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Variability of *Anthoxanthum* species in Poland in relation to geographical-historical and environmental conditions: morphological and anatomical variation

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Abstract: Three *Anthoxanthum* species are found in Poland: the native *A. odoratum* L. s. str. and *A. alpinum* Á. Löve & D. Löve, and the alien *A. aristatum* Boiss. Major problems within this genus concern: (1) population variation of the native *A. odoratum*, representing various phases of ecological expansion to anthropogenic habitats; (2) population variation of *A. odoratum* and *A. alpinum* along the altitudinal transect; and (3) variation between populations of *A. aristatum* colonizing new areas and habitats outside its natural range of distribution (chorological expansion). In this study, morphological and anatomical variation of the three Polish *Anthoxanthum* species was analysed in detail. The variation of *A. odoratum* and *A. aristatum* was analysed in respect of environmental differences: habitat types and soil parameters. In the Babia Góra massif, variability distribution along the altitudinal transect was analysed for two vicariants: *A. odoratum* and *A. alpinum*. *A odoratum* in this massif does not cross the upper forest limit (i.e. forest line), and lower montane populations are morphologically very similar to lowland populations. Morphological and anatomical differences were detected between populations of *A. alpinum* along the altitudinal transect in the Babia Góra massif, with distinct upper montane populations. Moreover, clear morphological differences were found between the two altitudinal vicariants. Lowland populations of *A. odoratum* are characterized by great morphological variation, only weakly correlated with the type of occupied habitat and the phase of ecological expansion. The detected morphological variation reflects only to a limited extent the environmental variation of occupied habitats, and is not significantly correlated with the phase of chorological expansion. Some soil parameters are significantly correlated with some morphological characters studied in all the *Anthoxanthum* species. The analysed anatomical features of stems and leaves show continuous variation in the three species.

Key words: Poaceae, *Anthoxanthum alpinum*, *Anthoxanthum aristatum*, *Anthoxanthum odoratum*, distribution, variation, morphology, anatomy, habitat, altitudinal transect, soil parameters, ecological expansion, chorological expansion

Contents

1. Introduction

The genus *Anthoxanthum* (vernal grasses) is represented in the Polish flora by three species: the native *A. alpinum* Löve and Löve and *A. odoratum* L., and the alien *A. aristatum* Boiss. Although differing in many respects, they are closely related taxonomically, genetically, chorologically, and ecologically. Thanks to this, they are jointly an interesting subject of research. Simultaneously, they differ in geographical-historical status and habitat preferences. All this makes it possible to investigate the mechanisms of natural and anthropogenic influence on species diversity.

Patterns of variation and distribution of natural plant populations are analysed in relation to current and historical events. The present distribution of species and their variation results from interpopulation and interspecific gene flow or genetic drift, but also geological history and climate change (Hewitt 1999).

Research on plant variation is carried out primarily with the use of methods based on phenotypic (structural) and genetic characters. An analysis of morphological variation makes it possible to determine if any differentiating trends can be noticed within a species, resulting from geographical distance or environmental variation. Similar studies concerned e.g. *Elymus repens* (Szczepaniak 2002, 2009), *Hordeum murinum* (Mizianty 2006), *Hordelymus europaeus*, and *Leymus arenarius* (Mizianty *et al.* 2007). One of the genera studied thoroughly in the last two decades is the genus *Calamagrostis*. The studies concern its taxonomy, karyology (Frey & Paszko 1999), anatomical variation (Paszko & Krawczyk 2005) or morphological variation (Drapikowska *et al.* 2007a, 2007b).

Microevolutionary mechanisms, initiated under the influence of human activity, are the subject of numerous studies, both theoretical and applied. This interest is perfectly understandable, because anthropogenic microevolutionary changes are relatively recent. Moreover, effects of the changes are very often evaluated negatively from the human point of view (Honnay & Jacquem 2007). That is why the studies usually concern plant species threatened with extinction (Kreivi *et al.*

2005), or invasive species with destructive effects on natural ecosystems and various crop fields. The habitat spectrum of invasive grass species in Poland includes chiefly ruderal and segetal habitats. Currently, intensive research concerns morphological and genetic variation of invasive species, e.g. *Avena fatua* (Paczos-Grzęda *et al*. 2009), *Hordeum murinum* (Mizianty 2006; Mizianty *et al.* 2007), *Bromus carinatus* (Sutkowska & Pasierbiński 2009), and *Apera spica-venti* (Warwick *et al.* 1987).

Molecular methods are used for research on genetic variation of natural populations in the geographical and geological context (Hewitt 2001, 2004; Schönswetter *et al.* 2005). Genetic processes in natural populations are dependent on internal and external factors. A basic task of population genetics is to estimate the intensity of gene flow between populations, with reference to natural selection and genetic drift. Many grass taxa have been studied in respect of distribution of genetic variation, e.g. *Bromus* species (Oja & Jaaska 1996), *Lolium perenne* (Bolaric *et al.* 2005), *Stipa capillata* (Hensen *et al.* 2010), *Calamagrostis arundinacea*, and *C. villosa* (Krzakowa *et al.* 2005; Krzakowa & Celka 2007, 2008; Krzakowa & Dunajski 2007).

