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Lifeforms as criterion for species delimitation: Are *Aristida adscensionis* and *A. coerulescens* (Aristidoideae, Poaceae) two species?

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Abstract

The distinction of the perennial *Aristida coerulescens* from the annual *A. adscensionis* and its taxonomic treatment have long been debated. We here include accessions from the Mediterranean and Macaronesia for molecular phylogenetic analyses and conducted a morphometric analysis to evaluate if both taxa are distinct. A lineage of *A. adscensionis*, *A. coerulescens* and *A. effusa* is well supported in phylogenetic trees. Moreover, a group of Mediterranean, Macaronesia and Arabian *A. coerulescens* and *A. adscensionis* is revealed where both taxa are intermingled. A morphological analysis of traditionally used spikelet characters does not indicate a clear separation of both taxa. We therefore conclude that *A. coerulescens* and *A. effusa* should best be treated as synonyms of *A. adscensionis*. The differential character of annual and perennial life forms seems to be plastic in this taxon, indicating rapid shifts between these two strategies.

Keywords: life history traits, morphometry, nrITS, *rpl16* intron, taxonomy, *trnL-F*

Introduction

Aristida Linnaeus (1753: 82) is a large genus with 250 to 290 species belonging to Poaceae subfamily Aristidoideae (Cerros-Tlatilpa *et al.* 2011). The taxonomy of the type species, *A. adscensionis* Linnaeus (1753: 82), and its delimitation from *A. coerulescens* Desfontaines (1798: 109) have long been debated. *Aristida adscensionis* was described by Linnaeus based on material from Ascension Island. This morphologically variable species has a worldwide distribution, occurring in thermophilous habitats in Southern Europe, Africa, Macaronesia, South and Middle Atlantic Ocean, Middle, East and tropical Asia, the Pacific region, North America (central and western USA and Mexico), South and Central America (Clayton *et al.* 2018). Linnaeus described *A. adscensionis* as having a caespitose habit and this taxon was considered to be an annual plant by Henrard (1929). Another, closely related taxon has been described by Desfontaines as *A. coerulescens*. By producing sterile innovations after blossom which can persist a whole vegetation period, this species shows a tendency to be perennial (Tutin 1980). The type material was collected from Kairouan in Tunisia (Henrard 1929, Auquier & Duvigneaud 1976, Peruzzi & Passalacqua 2004). This taxon is mainly of Mediterranean distribution.

There has been a long discussion about how to best treat *Aristida adscensionis* and *A. coerulescens* taxonomically. *Aristida adscensionis* is morphologically variable (Cerros-Tlatilpa *et al.* 2011). Auquier & Duvigneaud (1976) distinguished these taxa as follows: annual to perennial habits, interrupted panicles, shorter awns, and upper and lower glumes and longer lemmas in *A. adscensionis* and perennial habits, long, non-interrupted panicles, longer awns, and longer upper and lower glumes and shorter lemmas in *A. coerulescens*. They stated, however, that several of these quantitative characters vary to such an extent that they do not exclusively define both taxa. As a consequence, they treated *A. coerulescens* as subspecies of *A. adscensionis*. A place where both taxa are morphologically distinguishable and grow partly sympatrically is on the Canary Islands (Auquier & Duvigneaud 1976). This view is also followed by Acebes *et al.* (2010), who recognized subsp. *adscensionis* on La Palma, Fuerteventura, and Lanzarote and subsp. *coerulescens* (Desfontaines) Bourreil & Trouin ex Auquier & Duvigneaud (1976: 135) on all Canarian islands, except Lanzarote. The Near-East is another area where perennial and annual *Aristida* grow in relative proximity. In Israel, Jordan and Egypt the annuals are typical of the extreme desert and perennials of semi-desert and dry Mediterranean habitats.

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Aristida coerulescens has been treated in various ways. While some authors maintained species rank (Henrard 1929, Feinbrun-Dothan 1986, Jahn & Schönfelder 1995), many floras and studies followed Auquier & Duvigneaud (1976) treating *A. coerulescens* as subspecies of *A. adscensionis* (Peruzzi & Passalacqua 2004, Ghasemkhani *et al.* 2008). Cerros-Tlatilpa *et al.* (2011) regarded it as variety of *A. adscensionis*, and others regarded *A. coerulescens* as a synonym of *A. adscensionis* (Cope 1982, Press & Short 1994).

