in a competitive hierarchy and to establish whether there was any evidence of niche differentiation (*sensu* Fowler 1982) between them. Subsequent studies investigate the traits conferring a competitive advantage to the stronger competitors (Rösch 1996).

In replacement designs (De Wit 1960), the total density of plants is kept constant, while the relative frequencies of the two species are varied. Despite criticism (Connolly 1986; Taylor & Aarssen 1989; Snaydon 1991) this design has proved to be popular to study the interactive behaviour of components in mixed stands, because graphical presentation of the yield data allows the identification of the stronger competitor and the extent of niche overlap between species (Joliffe *et al.* 1984; Firbank & Watkinson 1985). Furthermore, it is applicable to a wide range of experimental situations from field to pot studies and no specialized techniques are needed (Hall 1974; Trenbath 1974; Mead 1979; Snaydon 1991).

Achenes of *D. sinuata*, *S. arenarius* and *U. cakilefolia* were collected in the Goegap Nature Reserve near Springbok. Plants were cultivated in a replacement-series (De Wit 1960) at a total density of four plants per pot, in pure stands and in pair-wise mixtures at ratios of 3:1, 2:2 and 1:3. All plants were grown in pots with a volume of 1 000 cm^3, filled with quartz sand, and received tap water daily, and once a week Arnon and Hoagland's complete nutrient solution (Hewitt 1962). The experiment was conducted out of doors at the University of Pretoria.

Four replicates of each treatment were harvested five months after sowing and the dry mass (g) of the leaves, stems and inflorescences, as well as total above-ground dry mass (g) were determined per pot and per plant. Plant parts were dried for one week at 60°C before determining the dry mass.

The following indices were calculated from the above-mentioned values:

(a) A, aggressivity (McGilchrist & Trenbath 1971):

$$A = 0.5\ (Y_{ij}/Y_{ii} - Y_{ji}/Y_{jj})$$

where Y_{ii} = yield of species i in a pure stand; Y_{jj} = yield of species j in a pure stand; Y_{ij} = yield of species i in a mixture of species i and species j; Y_{ji} = yield of species j in a mixture of species i and species j; all values being per pot.

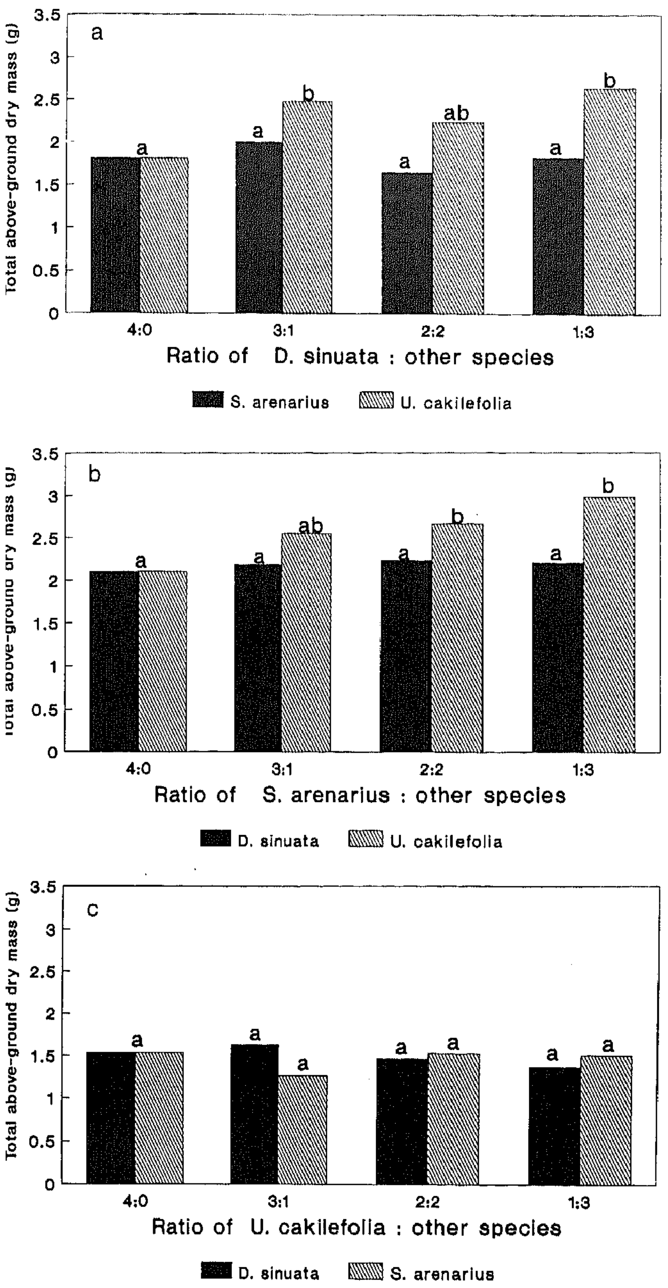
(b) C_b, competitive balance index (Wilson 1988):

