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RELATIONSHIPS AMONG SOME POPULATIONS OF *ANTHOXANTHUM ALPINUM* AND *A. ODORATUM*
(POACEAE, POOIDEAE): A MORPHOLOGICAL/ANATOMICAL APPROACH

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ABSTRACT

The genus *Anthoxanthum* s.l. (including *Hierochloë*) (Poaceae, Pooideae, Aveneae) comprises 35–50 species and has a cosmopolitan distribution. *Anthoxanthum alpinum* was described as a diploid perennial that is distributed in northern Eurasia and in the high mountains of central and eastern Europe. Difficulties in finding reliable morphological differences between this taxon and the widespread tetraploid *A. odoratum* have resulted in taxonomists treating them as conspecific, despite the cytological differentiation. The purpose of this study was to provide information that may help clarify the relationships between these taxa. Macromorphological, micromorphological, and anatomical data were gathered and analyzed for 14 populations representing both taxa from Scandinavia and the Iberian Peninsula. Statistical analyses were carried out to identify the most useful characters for taxonomy. The relationships among samples were based on different similarity coefficients and summarized using UPGMA clustering methods. The results show that geography has more statistical weight than ploidy level in explaining the relatedness among individuals and populations. A strong correlation between leaf micromorphological/anatomical characters and environmental parameters was detected. The results of the analyses do not support recognition of *A. alpinum* as a distinct species.

Key words: *Anthoxanthum alpinum*, *Anthoxanthum odoratum*, leaf anatomy, leaf micromorphology, morphometrics, Poaceae, polyploid complex.

INTRODUCTION

Traditionally, the genus *Anthoxanthum* L. s.s. (Poaceae, Pooideae, Aveneae) has comprised ca. 18 species, distributed in temperate and arctic-alpine regions of Europe, Asia, and Africa (Watson and Dallwitz 1992). However, Schouten and Veldkamp (1985) included *Hierochloë* R. Br. within *Anthoxanthum* (but see Clayton and Renvoize 1986). As a result, 35–50 species would be included in *Anthoxanthum* s.l., growing mainly in the temperate and arctic regions of both hemispheres, and also on tropical mountains (Clayton 1970; Hedberg 1976; Van Royen 1979; Tutin 1980; Phillips 1995). Seven of the species are present in Europe—*A. amarum* Brot., *A. aristatum* Boiss., *A. gracile* Biv., *A. nitens* (Weber) Y. Schouten & Veldkamp, *A. odoratum* L., *A. ovatum* Lag., and *A. pauciflorum* Adamovic—although this number is uncertain, since the status of some of these taxa is arguable and new species and subspecies have been proposed.

The most widely distributed species in the genus is the perennial *A. odoratum*, a morphologically extremely variable taxon that constitutes a diploid-tetraploid complex. It grows in a broad range of habitats in Eurasia, North Africa, Asia Minor, the Caucasus, and northern Asia. It also has been introduced in North and South America and in Oceania, where it may constitute an ecological problem (Cheeseman 1906; Hitchcock 1951; Tovar 1993).

Diploids of *A. odoratum* were first reported and described by Östergren (1942). Subsequently, Löve and Löve (1948) named these diploids *A. alpinum* Á. Löve & D. Löve, despite the difficult morphological distinction from the tetraploids. Later, names such as *A. odoratum* subsp. *alpinum* (Á. Löve & D. Löve) Hultén and *A. odoratum* var. *montanum* Asch.

& Graebn. were proposed for this taxon (Böcher 1961; Pundeva 1974).

Anthoxanthum alpinum is confined to the northernmost parts of the distribution range of *A. odoratum*, and also to the high mountains of central and eastern Europe (Hedberg 1969; Felber 1993; Felgrová and Krahulec 1999). It usually grows in arctic-alpine meadows, whereas the tetraploid *A. odoratum* occurs in a wide range of habitats.

Different karyotypes have been reported for both cytotypes. Jones (1964), studying Greek plants, was the first to point out the existence of a diploid karyotype “very much like *odoratum* in morphology and distinct from *A. alpinum*” whose taxonomic position “has still to be determined.” Later it was assigned by Hedberg (1986) to *A. odoratum*. Also, Hedberg (1970) was the first to report the existence of two karyotypes in tetraploid *A. odoratum*, confirmed by Teppner (1970).

Contradictory studies regarding morphological and karyological differences between the cytotypes and karyotypes (reviewed by Hedberg 1990) have led to disagreements on the taxonomic rank that should be applied to the ploidy levels. Tutin (1950), Rozmus (1958, 1960), Borrell (1961, 1963), Jones and Melderis (1964), Mayová (1982), Felber (1986, 1988, 1993), and Lauber and Wagner (2001) considered the diploids and tetraploids to represent well-defined species that can be distinguished by certain morphological characters (Table 1), whereas Böcher (1961) and Hedberg (e.g., 1970, 1986, 1990) concluded that the specific rank is not justified for *A. alpinum* since rather high morphological variability can be observed in natural populations.

The study of morphological and anatomical features is still an essential element of taxonomy, and approaches com-

Table 1. Characters traditionally employed for morphological differentiation of *Anthoxanthum odoratum* and *A. alpinum* (literature references in text).

<i>A. odoratum</i>	<i>A. alpinum</i>
Fertile floret smooth	Fertile floret scabrid
Lower glume with unicellular hairs	Lower glume smooth
Glume hairiness variable	Glumes with long soft hairs
Leaf blade planar	Leaf blade convolute
Spikelets greenish	Spikelets reddish
Leaves concolorous	Leaves discolorous
Stomata 44–52 µm long	Stomata 40–46 µm long
Leaf blade length/width ratio > than in <i>A. alpinum</i>	Leaf blade length/width ratio < than in <i>A. odoratum</i>

binning morphometric (qualitative and quantitative characters) and micromorphological/anatomical data have proven to be especially useful in Poaceae taxonomy (e.g., Metcalfe 1960; Dávila and Clark 1990; Acedo and Llamas 1999; Giraldo-Cañas 2001). The aims of this work were to (i) study the morphological and anatomical relationships among several Scandinavian and Iberian populations belonging to both cytotypes, (ii) evaluate the variation in relation to the *A. odoratum*–*A. alpinum* delimitation, and (iii) determine if a correlation exists between micromorphological/anatomical characters and environmental variables. We provide new data that could help clarify the taxonomy of *A. alpinum* and *A. odoratum*.