In a molecular study by Cerros-Tlatilpa *et al.* (2011) based on cpDNA (*trnL-F*, *rpl16* intron) and nuclear DNA (nrITS) *A. adscensionis*, mainly sampled from southern Africa and the Americas, is part of the 'annual core African' clade and paraphyletic including *A. effusa* Henrard (1926: 155). This study analyzed one accession of *A. coerulescens* from Iran, which was sister to all other samples of *A. adscensionis* and *A. effusa*.

We here address the distinctiveness of *A. coerulescens* and *A. adscensionis* using molecular and morphological data. For the molecular phylogenetic analysis, we extended the previous sampling by Cerros-Tlatilpa *et al.* (2011). We further discuss the evolution of annual versus perennial habits and address implications on the biogeography of this group in the Mediterranean region.

Material & Methods

Taxon sampling

We included 14 samples of *A. adscensionis* and 11 *A. coerulescens* from the Mediterranean and Macaronesia, because both species grow sympatrically in both regions. The attribution of individuals to one of these two taxa was based on regional floras (Feinbrun-Dothan 1986, Press & Short 1994, Jahn & Schönfelder 1995, Acebes *et al.* 2010), using an annual habit for *A. adscensionis* and a perennial one for *A. coerulescens* indicated by innovation shoots or observations of persisting plants in Israel (O. Fragman, pers. obs.). Two accessions from Madeira were attributed a priori to *A. coerulescens* because of the presence of innovation shoots. We also included all accessions of the *A. adscensionis* and *A. effusa* clade from Cerros-Tlatilpa *et al.* (2011) and chose the closely related *A. diffusa* Trinius (1836: 68), *A. anthoxanthoides* (Domin) Henrard (1926: 29), *A. congesta* Roemer & Schultes (1817: 401), *A. hordeacea* Kunth (1835: 15) and *A. rhiniochloa* Hochstetter (1855: 200) as outgroups. The used material is listed in Table 1.

DNA extraction, PCR amplification and sequencing

Total genomic DNA was extracted from herbarium or freshly collected material with the NucleoSpin Plant II (Macherey Nagel, Düren Germany) following the manufacturer's protocol. We followed Cerros-Tlatilpa *et al.* (2011) by using the same two cpDNA markers, the *trnL-F* region and the *rpl16* intron, and the nuclear ribosomal ITS. For the plastid regions, we used the primers and PCR settings described in Cerros-Tlatilpa *et al.* (2011). The primers for the amplification of nrITS were ITS-A, ITS-B, ITS-C, ITS-D (Blattner 1999). All PCRs were performed with a Sensoquest or Biometra cycler with DreamTaq DNA polymerase. PCR products were cleaned with PCR NucleoSpin Gel and PCR clean-up kit (Macherey Nagel, Düren, Germany). Both strands were obtained for each PCR product using the PCR primers and BigDye Terminator v3.1 Cycle Sequencing Kit (Thermo Fisher Scientific, Carlsbad, CA, USA). External sequencing service on an automated ABI 3730 XL sequencer (Applied Biosystems) was provided by LGC Genomics, Berlin. Sequence files were checked and consensus sequences were compiled using Geneious version 11.1.5 (http://www.geneious.com, Kearse *et al.* 2012). All newly generated sequences were deposited at GenBank of the National Center for Biotechnology Information (NCBI), and the corresponding accession numbers are listed in Table 1.

Phylogenetic analyses

Sequences were aligned using MAFFT v7.388 (Katoh *et al.* 2002) as implemented in GENEIOUS. Some hypervariable PolyA/T regions were excluded from analyses. These concern positions 106–107, 327–336, 635–637, 868–872 for trnL-F and for rpl16 positions 161–162 and 329–339. The alignment is deposited (Supplementary File 1). Because there were no contradicting clades in the cpDNA and nrDNA analyses with bootstrap (BS) support > 70% (Alfaro *et al.* 2003) we combined these data sets.