$$C_b = \log \frac{Y_{ij}/Y_{ji}}{Y_{ii}/Y_{jj}}$$

(c) RYP, relative yield per plant (Fowler 1982):

$$RYP_{ij} = Y_{ij}\ /\ (pY_{ii})$$

$$RYP_{ji} = Y_{ji}\ /\ (qY_{jj})$$



igure 1 The total above-ground dry mass (g) per plant of (a) *imorphotheca sinuata* in combination with *Senecio arenarius* or *rsinia cakilefolia*; (b) *S. arenarius* in combination with *D. sinuata* r *U. cakilefolia*; and (c) *U. cakilefolia* in combination with *D. sinuata* or *S. arenarius*, cultivated in a replacement series. Within a species, bars with the same letter do not differ significantly at α = 0.05.

vhere p = initial proportion of species i in a mixture; q = initial roportion of species j in a mixture so that $p + q = 1$ in a mixture f two species.

d) *RYT*, relative yield total (Fowler 1982):

$$RYT_{ij} = pRYP_{ij} + qRYP_{ji}$$

e) *LA*, allocation to leaves

f) *SA*, allocation to stems

g) *RA*, allocation to inflorescences

A, SA, RA = dry mass of particular organ as percentage of the otal above-ground dry mass

A one-way analysis of variance was used to test for statistially significant differences at α = 0.05. If significant, Tukey's test was used for all paired comparisons among treatments (Steyn *et al.* 1987). Statistically significant differences are indicated by different letters in the tables and figures.

The total above-ground dry mass per plant of *D. sinuata* and *S. arenarius* in monoculture was not significantly different from that in a mixture with each other, but in most cases was significantly lower than in a mixture with *U. cakilefolia* (Figure 1a & b). When grown with *U. cakilefolia*, the yield of both *D. sinuata* and *S. arenarius* was usually significantly higher than in a mixture with each other (Figure 1a & b). The yield of *U. cakilefolia* was not affected by the species composition of the plants in the pot (Figure 1c). Plant performance of the stronger competitors was therefore enhanced in a mixture with *U. cakilefolia*. However, *U. cakilefolia* performed just as well or better in a monoculture than in a mixture.

The relative competitive ability of the components in a mixture can either be expressed by the 'competitive balance index' (C_b) (Wilson 1988) or by 'aggressivity' (A) (McGilchrist & Trenbath 1971). Both C_b and A values (Wilson 1988) show that the competitive ability of *S. arenarius* was greater than that of *D. sinuata* and *U. cakilefolia*, while the competitive ability of *D. sinuata* was less than that of *S. arenarius*, but greater than that of *U. cakilefolia* (Table 1). The hierarchy of competitive power that was established was: *Senecio arenarius > D. sinuata > U. cakilefolia.*

The relative yield per plant (*RYP*) is the average performance of an individual in a mixture in comparison with the average performance of an individual of the same species in a pure stand at the same total density (Fowler 1982). If the *RYP* value is equal to one, then the growth of an individual is unaffected by the identity of the neighbouring individuals. An *RYP* value greater than one implies that individuals of that species suffer less interference from individuals of the other species (interspecific competition) than they do from individuals of their own species (intraspecific competition). The *RYP* values of *D. sinuata* as well as *S. arenarius* were approximately equal to one when these species were cultivated in a mixture. These species were therefore not affected by the identity of the neighbouring plants. However, when grown with *U. cakilefolia*, the *RYP* values of *D. sinuata* and *S. arenarius* were greater than one. This implies that intraspecific competition between individuals of *D. sinuata* or *S. arenarius* was stronger than interspecific competition from individuals of *U. cakilefolia*. The *RYP* of *U. cakilefolia* grown with *D. sinuata* or *S. arenarius* in most cases was slightly less than one, indicating that intraspecific competition between individuals of *U. cakilefolia* was less than interspecific competition with either *D. sinuata* or *S. arenarius* (Table 1).