MATERIALS AND METHODS

Plant Material

We sampled 14 populations of *A. odoratum* and *A. alpinum* from the Iberian Peninsula and Scandinavia during summer 2002 (Table 2). The areas were established to embrace a broad range of geographical and environmental variation in natural populations of *A. odoratum*. In addition, to ensure that both cytotypes were included in the analysis, the Scandinavian populations were selected following Hedberg (1967) wherein ploidy levels were reported. No populations

of *A. alpinum* have been recorded in the Iberian Peninsula (Hedberg 1990).

A total of 35 individuals per population were collected and pressed. Thirty and five individuals, respectively, were employed in the macromorphometric and micromorphological/anatomical analyses. A grand total of 490 specimens were analyzed. Voucher specimens were deposited in the Santiago de Compostela University Herbarium (SANT; Holmgren et al. 1990). Voucher numbers are provided in Table 2.

Morphometric Data

For the morphological study, 26 macroscopic characters (12 qualitative and 14 quantitative, including one ratio) were chosen and scored (Table 3). All of the characters listed in Table 1 were included in the survey except leaf color, as previous papers on *Anthoxanthum* and other grasses have reported that this character is highly influenced by the environment (Kjellqvist 1961; Hedberg 1967; Zeven 1986; Sahuquillo et al. 1991). To standardize the gathering of the data, leaf blade and ligule characters were scored for the second leaf from the base of the plant. In addition, spikelet characters were scored for the basal spikelet of the fourth branch of the inflorescence. To carry out the statistical analyses, the qualitative characters were transformed into binary variables.

The most informative taxonomic characters were identified by calculating the coefficient of variation (cv) for each character and performing a principal components analysis (PCA) for the quantitative data. Contingency tables were applied to qualitative characters. The similarity among samples was established using Manhattan distance and the Phi coefficient for quantitative and qualitative data, respectively. The relationships among populations were summarized in phenograms obtained using UPGMA clustering methods. Statistical analyses were carried out with SPSS vers. 11.0 for Windows (SPSS Inc., Chicago, Illinois, USA).

Micromorphological and Anatomical Data

A total of 29 leaf blade characters (14 from the abaxial epidermis and 15 from the transverse section) were chosen

Table 2. Populations sampled, corresponding habitats, and vouchers for the study of *Anthoxanthum odoratum* and *A. alpinum*. Population codes are in parentheses. I = Iberian Peninsula; SS = southern Scandinavia; NS = northern Scandinavia. Voucher numbers represent collections by the first author, deposited at SANT. Precise localities for populations are provided on the voucher labels.

Taxon	Population	Habitat	Voucher
<i>A. odoratum</i>	Trasigreja, Vilardevós, Ourense. (V1) I	Wet meadow	53412
	Arillo, Oleiros, A Coruña. (O1) I	Wasteland by a road	53361
	A Zapateira, A Coruña. (AZ) I	<i>Eucalyptus</i> plantation	52188
	Taro Blanco, O Courel, Lugo. (TB) I	Mountain meadow	53364
	Alunda, Uppland. (Al) SS	Birch forest	53396
	Angsö-Västerås, Västmanland. (AV) SS	Mixed forest	53389
	Lövudden, Västmanland. (Lö) SS	Birch forest	52199
	Skinnskatteberg, Västmanland. (Sk) SS	Birch forest	52200
	Ställdalen, Västmanland. (St) SS	Spruce forest	52201
<i>A. alpinum</i>	Nipfjället Mt., Dalarna. (Nip) NS	Mountain meadow	52182
	Vittangi, Lappland. (Vit) NS	Wasteland by a road	53393
	Nikkaluokta, Lappland. (Nik) NS	Birch forest	52198
	Björkliden, Lappland. NS. (Bjö)	Mountain meadow	52202
	5 km N Björkliden, Lappland. NS. (NB)	Mountain meadow	53395

Table 3. Quantitative and qualitative macromorphological characters used in the study. Quantitative characters: codes are in parentheses. Measurements were recorded in cm.

Quantitative characters	Qualitative characters
Plant height (Ph)	Leaf blade in transverse section (0 = planar; 1 = convolute)
Leaf blade length (LI)	Ligule shape (0 = round; 1 = pointed)
Leaf blade width at the middle (Lw)	Sheath hairiness (0 = glabrous; 1 = hairy)
Inflorescence length (II)	Upper glume hairiness (0 = glabrous; 1 = hairy)
First internode of inflorescence length (IntI)	Presence/absence of a mucro (0 = not mucronate; 1 = mucronate)
First inflorescence branch length (BI)	Lower glume hairiness (0 = glabrous; 1 = hairy)
Spikelet length (SI)	Presence/absence of a forked apex on upper sterile lemma (0 = not forked; 1 = forked)
Upper glume width (Ugw)	Ratio of sterile lemma hair length to the sterile lemma length (0 = hairs < lemma; 1 = hairs > lemma)
Lower glume width (Lgl)	Sterile lemma hairiness (0 = glabrous; 1 = hairy)
Upper sterile lemma length (Sfl)	Amount of overlap of fertile floret by sterile lemmas (0 = fertile floret not covered by sterile lemmas; 1 = fertile floret covered by sterile lemmas)
Upper sterile lemma width (Sfw)	Fertile floret scabridity (0 = smooth; 1 = scabrid)
Awn length (Al)	Spikelet color (0 = green; 1 = reddish)
Fertile floret length (Ffl)	
Leaf blade length/width (L/I)	

and scored (Table 4). The method used to obtain samples for microscopic observation was that of Devesa (1992), and the terminology followed Ellis (1976, 1979), Nicora and Rúgolo de Agrasar (1987), and Devesa (1992). Regarding the exodermic elements as defined by Devesa (1992), we made no distinction between prickles and hooks, because according to Metcalfe (1960), Snow (1996), and Aliscioni and Ariaga (1998), they intergrade. The quantitative data obtained for each specimen were the mean values of 12 different measures. The final values were transformed into binary variables.