Bayesian Inference (BI) and Maximum likelihood (ML) trees were calculated using MrBayes (Huelsenbeck & Ronquist 2001) and PHYML (Guindon & Gascuel 2003) in GENEIOUS. According to the outcomes of JMODELTEST (Darriba *et al.* 2012), we used the GTR model with four gamma categories, with estimated proportion of variable sites and gamma distribution parameters. For MrBayes the chain length was 1,100,000 generations. Four heated chains with temperature of 0.2, a sample frequency of 200 and a burn-in of 10% were used. For ML nearest-neighbour interchange was used for the tree searches. Using the same options, 100 ML bootstrap replicates were conducted.

Morphometric analysis

The length of central awns, upper glumes, lower glumes and lemmas was measured on 10 spikelets from eight herbarium specimens of each *A. adscensionis* and *A. coerulescens* (SI Table 1). To see if the two taxa can be distinguished by these characters a Principal Components Analysis (PCA) was carried out using JMP (SAS Campus Drive Cary, USA).

TABLE 1. Material used for phylogenetic analyses. Taxa with their origin, voucher specimens and GenBank numbers.

No.	Subsp.	origin	collector & no.	Herbarium	Genbank no. nrITS	Genbank no. *trnL-F*	Genbank no. *rplL16* intron
1	*A. adscensionis*	Egypt	Danin 51600	HUJ	MK119156	MK119129	-
2	*A. adscensionis*	Israel	Thiv 5580	STU	MK119155	MK119128	MK119142
3	*A. adscensionis*	Israel	Thiv 5543	STU	MK119164	MK119139	MK119151
4	*A. adscensionis*	Spain, Lanzarote	Reyes-Betancort SMNS-482	STU	MK119158	MK119130	MK119143
5	*A. adscensionis*	Socotra	Hannon 810	RSA	-	DQ172200	DQ172083
6	*A. adscensionis*	Peru	Columbus 3539	RSA	DQ171976	DQ172201	DQ172090
7	*A. adscensionis*	Argentina	Columbus 3110	RSA	DQ171974	DQ172198	DQ172088
8	*A. adscensionis*	Namibia	Mannheimer 3369	RSA	-	GQ924358	GQ924251
9	*A. adscensionis*	Mexico	Columbus 2869	RSA	DQ171973	DQ172197	DQ172087
10	*A. adscensionis*	Mexico	Columbus 2991	RSA	DQ171972	DQ172196	DQ172086
11	*A. adscensionis*	Mexico	Columbus 3035	RSA	DQ171970	DQ172194	DQ172085
12	*A. adscensionis*	Mexico	Columbus 2716	RSA	DQ171975	DQ172199	DQ172089
13	*A. adscensionis*	Namibia	Mannheimer 3354	RSA	GQ924143	GQ924357	GQ924250
14	*A. adscensionis*	South Africa	Cerros 2884	RSA	GQ924143	GQ924356	GQ924249
15	*A. coerulescens*	Crete	Thiv 5754	UPA, STU	MK119163	MK119133	MK119146
16	*A. coerulescens*	Crete	Thiv 5773	UPA, STU	MK119159	MK119134	MK119147
17	*A. coerulescens*	Crete	Orshan 10502	HUJ	-	MK119135	MK119148
18	*A. coerulescens*	Crete	Thiv 5750	UPA, STU	MK119162	MK119132	MK119145
	A. coerulescens	Egypt	Danin 51733	HUJ	MK119160	MK119137	MK119149
20	*A. coerulescens*	Jordan	Danin 51697	HUJ	MK119157	MK119136	-
21	*A. coerulescens*	Israel	Thiv 5665	STU	MK119165	MK119140	MK119152
22	*A. coerulescens*	Spain, Tenerife	Reyes-Betancort SMNS-483	STU	MK119161	MK119131	MK119144
23	*A. coerulescens*	Portugal, Madeira	Thiv 5808	STU	MK119152	MK119138	MK119150
24	*A. coerulescens*	Portugal, Madeira	Thiv 5830	STU	MK119154	MK119127	MK119141
25	*A. coerulescens*	Iran	Jacobs 6785	RSA	DQ171971	DQ172195	DQ172084
26	*A. anthoxanthoides*	Australia	Columbus 5249	RSA	GQ924146	GQ924360	GQ924253
27	*A. congesta*	South Africa	Cerros 2843	RSA	GQ924154	GQ924368	GQ924261
28	*A. diffusa*	South Africa	Cerros 2832	RSA	GQ924161	GQ924376	GQ924267
29	*A. effusa*	Namibia	Mannheimer 3340	RSA	GQ924165	GQ924380	GQ924271
30	*A. effusa*	Namibia	Mannheimer 3352	RSA	GQ924166	GQ924381	GQ924272
31	*A. effusa*	Namibia	Mannheimer 3333	RSA	GQ924164	GQ924379	GQ924270
32	*A. effusa*	Namibia	Mannheimer 3370	RSA	GQ924167	GQ924382	GQ924273
33	*A. hordeacea*	Senegal	Laegard 17891	MO	DQ172005	DQ172230	DQ172121
34	*A. rhiniochloa*	Namibia	Mannheimer 3337	RSA	GQ924200	GQ924414	GQ924305