The genus *Anthoxanthum* L. is found in Australia, Africa, Europe, West-Asia and North America (Meusel *et al.* 1965, Fig. 1). It was first described by Linnaeus in 1754, in his book *Genera Plantarum* (Linnaeus 1754). The genus belongs to the family Poaceae, subfamily Pooideae, tribe Aveneae, and subtribe Phalaridinae (Frey 2007, after Clayton & Renvoize 1986), and globally is represented by 18 species (Mabberley 1997). From Europe, 6 species are reported by Tutin (2005), whereas 8 species by Pimentel Pereira *et al.* (2007a). These include 5 perennials: *A. odoratum* L. s. str. *A. alpinum* Löve and Löve, *A. armarum* Brot., *A. maderense* Teppner, and *A. pauciflorum* Adamovic; as well as 3 annuals: *A. aristatum* Boiss., *A. ovatum* Lag., and *A. gracile* Biv. (Tutin 2005; Pimentel Pereira *et al.* 2007a).

Population studies involving European populations of the genus *Anthoxanthum* have been conducted primarily by Pimentel Pereira *et al.* (2007a, 2007b). Morphological-genetic research shows that the major cause of differentiation of European species of the genus *Anthoxanthum* was probably the colder period in the early Eocene (55 million years ago), which initiated the spread of tall grasses and differentiation of grass species resistant to drought. At that time, annual Mediterranean

Fig. 1. Distribution of the genus *Anthoxanthum* in the world (according to Meusel *et al.* 1965)
Explanation: sa – synanthropic site

species were separated from perennial Euro-Siberian species. The next stage of rapid differentiation took place during Pleistocene glaciation, when polyploid species (e.g. *A. odoratum*), resulting from hybridization in the contact zone of diploid species, differentiated from parental diploid species (*A. alpinum*), whose distribution range covers northern Europe and Asia and higher parts of mountains (e.g. *A. alpinum*) or the Mediterranean region (e.g. *A. aristatum*). Moreover, clear morphological and genetic differences were found between populations of *A. odoratum* and two other European species: *A. armarum* and *A. alpinum* (Pimentel *et al.* 2007b). Research on morphological variation of *A. odoratum* in Poland (Drapikowska *et al.* 2008, 2011) showed a high degree of intraspecific variation and small interpopulation variation, but a lack of correlation with habitat type.

Polyploidization has played an important role in grass evolution, as about 70% of grass species are polyploids (Mizianty 2007). The origins of polyploid species of the genus *Anthoxanthum*, including *A. odoratum*, have been studied for many years (Jones 1964; Teppner 1969; Hedberg 1986; Felber 1996; Bretagnolle 2001). Cytological analysis of specimens classified as *A. odoratum* shows that like in other parts of Europe, also in Poland, *A. odoratum* is a collective species and includes two cytotypes (Rozmus 1958): diploid ($2n = 10$), whose distribution is limited to the subalpine and alpine zones, and tetraploid ($2n = 20$), found in lowlands and at lower altitudes in mountains, below the forest line. Those studies confirmed that *A. alpinum*, first described by Löve and Löve (1948), is a valid species. In the 1960s, experiments were conducted to investigate the evolution of *Anthoxanthum* species (Borril 1963). Controlled hybridization of diploid species *A. ovatum* Lag. and *A. alpinum* with the tetraploid *A. odoratum* indicated e.g. that *A. odoratum* is most closely linked to *A. ovatum* and distinct from *A. alpinum* and *A. aristatum*. Borrill (1963) found also that potential ancestors of the tetraploid *A. odoratum* were two diploid species with genomes similar to those of *A. ovatum* and *A. aristatum*. A comparative analysis of karyotypes, aimed to explain the origin of the tetraploid *A. odoratum*, proved that *A. odoratum* is an allotetraploid, significantly different from the diploid *A. alpinum* (Jones 1964). Recent cytogenetic investigations have revealed that *A. odoratum* has 4 genes encoding 5S rDNA and 6 genes encoding 45S rDNA in meristematic root cells. It was also found that genome size in *A. odoratum* amounts to 13.252 pg/2C DNA. Measurements of stomata on both sides of the leaf show that their size depends on ploidy level and stomatal length vary widely within the allotetraploid *A. odoratum* (Drapikowska *et al.* 2013).

Anthoxanthum odoratum is a polymorphic species, varying in leaf blade morphology, shape and colour of individual parts of the plant, and selected reproductive characters. On the basis of those characters, many varieties, subvarieties, and forms have been defined (Hegi 1909). Some of the forms were next attributed to characteristic habitats: *A. odoratum* subvar. *tenerum* Beck and *A. odoratum* subvar. *umbrosum* Bolle on shaded sites, *A. odoratum* subvar. *villosum* Loisel. on dry sites, and *A. odoratum* subvar. s*ilvaticum* Arch. and Graebn. in open forests (Hegi 1909; Falkowski 1982).