The statistical analyses applied to these data were the same as those used for the qualitative macroscopic traits. To determine if correlations exist between micromorphological/anatomical characteristics and environmental variables, a canonical correspondence analysis (CCA) was performed using CANOCO vers. 4.0. (Ter Braak 1987; Ter Braak and Smilauer 1998; Lepš and Smilauer 2003). The environmental parameters considered were soil pH (following Guitián and Carballos 1976); mean, minimum, and maximum annual temperature (°C); drought period; and mean annual rainfall (mm). Climatic data for the Iberian Peninsula were gathered from Carballeira et al. (1983), and for Scandinavia from the Swedish Meteorological and Hydrological Institute (www.smhi.se). The meteorological stations nearest to the collection localities were selected.

RESULTS AND DISCUSSION

The analyses of quantitative data showed that vegetative characters were more variable than reproductive characters for all populations. Some vegetative characters used to cir-

Table 4. Leaf blade micromorphological (abaxial epidermis) and anatomical (transverse section) characters used in the study. Selected character codes are in parentheses. VB = vascular bundle.

Epidermis		Anatomy
Epidermis type (0 = homogeneous; 1 = siliceous-homogeneous)		
Intercostal zones	Long cell type (0 = 12; 1 = 13)(Devesa 1992)	VB sheath outline (0 = round; 1 = elliptical)
	Long cell length (LCI)(1 = 101–200 μ m; 2 = 301–400 μ m; 3 = 401–500 μ m; 4 = 501–600 μ m; 5 = 601–700 μ m)	VB sheath cell shape (0 = round; 1 = angular)
	Presence/absence of short cells (SI)(0 = absent; 1 = present)	VB sheath cells equal/unequal in size (0 = equal; 1 = not equal)
	Short cell length (LSI)(1 = 11–20 μ m; 2 = 21–40 μ m; 3 = 41–50 μ m)	Median VB sheath type (0 = single; 1 = complete)
	Presence/absence of exodermic elements (0 = present; 1 = absent)	Median VB sheath cell diameter (M) (0 = <15 μ m; 1 = $\geq$ 15 μ m)
Stomate type (0 = parallel-sided; 1 = dome-shaped)		Number of cells in VB sheath (0 = <17; 1 $\geq$ 17)
Costal zones	Long cell type (0 = 12; 1 = 13)(Devesa 1992)	Number of bulliform cells per group (0 = <6; 1 = $\geq$ 6)
	Long cell length (LCN)(1 = 101–200 μ m; 2 = 201–300 μ m; 3 = 301–400 μ m; 4 = 401–500 μ m)	Number of VBs per leaf (VB)(0 = <15; 1 = $\geq$ 15)
	Presence/absence of short cells (SN)(0 = absent; 1 = present)	Median VB type—free or joined to epidermis by sclerenchyma girders (VBT)(0 = free; 1 = joined)
	Short cell length (0 = <50 μ m; 1 = $\geq$ 50 μ m)	Median VB diameter (maximum diameter measured horizontally; VBD)(0 = <75 μ m; 1 = $\geq$ 75 μ m)
	Presence/absence of exodermic elements (0 = present; 1 = absent)	Presence/absence of a radial chlorenchyma (0 = absent; 1 = present)
Presence/absence of bulliform cells (0 = absent; 1 = present)		Presence/absence of a colorless parenchyma (0 = absent; 1 = present)
Leaves pruinose or not (0 = not pruinose; 1 = pruinose)		Presence/absence of ribs and furrows (0 = absent; 1 = present)
		Presence/absence of developed keel (0 = absent; 1 = present)
		Bulliform cell width (0 = <30 μ m; 1 = $\geq$ 30 μ m)

Fig. 1.—Box plots for some of the quantitative characters studied. Line in box represents the mean. Box represents 95% confidence interval. Units are cm.—A. Leaf blade width.—B. Plant height.—C. Spikelet length.—D. Lower glume length. I = Iberian Peninsula; SS = southern Scandinavia; NS = northern Scandinavia.

cumscribe *A. alpinum*, such as plant height (Ph) and leaf width (Lw), had high cv values and ranges of variation that greatly overlapped (Appendices 1, 2; Fig. 1). Conversely, reproductive characters such as spikelet (SI) and lower glume (Lgl) length yielded lower cv values and non-overlapping ranges of variation between both cytotypes, at least for values inside the 95% confidence interval (Appendix 1, Fig. 1). These results also have been observed in two other *Anthoxanthum* species, the Mediterranean *A. aristatum* and *A. ovatum* (Pimentel and Sahuquillo 2003), and reinforce the use of reproductive characters in the differentiation of *Anthoxanthum* taxa.

The mean cv for all tetraploid populations was quite similar to that for all populations of the diploid *A. alpinum* (0.17 and 0.16, respectively; Appendix 2). Higher variability could be expected in the tetraploid populations, since they occur in a wider range of habitats over a greater geographical area, whereas the diploid populations are located in climatically homogeneous areas of northern Sweden (Table 2). Accumulation of snow during the winter is thought to be the most

important factor in determining the distribution of *A. alpinum* (Hedberg 1967).