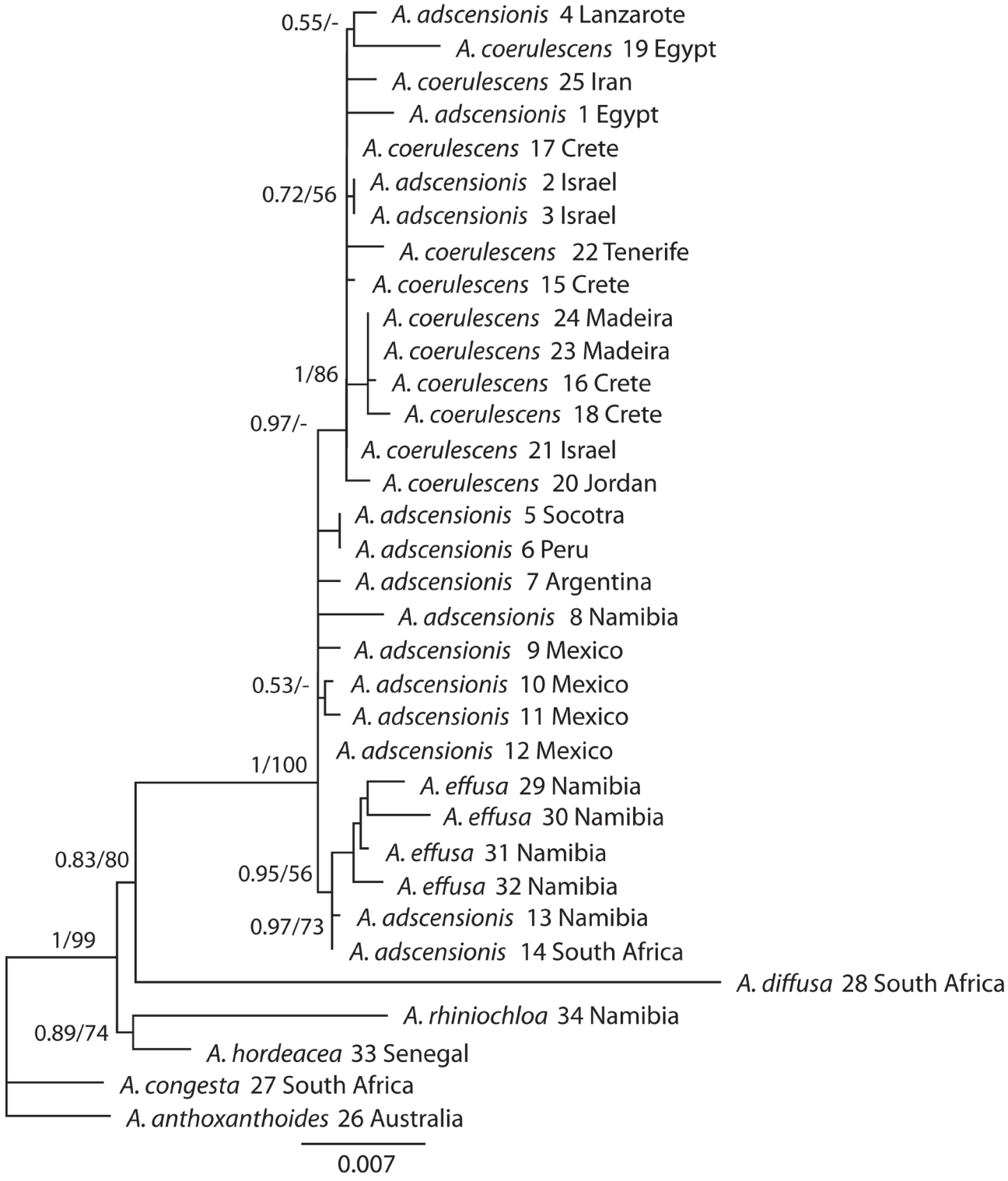


FIGURE 1. Combined *trnL-F*, *rpl16* intron and nrITS ML tree of the *Aristida adscensionis* group. Numbers behind taxon names refer to Table 1 and geographical origins of each accession is given. The first number along a branches indicates PP, and the second number BS>50%. *A.* = *Aristida.*

Results

Our study included 14 new accessions of *A. adscensionis* and *A. coerulescens*. The aligned sequence length (combined matrix) was 2531 bp. A few amplifications failed, leading to 5% missing data (Table 1). The BI analyses yielded trees with a mean log-likelihood of-5342.82 with a standard deviation of 0.176, lower 95% HPD of-5355.79, upper 95% HPD-5329.93 and an effective sample size of >200. The ML tree had a log-likelihood of-5300.40. Pairwise distances varied between 0 and 0.0071 in the ingroup and 0 and 0.0502 in the entire alignment. There were no topological differences between the BI and ML analyses; the trees mainly differed in their support values.

A clade of *A. adscensionis*, *A. coerulescens* and *A. effusa* received high support (PP 1, BS 100). Resolution within this lineage is low. A clade with *Aristida effusa* (PP 0.98, BS <50) from Namibia and *A. adscensionis* from Namibia (one of two samples) and South Africa (PP 0.95, BS 56) is revealed. Two Mexican accessions of *A. adscensionis* (PP 0.53, BS <50) group together. Accessions of *A. adscensionis* from Socotra, Namibia, Peru, Mexico and Argentina are unresolved in the tree. All *A. coerulescens* fall into a group of Mediterranean, Macaronesian and Arabian *A. adscensionis* and *A. coerulescens* accessions (PP 0.97, BS <50). In this clade two Israeli accessions of *A. adscensionis* (PP 0.72, BS 56), *A. adscensionis* from Lanzarote and *A. coerulescens* from Egypt (PP 0.55, BS <50), and Madeiran and Cretian *A. coerulescens* (PP 1, BS 86) group together. The relationships of the remaining accessions from Iran, Jordan, Crete, Egypt, Israel and Tenerife are unresolved.

The results of the morphometric analysis are shown in SI table 2 and Fig. 2. Except for some outliers which belong to specimen C1 in SI Table 1, no overall separation between a priori attributed *A. adscensionis* and *A. coerulescens* was found. Slight differences were indicated when testing both species against the first component (t-test: P = 0.0253, t ratio = 1.97). The length of the awn explained 0.99 of the first component. When removing the outliers C1, differences between both species were not significant.