The relative yield total (*RYT*) reflects the sum of the proportional changes in yield in a mixture and if the species compete for the same resource, *RYT* will be equal to 1. If the two species use somewhat different resources, for example different rooting zones, the proportional gain to individuals of one species from growing in a mixture will be greater than the loss to the other, and the RYT will be greater than 1 (Fowler 1982). The *RYT* values of *D. sinuata* in combination with *S. arenarius* were approximately 1, indicating competition for the same resources. However, *RYT* values of these two species in mixture with *U. cakilefolia* were greater than one, implying some degree of niche differentiation and therefore the possibility of species coexistence (Fowler 1982).

The biomass allocation patterns of a species are the result of selection for that particular pattern in which energy and sources are allocated optimally to processes such as growth and reproduction (Abrahamson 1979). The selection of allocation patterns of ephemerals has apparently been influenced by the unpredictability of the rainfall with respect to space and time as well as sea-

Table 1 Competitive balance index (C_b), aggressivity (A), relative yield per plant (RYP) and relative yield total (RYT) of plants of *Dimorphotheca sinuata*, *Senecio arenarius* and *Ursinia cakilefolia* cultivated in a replacement-series

		D. sinuata			*S. arenarius*			*U. cakilefolia*			
Mixture	Ratio	C_b	A	RYP	C_b	A	RYP	C_b	A	RYP	RYT
D. sinuata	3:1			1.106			1.050				1.093
with	2:2	−0.130	−0.038	0.913	+0.130	+0.038	1.196				1.055
S. arenarius	1:3			1.012			1.040				1.033
D. sinuata	3:1			1.373						0.892	1.252
with	2:2	+0.246	+0.071	1.105				−0.246	−0.071	0.957	1.032
U. cakilefolia	1:3			1.461						1.059	1.159
S. arenarius	3:1						1.218			0.981	1.159
with	2:2				+0.243	+0.063	1.261	−0.243	−0.063	1.018	1.140
U. cakilefolia	1:3						1.421			0.826	0.975

sonal temperature extremes in desert environments (Bell *et al.* 1979; Clark & Burk 1980). During the growth of plants under density stress the allocation of assimilates between different structures may become proportionately altered (Harper 1977). In general, biomass allocation patterns of the three species in this study showed no specific trend in response to competitive stress. Reproductive allocation was only significantly affected by competition in the case of *D. sinuata* where it was decreased due to interspecific competition from *S. arenarius*.

The three species in this study could be arranged in a hierarchy, the two strongest competitors being nearly equivalent. The interaction between *D. sinuata* and *S. arenarius* could therefore be classified as symmetrical, whereas that between *U. cakilefolia* and either of the other two species was asymmetrical. In a study on 15 pioneer species from Namaqualand, which included the three of this study, Rösch (1996) found that competitive ability was related to plant size. Shipley & Keddy (1994) hypothesized that the internal force maintaining a competitive hierarchy was that competitive performance was a function of plant size. The forces preventing competitive exclusion were however external, i.e. all those factors causing density-independent mortality (Shipley & Keddy 1994).

Shipley & Keddy (1994) have emphasized the importance of determining whether symmetrical or asymmetrical interactions are most common in multispecies assemblages since the answer to this question determines the approach used in future studies. The three species evaluated in this study provided no decisive answer to this question as both types of interactions occurred.

According to the competitive exclusion principle, as it was originally expressed by Gause (1934), species with equivalent competitive abilities should be least likely to coexist through time because of the intense competition between them. Stable coexistence would be obtained if there was niche separation between the species. As the results of the replacement series indicated a degree of niche differentiation between *U. cakilefolia* and both *D. sinuata* and *S. arenarius* (RYT values > 1), *U. cakilefolia* would be able to coexist with either of the other two species according to Gause's principle. Although this study did not attempt to qualify the different niches, separation in timing of growth patterns (phenology), use of pollinators, response to microtopography, soil moisture, temperature or nutrients may contribute to the coexistence of Namaqualand ephemeral species (van Rooyen 1988).

The competitive exclusion principle does, however, not explain how *S. arenarius* and *D. sinuata*, with their similar competitive abilities can coexist. Various theories have been put forward to reconcile coexistence with the competitive exclusion principle (Silvertown & Lovett Doust 1993). In the case of *S. arenarius* and *D. sinuata*, different mechanisms are probably operating. Although these species occur in mixtures under field conditions, they often produce patches where one species dominates. These spatial refuges provided by the aggregation of the species reduce the rate of encounter between the competitors. Temporal refuges from competition may be provided by differences in the regeneration niche. Lauri and Cowling (1994) have developed a general lottery model that avoids the requirements of overlapping generations, which could also explain coexistence of annual species.