The first three components of the PCA explained 61% of the variation (Table 5). The PCA plot of these components showed a continuum between the diploid *A. alpinum* and the tetraploid *A. odoratum*, although loosely cohesive groups for each region and cytotype were observed (Fig. 2). The scant separation among the groups was mainly owed to the first component that accounted for 31.6% of the variance. The characters with highest loadings on the first component were leaf blade (LI), inflorescence (II), and spikelet (SI) lengths. According to Östergren (1942), Knaben (1950), and Tutin (1950), a weak differentiation between cytotypes based on these characters may be manifest. However, variation ranges they observed in populations from Scandinavia and the British Isles reduced the taxonomic utility of these characters. In addition, Hedberg (1967) demonstrated in garden experiments that leaf width and length, as well as inflorescence length, are easily modified by the environment. Moreover, traits usually viewed as taxonomically useful, such as fertile

Table 5. Quantitative macromorphological characters showing factor loadings on the first three components from the principal components analysis (Fig. 2). Percentage of total variation explained by each component is provided in parentheses. See Table 3 for explanation of character codes.

Character	Component 1 (31.6%)	Component 2 (15.1%)	Component 3 (14.9%)
Ph	0.44	0.29	-0.37
Li	0.87	-0.28	-0.066
Lw	0.53	-0.36	-0.29
Il	0.88	-0.07	0.14
Intl	0.61	0.04	0.43
Bl	0.57	0.03	-0.35
Sl	0.74	0.29	0.40
Ugw	0.54	-0.27	0.65
Lgl	0.58	0.46	0.36
Sfl	-0.35	0.58	-0.19
Sfw	-0.016	-0.08	0.63
Al	0.11	0.71	-0.17
Ffl	0.17	0.65	0.36
L/l	0.59	0.03	0.20

floret length (Ffl) and upper sterile lemma width (Sfw) (Pau-nero 1953; Valdés 1973; Tutin 1980), were weakly correlated with all three components, indicating their weak discriminating value (Table 5). In our results, only spikelet length (Sl; Mann-Whitney *U*-test, $P = 0.003$) and the ratio of leaf blade length to width (L/l; $P = 0.006$) showed a slight differentiation between cytotypes.

The PCA results suggest that geography is as important as ploidy level in the morphological differentiation of groups. Recognition of *A. alpinum* at the specific rank therefore seems untenable based on morphological characters, and infraspecific status instead should be considered. Limited morphological separation in plants has led authors to widely different taxonomic conclusions. For instance, Chiappella (2000) and Gengler-Nowak (2002), studying *Deschampsia* P. Beauv. (Poaceae) and *Malesherbia* Ruiz & Pav. (Malesherbiaceae), respectively, concluded that continuous morphological variation among groups precluded recognition of the groups as species. Conversely, similar morphological overlap led Dufrêne et al. (1991) to differentiate species within the *Dactylorhiza maculata* (L.) Soó group (Orchidaceae).

In the dendrogram obtained from cluster analysis of quantitative characters (not shown) no clear pattern was observed, and individuals from different populations and regions were intermixed.

Traditionally, qualitative characters have been used more often than quantitative characters for diagnosis of *A. alpinum* (Table 1). Although we found significant differences among populations to be common with respect to qualitative characters, the variation was not partitioned according to cytotype. For instance, the presence or absence of hairs on the lower glume, the latter considered diagnostic for *A. alpinum* (Knaben 1950; Tutin 1950; Jones and Melderis 1964; Lauber and Wagner 2001), was variable in some of the diploid populations studied, such as those at Nipfjället Mt. and Björkliden. This previously has been reported by Borrill (1963) and Hedberg (1964, 1967) for populations in the British Isles, Scandinavia, and the Alps.

Fig. 2.—Plot from a principal components analysis of 14 quantitative macromorphological characters representing 30 plants from each of nine populations (five Scandinavian and four Iberian) of the tetraploid *Anthoxanthum odoratum* and five Scandinavian populations of the diploid *A. alpinum*. I = Iberian Peninsula, SS = southern Scandinavia, NS = northern Scandinavia.

A cluster analysis of qualitative characters (Fig. 3) showed some differentiation of cytotypes. It is worth noting that while 12% of the tetraploids (*A. odoratum*) clustered with diploids (*A. alpinum*), only 2% of the diploids clustered with tetraploid populations. Sheath and glume pubescence seem to be the most important characters for separating the cytotypes. This is consistent with the results of Hedberg (1967), who also found greater variability in pubescence in tetraploids than in diploids. Populations clustered at low levels of similarity with one exception, the Taro Blanco population with hairy sheaths and glabrous glumes. This population is situated in a mountainous area in the northwestern Iberian Peninsula, characterized by extreme climatic conditions, in terms of minimum temperatures, compared to the remaining Iberian tetraploid populations. Noteworthy character states for which a population or cluster was fixed include reddish spikelets, glabrous sheaths and glumes, and the upper sterile lemma having a forked apex. Various studies of grasses have suggested that characteristics such as color or pubescence are highly dependent on the conditions under which the plants grow and, therefore, can hardly be considered distinctive characters (Hedberg 1964, 1967, 1990; Zeven 1986; Sahuquillo et al. 1991; Ramesar-Fortner et al. 1995; Chiappella 2000).

Numerous studies have demonstrated the importance of leaf micromorphology and anatomy in grass systematics (e.g., Metcalfe 1960; Ellis 1976, 1979; Acedo and Llamas 1999; Aliscioni 2000; Giraldo-Cañas 2001). To test their usefulness in the *A. odoratum*–*A. alpinum* complex, a cluster analysis was performed using data from the abaxial epidermis and transverse section of the leaf blade.