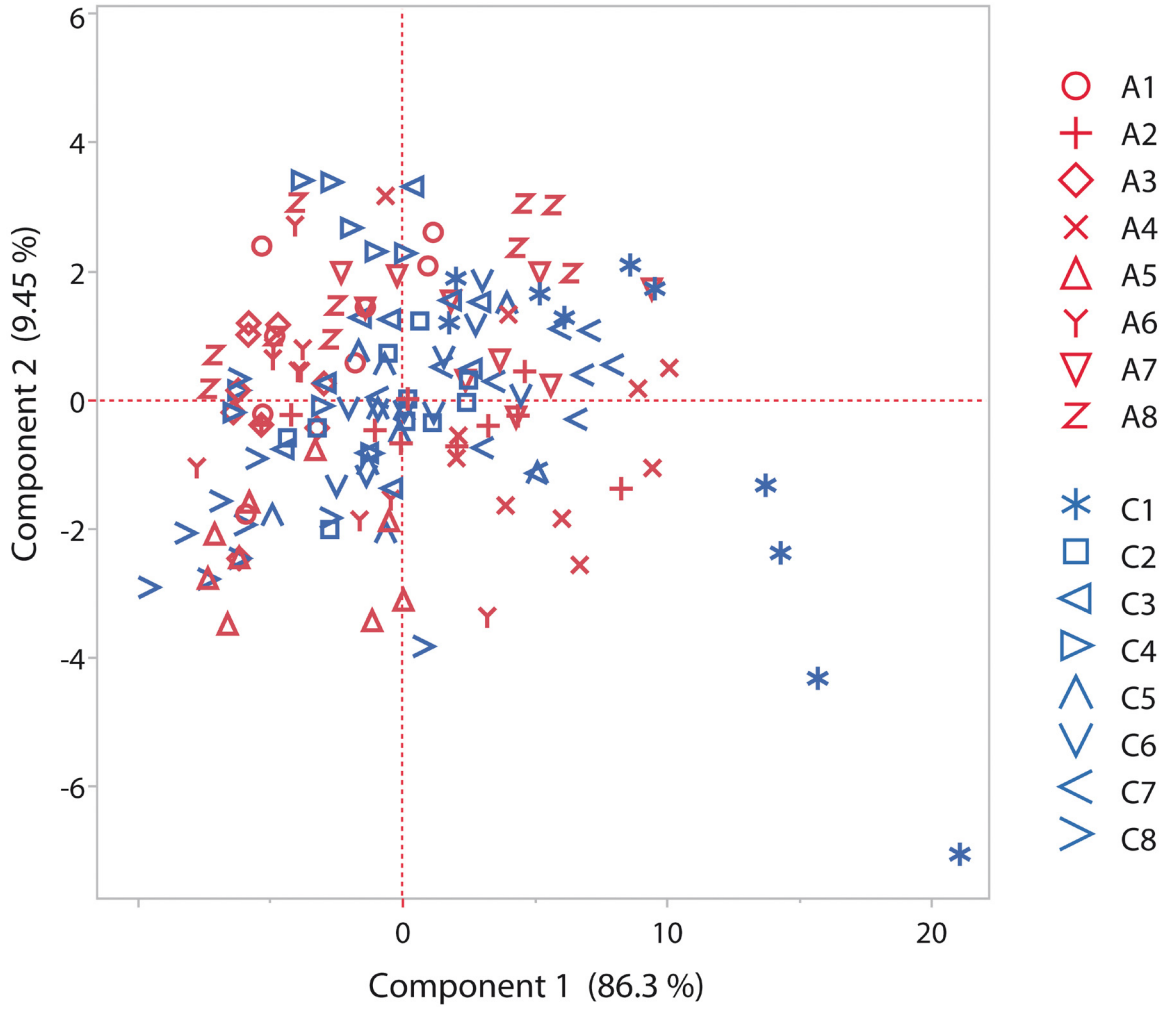


FIGURE 2. Principal component analysis (PCA) of morphological variation of spikelet characters of eight specimens of *Aristida adscensionis* (red) and *A. coerulescens* (blue). A1-8 and C1-8 refer to specimens in SI Table 1.

Discussion

The strong support for the clade of *A. adscensionis*, *A. coerulescens* and *A. effusa* and the low genetic variation among individuals within this lineage (< 1%) support treating this group at species rank, as *A. adscensionis*. So far, the species has been sampled in molecular analyses from Central and South America, southern Africa, the Mediterranean, Arabia and Macaronesia. A cluster of Mediterranean, Macaronesian and Arabian *A. adscensionis* and *A. coerulescens* is moderately supported in the BI analysis and may represent a geographic evolutionary subgroup. All sampled *A. coerulescens* fall into this clade. Inside this group, there is no subclustering for *A. coerulescens* nor for *A. adscensionis*. The two taxa are intermingled. Based on the present molecular data a distinction between *A. adscensionis* and *A. coerulescens* is not corroborated. The morphometric results confirm broad variation in spikelet characters, as stated by Auquier & Duvigneaud (1976); the morphological characters analysed do not distinguish the taxa. We therefore support the taxonomic view of Cope (1982), Meikle (1985) and Press & Short (1994) treating *A. coerulescens* as synonym of *A. adscensionis*.