In any plant community, some species are more abundant than others. While some researchers have suggested or found that a species' relative abundance in a community is related to competitive ability, other studies could not demonstrate a relationship (Duralia & Reader 1993). Under field conditions, the three species examined in this study often occur in mixtures, yet they also produce patches where one species dominates. In mixtures, the stronger competitors (*S. arenarius* and *D. sinuata*) are favoured, while the weakest (*U. cakilefolia*) is favoured in the absence of interspecific competition.

The unpredictable nature of the climate in Namaqualand changes the competitive milieu of the species each season and these constantly changing conditions promote coexistence, as no species is able to retain a competitive advantage long enough to exclude the others (van Rooyen 1988).

Acknowledgements

The authors thank the University of Pretoria, the Department of Environmental Affairs and Tourism and the Foundation for Research Development for their financial support.

References

AARSSEN, L.W. 1983. Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. *Am. Nat.* 122: 707–731.

ABRAHAMSON, W.G. 1979. Patterns of resource allocation in wildflower populations of fields and woods. *Am. J. Bot.* 66: 71–79.

S. Afr. J. Bot. 1996, 62(6): 345–347

BELL, K.L., HIATT, H.D. & NILES, W.E. 1979. Seasonal changes in biomass allocation in eight winter annuals of the Mojave Desert. *J. Ecol.* 67: 781–787.

BENEKE, K., VAN ROOYEN, M.W. & THERON, G.K. 1992. Fruit polymorphism in ephemeral species of Namaqualand: 6. Intermorphic competition among plants cultivated from dimorphic diaspores. *S. Afr. J. Bot.* 58: 461–468.

CLARK, D.D. & BURK, J.H. 1980. Resource allocation patterns of two California Sonoran Desert ephemerals. *Oecologia (Berlin)* 46: 86–91.

CONNOLLY, J. 1986. On difficulties with replacement-series methodology in mixture experiments. *J. appl. Ecol.* 23: 125–137.

DE WIT, C.T. 1960. On competition. *Verslag Landbouwkundige Onderz.* 66: 1–82.

DURALIA, T.E. & READER,R.J. 1993. Does abundance reflect competitive ability?: A test with three prairie grasses. *Oikos* 68: 82–90.

FIRBANK, L.G. & WATKINSON, A.R. 1985. On the analysis of competition within two species mixtures of plants. *J. appl. Ecol.* 22: 503–517.

FOWLER, N. 1982. Competition and coexistence in a North Carolina grassland. *J. Ecol.* 70: 77–92.

GAUSE, G.F. 1934. The struggle for existence. Waverly, Baltimore.

GOLDBERG, D.E. & BARTON, A.M. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *Am. Nat.* 139: 771–801.

HALL, R.L. 1974. Analysis of the nature of interference between plants of different species: 1. Concepts and extension of the De Wit analysis to examine effects. *Austr. J. agric. Res.* 25: 739–747.

HARPER, J.L. 1977. Population biology of plants. Academic Press, London.

LAURI, H. & COWLING, R.M. 1994. Lottery coexistence models extended to plants with disjoint generations. *J. veg. Sci.* 5: 161–168.

HEWITT, E.T. 1962. Sand and water culture methods used in the study of plant nutrition. Farnham Royal, Bucks, Commonwealth Agricultural Bureau.

JOLIFFE, P.A., MINJAS, A.N. & RUNECKLES, V.C. 1984. A reinterpretation of yield relationships in replacement series experiments. *J. appl. Ecol.* 21: 227–243.

KEDDY, P.A. 1989. Competition. Chapman & Hall, London.

MACK, R.N. & HARPER, J.L. 1977. Interference in dune annuals: Spatial pattern and neighbourhood effects. *J. Ecol.* 65: 345–363.

MCGILCHRIST, C.A. & TRENBATH, B.R. 1971. A revised analysis of plant competition experiments. *Biometrics* 27: 659–671.

MEAD, R. 1979. Competition experiments. *Biometrics* 35: 41–54.

RöSCH, H. 1996. Life history strategies of Namaqualand pioneer plant species. M.Sc. dissertation, University of Pretoria, Pretoria.

SHIPLEY, B. & KEDDY, P.A. 1994. Evaluating the evidence for competitive hierarchies in plant communities. *Oikos* 69: 340–345.

SHMIDA, A. & ELLNER, S.P. 1984. Coexistence of plants with similar niches. *Vegetatio* 58: 29–55.