In the resulting phenogram, no clear groupings of populations or cytotypes were evident except for a certain separation between the Scandinavian and most Iberian populations (Fig. 4). Differentiating characters included the presence or absence of short cells in the intercostal (SI) and

Fig. 3.—UPGMA phenogram based on 12 qualitative macromorphological characters representing 30 plants from each of nine populations (five Scandinavian and four Iberian) of *Anthoxanthum odoratum* and five Scandinavian populations of *A. alpinum*. The number of specimens per population included in each cluster is indicated in parentheses. FASL = presence of a forked apex on upper sterile lemma; USL = upper sterile lemma. I = Iberian Peninsula, SS = southern Scandinavia, NS = northern Scandinavia.

Fig. 4.—UPGMA phenogram based on 29 leaf blade micromorphological (abaxial epidermis) and anatomical (transverse section) characters representing five plants from each of nine populations (five Scandinavian and four Iberian) of *Anthoxanthum odoratum* and five Scandinavian populations of *A. alpinum*. The number of specimens per population included in each cluster is indicated in parentheses. LCI = long cell length in intercostal zones; LCN = long cell length in costal zones; LSI = short cell length in intercostal zones; M = median vascular bundle sheath cell diameter; SI = presence/absence of short cells in intercostal zones; SN = presence/absence of short cells in costal zones; VBD = median vascular bundle diameter; VBT = median vascular bundle type. I = Iberian Peninsula; SS = southern Scandinavia; NS = northern Scandinavia.

Fig. 5.—Plot from a canonical correspondence analysis of 29 leaf blade micromorphological (abaxial epidermis) and anatomical (transverse section) characters representing five plants from each of nine populations of the tetraploid *Anthoxanthum odoratum* and the diploid *A. alpinum*. All Scandinavian diploid populations (*A. alpinum*) were plotted together (as “N Scandinavia 2x”). Number at end of character codes corresponds to character state explained in Table 4. I = Iberian Peninsula; SS = southern Scandinavia.

costal (SN) zones, the diameter of the median vascular bundle (VBD), and the diameter of the vascular bundle sheath cells (M). It is noteworthy that plants from the Iberian Taro Blanco population cluster with the Scandinavian ones. The position of the Taro Blanco population in the phenogram, as well as the arrangement of populations in a north-south gradient, suggest that the expression of the micromorphological/anatomical characters could be influenced by the environment.

The correlation between the environment and micromorphological/anatomical characters has been pointed out by various authors (e.g., Aiken and Lefkovitch 1984; Ramesar-Fortner et al. 1995). To explore a possible relationship in our

study, a CCA was performed using the characters that were most discriminating in the phenogram (Fig. 4). A high correlation between these characters and the environmental parameters was obtained (0.91 and 0.81, first and second axes, respectively; Fig. 5). Shorter long cells in both costal and intercostal areas were related to high temperatures and the availability of water. Also, the number of vascular bundles per leaf and the diameter of the median vascular bundle increased with higher temperatures. Conversely, presence and length of short cells were related to low temperatures. Regarding the populations, diploids appeared to be associated with low temperatures, whereas all Iberian tetraploids, except the Taro Blanco population, were associated with high

temperatures. As a consequence, these characters should be used with caution when employed for taxonomic purposes in this group.

The limited morphological differentiation observed and the influence of the environment on the micromorphological, anatomical, and qualitative characters do not support recognition of multiple taxonomic species inside the diploid-tetraploid complex. However, unpublished results based on AFLP markers show a higher than expected genetic differentiation between cytotypes (Pimentel et al. unpubl. data). In light of this, and despite the minimal morphological distinction between the cytotypes, their ecological, geographical, and genetic differentiation might be sufficient to assign subspecific status to the diploid. To build on this study, all *A. odoratum*–*A. alpinum* karyotypes should be sampled. Moreover, sampling of additional populations in other areas of the distribution, such as the Alps or the eastern Mediterranean mountains, should be carried out.

CONCLUSIONS

Analyses of morphological and anatomical characters do not support recognition of the cytotypes as different species. Moreover, the quantitative characters that have been used to distinguish *A. alpinum* and *A. odoratum* appear to be too variable and overlap. Only spikelet length, lower glume length, and the ratio of leaf blade length to width are able to slightly separate the cytotypes.

Micromorphological, anatomical, and qualitative macroscopic characters are not discriminant in the *A. odoratum*–*A. alpinum* complex and are more related to geography than to ploidy level. A correlation between micromorphological/anatomical characters and the environment was detected.

The morphological continuum observed between the cytotypes representing populations from distant geographical regions, as well as the ecological and geographical differentiation, suggest that taxonomic separation at the infraspecific level is possible. Unpublished genetic analyses likewise support subspecific status for the diploids.

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Appendix 1. Variation in quantitative macromorphological characters in the populations of *Anthoxanthum odoratum* and *A. alpinum* studied. For population and character codes, see Tables 2 and 3, respectively. Units are in cm. I = Iberian Peninsula; SS = southern Scandinavia; NS = northern Scandinavia; SD = standard deviation; M = maximum value; m = minimum value; CI = 95% confidence interval around the mean.