Aristida effusa from Namibia, already included in the molecular analysis by Cerros-Tlatilpa *et al.* (2011), is nested inside *A. adscensionis*. It is closely related to South African accessions of *A. adscensionis*. *Aristida effusa* was described to be an annual grass with 7 mm long lower glumes, 8 mm long upper glumes, 9 mm long lemmas and central awns of maximum 12 mm length (Henrard 1926). These dimensions fall into the range of measurements of *A. adscensionis* (SI Table 1). Therefore, *A. effusa* should be treated as synonym of *A. adscensionis*.

One of the main characters that has been used to differentiate taxa in this complex, the annual versus perennial life form, is likely plastic in *A. adscensionis*. Whether shifts between these two life-histories are genetically fixed or possibly triggered by ecological parameters is still unclear. Greenhouse cultivation experiments attempted in Germany, in which perennial and annual *Aristida* were grown under the same conditions to see if the lifeform is under genetic control or an environmental modification, were unsuccessful (M. Thiv, unpublished data). Evolutionary shifts between annual and perennial life forms have been detected in several plant groups, e.g., in *Nemesia* Ventenat (Scrophulariaceae), linked to climate changes (Datson *et al.* 2008) or *Lupinus* Linnaeus (Fabaceae, Drummond 2008). Accelerated evolutionary rates in annual plants as observed on larger scale (Yue *et al.* 2010) are not visible in branch length differences in *A. adscensionis* and *A. coerulescens*. The presence of innovation shoots may not be equally distributed in a population. On Madeira only some individuals were observed to have innovation shoots. Considering the close genetic proximity between these forms, the time period necessary to switch between annual and perennial life forms seems to be short and may be underlain by minor genetic controls, possibly induced by ecological parameters. Still, these shifts between annuals and perennials are not yet well understood on a genetic level (Anderson *et al.* 2011).

The present sampling allows us to draw some taxonomic conclusions, but implications on the evolution of *A. adscensionis* in space and time are still limited. A more comprehensive biogeographic study should include a broader, worldwide sampling of this species. At present, the reconstruction of a Mediterranean, Macaronesian and Arabian lineage of *A. adscensionis* is moderately supported. Macaronesian accessions from Tenerife, Lanzarote and Madeira are found in different positions in the phylogenetic trees. While being aware of the low sampling, this may indicate that the Macaronesian colonization could possibly be explained by independent long distance dispersals perhaps from the Mediterranean. The Madeiran plants group with accessions from Crete, not ruling out that unsampled *Aristida* from the western Mediterranean areas may also fall into this subclade.

Taxonomy

Aristida adscensionis Linnaeus (1753: 82)

Lectotype designated by Hitchcock (1924): Aristida adscensionis, Ex insula ascensionis [Osbeck] No. 98.1 (LINN!) http://linnean-online.org/1600/

Synonyms: *Aristida coerulescens* Desfontaines (1798: 109). *Aristida adscensionis* subsp. *coerulescens* (Desf.) Bourreil & Trouin ex Auquier & Duvigneaud (1976: 134). *Aristida adscensionis* var. *coerulescens* (Desf.) Durand & Schinz (1895: 799) (cf. Auquier & Duvigneaud 1976).

Lectotype designated by Peruzzi & Passalacqua (2004): Desfontaines (P-267793)

Aristida effusa Henrard (1926: 155). Type: Africa anstro-occidentalis; Damara. prope Karibib 1200 m. s. m. April 1913 leg. A. Engler, no. 6162 in Herb. Mus. Bot. Berolin.

This type specimen could not be found in the herbarium B (R. Vogt, pers. comm.) and was probably destroyed during World War II. We here refrain from designating a neotype because we cannot rule out the existence of isotypes or other original material.

Conclusion

Inferring from our data, a separation as subspecies or species of *A. coerulescens* is not supported and a treatment of this taxon and *A. effusa* as synonyms of *A. adscensionis* is warranted. Overall, a comprehensive taxonomy and the reconstruction of its biogeographic history still await a denser sampling on the population level and the use of more variable DNA marker systems. Because the Mediterranean-Macaronesian-Irano-Turanian group of *A. adscensionis* exemplifies a high plasticity of annual and perennial habits, this species may serve as an excellent case to study the shifts between life history traits in relation to climate, vegetation and genetics at a low taxonomic level.

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