SILVERTOWN, J.W. & LOVETT DOUST, J. 1993. Introduction to plant population biology. Blackwell, Oxford.

SNAYDON, R.W. 1991. Replacement or additive design for competition studies? *J. appl. Ecol.* 28: 930–946.

STEYN, A.G.W., SMITH, C.F. & DU TOIT, S.H.C. 1987. Moderne statistiek in die praktyk, 4th edn. Sigma, Pretoria.

TAYLOR, D.R. & AARSSEN, L.W. 1989. On the density dependence of replacement series competition experiments. *J. Ecol.* 77: 975–988.

TRENBATH, B.R. 1974. Biomass productivity of mixtures. *Adv. Agron.* 26: 177–210.

VAN ROOYEN, M.W. 1988. Ekofisiologiese studies van die efemere van Namakwaland. Ph.D. thesis, University of Pretoria, Pretoria.

WILSON, J.B. 1988. Shoot competition and root competition. *J. appl. Ecol.* 25: 279–296.

The taxonomic status of *Sarcocaulon* (Geraniaceae)

F. Albers

Institut für Botanik, Westfälische-Wilhelms-Universität,
Schlossgarten 3, D-48149 Münster, Germany

Received 1 October 1996; revised 24 October 1996

The circumscription of *Sarcocaulon* and *Monsonia* is reconsidered in view of the morphological diversity in the closely related genus *Pelargonium*. SEM studies of the androecium ontogeny reveal that there is no reason for maintaining *Sarcocaulon* and *Monsonia* as separate genera. The gross morphological characters currently used to separate the two genera occur also in several sections of *Pelargonium*. Karyologic, chemotaxonomic and DNA studies also support the lumping of the two genera. The necessary taxonomic changes are made.

Keywords: Generic delimitation, Geraniaceae, *Monsonia*, *Sarcocaulon*.

De Candolle (1824) described *Sarcocaulon* as a new section within the genus *Monsonia* L. (Geraniaceae). However, Sweet (1826) excluded *Sarcocaulon* and raised it to generic rank. Knuth (1912) used androecium morphology characters, apart from growth form characters, as further evidence for maintaining the two as separate genera. *Sarcocaulon* has since been distinguished from *Monsonia* on the basis of its thick, more or less succulent and often woody stems and free stamens as opposed to the mostly herbaceous stems and basally connate stamens in *Monsonia*. Moffett (1979) and Venter (1979) adopted this classification and presented revisions of *Sarcocaulon* and *Monsonia* respectively, maintaining them as separate genera. They also provided historical reviews and nomenclatural changes, and created sections within these genera. Multidisciplinary studies of most of the species in the closely related genus, *Pelargonium*, have cast serious doubt on the long-held views on *Sarcocaulon* and *Monsonia* as two distinct genera. The key characters used to separate them occur also in a range of *Pelargonium* sections.

The differentiation of *Monsonia* and *Sarcocaulon* is mainly based on the gross morphology. In contrast to the predominantly herbaceous stems of *Monsonia* species, those of *Sarcocaulon* form thick, more or less woody to succulent, often spinescent stems. In closely related *Pelargonium* species, similar differences in growth forms are frequently found in comparable habitats. Many species of *Pelargonium* sect. *Cortusina* (DC.) Harv. (e.g. Dreyer *et al.* 1992) and sect. *Otidia* exhibit similar growth forms and often share the arid habitats with species of *Sarcocaulon*. *Monsonia* and *Sarcocaulon* have a similar flower structure but Knuth (1912) observed a difference in the androecium in selected species of the two genera. He pointed out that the 15 stamens of *Monsonia* are grouped together and are connate at the base, whereas in *Sarcocaulon*, the 15 stamens are all free. This was why he maintained *Sarcocaulon* and Monsonia as separate genera. SEM studies on the ontogeny of androeceium development have demonstrated that there is no difference between *Monsonia* and *Sarcocaulon* (Löbbert 1994; Albers & Löbbert 1996), a fact also noted by Venter (1979).

Studies on non-morphological aspects such as phenolic compounds (Marschewski 1995), protein patterns (Touloumenidou 1996) and a variety of basic chromosome numbers (*Monsonia*, $x = 8, 9, 10, 11, 12$; *Sarcocaulon*, $x = 11$) (Albers, unpublished) support the lumping of the two taxa. Based on *rbcL* sequence comparisions, Price and Palmer (1993) observed that *Monsonia* and *Sarcocaulon* are either sister genera or congeneric. The dif-