Population	Statistic	LI	Lw	Ph	L/I	II	BI	Intd
VI (I)	Mean (M-m)	7.78 (10.9-3.2)	0.36 (0.5-0.2)	62.9 (89.1-9.8)	22.8 (8.2-54.5)	5.37 (8.6-3.2)	1.3 (1.7-1)	1.01 (1.4-0.8)
	SD (CI)	1.9 (7.7-8.5)	0.085 (0.32-0.39)	20.5 (55.2-70.5)	8.6 (19.6-26)	1.26 (4.9-5.8)	0.21 (1.2-1.4)	0.17 (0.95-1.1)
	Mean (M-m)	9.3 (13.9-3.6)	0.55 (0.8-0.3)	41.6 (70.4-21.6)	17.3 (6.4-34.5)	5.9 (8.1-3.8)	0.36 (0.43-0.26)	1.56 (2.2-1)
	SD (CI)	2.72 (8.3-10.3)	0.13 (0.5-0.6)	10.7 (37.6-45.6)	5.4 (15.2-19.3)	1.2 (5.4-6.3)	0.042 (0.35-0.38)	0.32 (1.4-1.68)
OI (I)	Mean (M-m)	7.23 (12.1-4.1)	0.46 (0.7-0.3)	34.6 (45.4-19.2)	16.2 (8.8-25.5)	5.2 (7.4-3.4)	0.39 (0.44-0.32)	1.4 (2.4-0.7)
	SD (CI)	1.9 (6.5-7.9)	0.103 (0.42-0.5)	6.16 (32.3-36.9)	4.9 (14.3-18)	0.9 (4.8-5.5)	0.027 (0.38-0.4)	0.4 (1.2-1.5)
	Mean (M-m)	4.3 (7.25-2.5)	0.36 (0.62-0.2)	19.8 (26.7-10.3)	12.4 (6.6-18.1)	3.5 (6.7-1.4)	1.2 (2.1-0.7)	0.64 (1-0.4)
	SD (CI)	1.19 (3.9-4.8)	0.11 (0.32-0.4)	4.73 (18.1-21.6)	3.4 (11.1-13.7)	1.2 (3.1-4)	0.38 (1.07-1.36)	0.17 (0.57-0.7)
AI 4x (SS)	Mean (M-m)	4.2 (6.7-0.8)	0.24 (0.4-0.15)	43.1 (56.2-21.8)	17.7 (4-31.4)	4.4 (6.2-3)	1.3 (1.8-0.8)	0.78 (1.3-0.4)
	SD (CI)	1.32 (3.75-4.7)	0.06 (0.2-0.26)	5.4 (41.1-45.2)	5.7 (15.6-19.9)	0.7 (4.2-4.8)	0.24 (1.2-1.4)	0.2 (0.7-0.86)
	Mean (M-m)	3.8 (8.6-1.7)	0.23 (0.36-0.16)	48.1 (64.7-26.6)	16.9 (9.3-33.7)	3.6 (4.9-2.5)	1.2 (1.9-1.8)	0.78 (1.3-0.4)
	SD (CI)	1.01 (3.37-4.4)	0.05 (0.21-0.25)	9.45 (44.5-51.6)	5.8 (14.7-19.1)	0.54 (3.4-3.8)	0.2 (1.13-1.2)	0.21 (0.7-0.86)
Lô 4x (SS)	Mean (M-m)	3.9 (9.3-2.1)	0.23 (0.4-0.1)	41.2 (53.9-28.9)	18.1 (6.5-32.2)	3.6 (4.9-2.3)	1.15 (1.9-0.6)	0.61 (0.9-0.4)
	SD (CI)	1.1 (3.3-4.65)	0.07 (0.2-0.26)	5.4 (39.9-43.9)	7.3 (15.3-18.5)	0.57 (3.4-3.9)	0.23 (1.07-1.25)	0.13 (0.4-0.9)
	Mean (M-m)	3.2 (7-1.4)	0.21 (0.31-0.13)	41.6 (60.7-14.3)	15.8 (6.4-35)	3.3 (5-2.2)	1.06 (1.7-0.8)	0.51 (1-0.3)
	SD (CI)	1.4 (2.7-3.7)	0.04 (0.19-0.22)	9.7 (37.9-45.2)	7.2 (13-18.5)	0.63 (3.1-3.6)	0.2 (0.9-1.14)	0.15 (0.45-0.56)
St 4x (SS)	Mean (M-m)	4.8 (9.1-3)	0.29 (0.5-0.2)	41.1 (60-29.5)	17.1 (9-29.4)	4.1 (6-2.2)	1.17 (1.9-0.8)	0.72 (1.3-0.4)
	SD (CI)	1.4 (4.3-5.4)	0.07 (0.27-0.32)	6.53 (38.7-43.5)	5.9 (14.8-19.3)	0.95 (3.7-4.45)	0.23 (1.08-1.25)	0.2 (0.63-0.79)
Nip 2x (NS)	Mean (M-m)	2.8 (5.5-1.4)	0.36 (0.65-0.2)	33.1 (40.6-22)	7.7 (3.8-13.7)	2.9 (3.9-2)	1.17 (1.9-0.6)	0.58 (0.8-0.3)
	SD (CI)	1.01 (2.4-3.1)	0.09 (0.33-0.4)	5.02 (31.3-35)	2.7 (6.7-8.7)	0.49 (2.7-3.12)	0.29 (1.06-1.27)	0.14 (0.52-0.62)
	Mean (M-m)	3 (6.9-1)	0.21 (0.4-0.13)	36.8 (51.7-18.8)	14.6 (5-36.3)	3 (5.2-1.7)	1.05 (1.6-0.4)	0.69 (1.2-0.3)
	SD (CI)	1.4 (2.5-3.5)	0.05 (0.19-0.23)	7.53 (33.9-39.5)	6.7 (12.1-17.1)	0.78 (2.7-3.3)	0.26 (0.95-1.14)	0.19 (0.61-0.75)
Nik 2x (NS)	Mean (M-m)	3.4 (6.8-1.3)	0.23 (0.4-0.11)	40.6 (55.4-21.6)	14.8 (6.2-31.5)	3.2 (4.8-2.1)	1 (1.4-0.7)	0.7 (1-0.3)
	SD (CI)	1.52 (2.8-3.9)	0.11 (0.21-0.26)	7.8 (37.7-43.5)	5.9 (12.5-17)	0.75 (2.9-3.5)	0.15 (0.34-1.05)	0.15 (0.6-0.71)
	Mean (M-m)	1.7 (5-0.9)	0.25 (0.4-0.17)	19.3 (25.6-11.1)	6.7 (2.5-17.9)	2.6 (3.9-1.8)	1.06 (1.6-0.8)	0.44 (0.7-0.2)
	SD (CI)	0.9 (1.3-2.03)	0.06 (0.23-0.27)	3.3 (18.1-20.5)	3.1 (5.5-7.8)	0.5 (2.4-2.8)	0.2 (0.99-1.14)	0.11 (0.4-0.5)
NB 2x	Mean (M-m)	2.9 (4.8-1.1)	0.33 (0.41-0.21)	53.6 (66.9-39.2)	9.1 (3.9-17.1)	3.6 (4.5-2.9)	1.4 (1.9-1)	0.9 (1.2-0.7)
	SD (CI)	0.95 (2.5-3.3)	0.05 (0.31-0.35)	8.1 (50.6-56.6)	3.4 (7.8-10.4)	0.38 (3.4-3.7)	0.26 (1.3-1.51)	0.16 (0.8-0.97)

Appendix 1. Continued.

Population	Statistic	SI	Lgl	AI	Ugw	Sfw	Sfl	Ffl
VI (I)	Mean (M-m)	0.79 (0.9-0.7)	0.39 (0.5-0.3)	0.79 (1.1-0.55)	0.35 (0.42-0.29)	0.11 (0.17-0.1)	0.31 (0.41-0.29)	0.21 (0.25-0.15)
	SD (Cl)	0.074 (0.76-0.8)	0.055 (0.3-0.5)	0.12 (0.75-0.83)	0.04 (0.34-0.37)	0.024 (0.11-0.13)	0.036 (0.29-0.32)	0.024 (0.19-0.22)
	Mean (M-m)	0.77 (0.87-0.63)	0.42 (0.58-0.3)	0.77 (0.9-0.44)	0.2 (0.25-0.12)	0.08 (0.1-0.05)	0.29 (0.4-0.26)	0.26 (0.32-0.2)
OI (I)	SD (Cl)	0.063 (0.74-0.79)	0.066 (0.39-0.44)	0.096 (0.73-0.8)	0.025 (0.19-0.21)	0.02 (0.076-0.09)	0.04 (0.27-0.33)	0.035 (0.25-0.28)
	Mean (M-m)	0.76 (0.9-0.55)	0.4 (0.5-0.3)	0.76 (1-0.6)	0.2 (0.27-0.14)	0.088 (0.1-0.06)	0.3 (0.36-0.24)	0.28 (0.34-0.19)
	SD (Cl)	0.08 (0.73-0.8)	0.04 (0.38-0.42)	0.09 (0.72-0.8)	0.019 (0.19-0.21)	0.01 (0.08-0.09)	0.042 (0.28-0.32)	0.028 (0.28-0.3)
TB (I)	Mean (M-m)	0.77 (0.91-0.62)	0.37 (0.42-0.29)	0.82 (1.02-0.62)	0.4 (0.46-0.33)	0.12 (0.18-0.07)	0.29 (0.4-0.21)	0.19 (0.23-0.15)
	SD (Cl)	0.078 (0.74-0.8)	0.035 (0.36-0.39)	0.12 (0.77-0.87)	0.03 (0.38-0.4)	0.03 (0.1-0.13)	0.05 (0.27-0.31)	0.019 (0.18-0.2)
AI 4x (SS)	Mean (M-m)	0.79 (0.84-0.69)	0.5 (0.55-0.41)	0.85 (1.06-0.7)	0.3 (0.39-0.27)	0.09 (0.12-0.07)	0.31 (0.36-0.27)	0.23 (0.26-0.21)
	SD (Cl)	0.04 (0.76-0.79)	0.04 (0.46-0.49)	0.09 (0.81-0.88)	0.07 (0.3-0.33)	0.01 (0.09-0.1)	0.02 (0.3-0.32)	0.012 (0.22-0.24)
	Mean (M-m)	0.77 (1.01-0.65)	0.42 (0.52-0.33)	0.81 (1.08-0.52)	0.32 (0.42-0.25)	0.105 (0.13-0.08)	0.3 (0.41-0.25)	0.21 (0.27-0.19)
AV 4x (SS)	SD (Cl)	0.082 (0.74-0.8)	0.046 (0.4-0.43)	0.1 (0.77-0.84)	0.038 (0.31-0.34)	0.013 (0.1-0.11)	0.031 (0.29-0.32)	0.016 (0.2-0.22)
	Mean (M-m)	0.75 (0.84-0.62)	0.43 (0.51-0.34)	0.86 (1.02-0.72)	0.31 (0.36-0.25)	0.1 (0.13-0.08)	0.31 (0.36-0.26)	0.22 (0.25-0.18)
	SD (Cl)	0.06 (0.72-0.77)	0.04 (0.42-0.45)	0.08 (0.83-0.88)	0.03 (0.29-0.32)	0.014 (0.09-0.13)	0.025 (0.3-0.32)	0.018 (0.21-0.23)
Sk 4x (SS)	Mean (M-m)	0.75 (0.84-0.62)	0.43 (0.51-0.34)	0.86 (1.02-0.72)	0.31 (0.36-0.25)	0.1 (0.13-0.08)	0.31 (0.36-0.26)	0.22 (0.25-0.18)
	SD (Cl)	0.06 (0.72-0.77)	0.04 (0.42-0.45)	0.08 (0.83-0.88)	0.03 (0.29-0.32)	0.014 (0.09-0.13)	0.025 (0.3-0.32)	0.018 (0.21-0.23)
	Mean (M-m)	0.73 (0.75-0.71)	0.42 (0.51-0.32)	0.8 (0.91-0.6)	0.31 (0.35-0.28)	0.09 (0.11-0.08)	0.3 (0.33-0.23)	0.22 (0.26-0.18)
St 4x (SS)	SD (Cl)	0.05 (0.71-0.75)	0.05 (0.4-0.44)	0.06 (0.78-0.83)	0.018 (0.3-0.32)	0.01 (0.09-0.1)	0.025 (0.27-0.29)	0.02 (0.21-0.23)
Nip 2x (NS)	Mean (M-m)	0.67 (0.73-0.6)	0.37 (0.45-0.31)	0.78 (0.93-0.64)	0.29 (0.35-0.22)	0.1 (0.12-0.09)	0.36 (0.4-0.31)	0.21 (0.25-0.16)
	SD (Cl)	0.036 (0.66-0.69)	0.037 (0.35-0.38)	0.06 (0.76-0.81)	0.04 (0.27-0.3)	0.008 (0.1-0.12)	0.028 (0.35-0.37)	0.02 (0.2-0.22)
	Mean (M-m)	0.58 (0.68-0.5)	0.33 (0.43-0.27)	0.75 (0.91-0.61)	0.27 (0.32-0.18)	0.12 (0.15-0.07)	0.33 (0.41-0.21)	0.21 (0.24-0.18)
Vit 2x (NS)	SD (Cl)	0.04 (0.56-0.6)	0.038 (0.31-0.34)	0.08 (0.73-0.79)	0.03 (0.26-0.28)	0.015 (0.11-0.12)	0.04 (0.31-0.34)	0.013 (0.2-0.21)
	Mean (M-m)	0.58 (0.67-0.44)	0.28 (0.37-0.22)	0.73 (0.89-0.6)	0.26 (0.34-0.2)	0.11 (0.15-0.07)	0.31 (0.35-0.27)	0.18 (0.21-0.14)
	SD (Cl)	0.05 (0.56-0.6)	0.037 (0.27-0.3)	0.07 (0.7-0.76)	0.03 (0.25-0.28)	0.02 (0.1-0.15)	0.02 (0.3-0.32)	0.014 (0.18-0.2)
Bjö 2x (NS)	Mean (M-m)	0.6 (0.66-0.47)	0.31 (0.37-0.28)	0.78 (0.95-0.65)	0.27 (0.35-0.23)	0.1 (0.12-0.09)	0.34 (0.41-0.29)	0.21 (0.24-0.2)
	SD (Cl)	0.04 (0.57-0.6)	0.02 (0.3-0.32)	0.06 (0.75-0.8)	0.027 (0.26-0.28)	0.01 (0.1-0.11)	0.03 (0.33-0.35)	0.011 (0.21-0.23)
	Mean (M-m)	0.62 (0.71-0.55)	0.35 (0.4-0.31)	0.96 (1.04-0.85)	0.17 (0.21-0.15)	0.05 (0.06-0.05)	0.36 (0.41-0.34)	0.19 (0.23-0.18)
NB 2x (NS)	SD (Cl)	0.04 (0.61-0.64)	0.017 (0.34-0.35)	0.05 (0.11-0.13)	0.016 (0.16-0.18)	0.002 (0.04-0.06)	0.02 (0.35-0.38)	0.014 (0.19-0.23)

Appendix 2. Coefficient of variation of each quantitative macromorphological character for each population studied. For population and character codes, see Tables 2 and 3, respectively. OV = overall value; MV = mean value per population.

		Character														MV
		LI	Lw	Ph	L/l	Il	Bl	Intl	Sl	Lgl	Al	Ugw	Sfw	Sfl	Ffl	
Population	VI	0.24	0.23	0.32	0.37	0.23	0.16	0.17	0.09	0.14	0.15	0.11	0.2	0.12	0.11	0.17
	Ol	0.29	0.24	0.26	0.31	0.2	0.2	0.37	0.08	0.16	0.12	0.11	0.24	0.13	0.13	0.19
	AZ	0.28	0.22	0.18	0.3	0.17	0.29	0.35	0.08	0.1	0.12	0.07	0.11	0.1	0.09	0.19
	TB	0.28	0.3	0.24	0.27	0.34	0.31	0.26	0.1	0.09	0.15	0.08	0.24	0.17	0.1	0.2
	Al	0.3	0.24	0.13	0.32	0.17	0.18	0.27	0.05	0.08	0.1	0.09	0.11	0.07	0.05	0.14
	AV	0.35	0.22	0.2	0.34	0.15	0.18	0.27	0.1	0.11	0.13	0.12	0.12	0.1	0.08	0.16
	Lö	0.46	0.32	0.13	0.4	0.15	0.2	0.22	0.08	0.1	0.1	0.09	0.14	0.08	0.08	0.16
	Sk	0.44	0.21	0.23	0.45	0.19	0.2	0.31	0.08	0.08	0.09	0.09	0.15	0.09	0.07	0.17
	St	0.29	0.23	0.16	0.34	0.23	0.2	0.31	0.07	0.12	0.07	0.06	0.11	0.09	0.09	0.15
	Nip	0.36	0.25	0.15	0.35	0.23	0.25	0.24	0.05	0.1	0.08	0.14	0.08	0.08	0.11	0.16
	Vit	0.46	0.27	0.2	0.45	0.26	0.25	0.28	0.08	0.12	0.11	0.11	0.13	0.13	0.07	0.19
	Nik	0.45	0.3	0.19	0.4	0.24	0.15	0.23	0.08	0.13	0.1	0.12	0.18	0.07	0.08	0.18
	Bjö	0.53	0.23	0.17	0.45	0.19	0.18	0.26	0.07	0.07	0.08	0.1	0.09	0.09	0.05	0.16
	NB	0.33	0.15	0.15	0.37	0.1	0.18	0.18	0.07	0.05	0.05	0.1	0.05	0.06	0.07	0.11
	OV	0.58	0.41	0.35	0.47	0.32	0.25	0.35	0.14	0.17	0.12	0.2	0.23	0.13	0.1	