Anthoxanthum alpinum was distinguished in Poland on the basis of taxonomic and cytological research conducted by Rozmus (1960). Gluch and Rostański (1994) presented the karyotype of meristematic cells of *A. alpinum* from Babia Góra (altitude 1660 m). Population ecology of *A. alpinum* in the Babia Góra massif was studied by Szwed (1986). Distribution of *A. alpinum* was studied e.g. in the Karkonosze Mts. (Mądalski & Serwatka 1963; Rostański 1977), in the massif of Śnieżnik (Králický Sněžník), and Bialskie Mountains (Szeląg 2000). As reported in earlier studies, *A. odoratum* and *A. alpinum* differ in plant structure (Rostański 1996; Drapikowska *et al.* 2012b). Contact zone of these species (in the upper montane zone) is very narrow. *A. alpinum* can sporadically be found below 1000 m a.s.l.

For many years botanical research has concerned the effect of altitude on morphological, genetic, and cytological variation of *A. odoratum* and *A. alpinum* in the Western Carpathians, Massif Central in France, and the Karkonosze Mts. In Austria, detailed chorological and karyological studies were conducted by Teppner (1969, 1970), who found autotetraploid individuals of *A. alpinum* and reported that in the Austrian Alps *A. alpinum* reaches altitudes of up to 1200 m. Bretagnole (2001) came to a conclusion that within diploid populations of *A. alpinum*, polyploidization occurs spontaneously at a rate of 2 triploids per 1000 seeds. Other studies have focused on life history of both species at various altitudes. For example, Flegrová and Krahulec (1999) reported that limitations of sexual reproduction (e.g. difficulties in seed germination) of *A. odoratum* and *A. alpinum* limit the expansion of these species to sites occupied by the other vicariant. The distribution of cytodemes (i.e. groups of taxa sharing a common chromosome complement) in Switzerland and France was investigated by Felber (1986, 1988; Felber-Girard *et al.* 1996). Filipová and Krahulec (2006), when analysing the contact zone between *A. odoratum* and *A. alpinum* in the Karkonosze Mts., found that the potential hybridization zone of these vicariants covers the altitudes of 800-1290 m and that *A. alpinum* sometimes appears in the lower montane zone. Besides, those authors noticed that *A. odoratum* prefers south-facing slopes, where it is more abundant. Morphological and genetic variation was also studied in

Scandinavian populations and montane Iberian populations of two closely related species: *A. odoratum* and *A. alpinum* (Pimentel & Sahuquillo 2008). The results show that both species are characterized by continuous variation of morphological and anatomical characters, and there are no genetic differences between two cytotypes: diploid and tetraploid. Gui-Fang *et al.* (2000) found significant genetic variation of populations of *A. alpinum* studied along the altitudinal transect.

Intraspecific variation is noticeable in *A. aristatum.* According to most authors, *A. aristatum* Boiss. is a synonym of *A. puelii* Lecoq & Lamotte (e.g. Häfliger & Scholz 1981). However, some authors (e.g. Pinto da Silva *et al*. 1971) distinguish two subspecies: *A. aristatum* Boiss. subsp. *aristatum*, recorded mostly in the west-Mediterranean part of its geographical range, and *A. aristatum* Boiss. subsp. *puelli* Lecoq & Lamotte, distributed in the Atlantic part of West and Central Europe. Other concepts distinguish within *A. aristatum* subsp. *aristatum* two varieties: var. *aristatum* and var. *welwitschii* Ricci (Valdés 1973). According to Schneider *et al.* (1994), both varieties are found in Germany and their geographical ranges overlap. Intensive population studies and comparative taxonomic studies on *A. aristatum* were conducted within its natural range (Pimentel *et al* 2006, 2010). Their results show that there is a high morphological and genetic variation in Mediterranean populations of *A. aristatum*, and the species hybridizes with the closely related *A. ovatum*.

Anthoxanthum aristatum is characterized by phenotypic plasticity. A preliminary biometric analysis of populations of this species from various habitats (fields, ruderal sites, roadsides, forest edges) has revealed significant variation between them. Additionally, the degree of morphological variation was found to be correlated with the type of occupied habitat (Drapikowska *et al.* 2012a). The presence of populations of *A. aristatum* for over 100 years in the immediate vicinity of lowland populations of *A. odoratum* raises a question about the possibility of interspecific hybridization. Falkowski (1982) after Knobloch (1968) noted that the diploid *A. aristatum* can hybridize with the tetraploid *A. odoratum*. Cytogenetic analyses show that *A. aristatum* and *A. odoratum* differ in DNA content, estimated at 6.863 pg/2C DNA in *A. aristatum* and 13.252 pg/2C DNA in *A. odoratum*. These two species also differ in location and number of loci of 45 rDNA and 5S rDNA. The detected close location of genes of 45 rDNA and 5S rDNA on the same chromosome pair can serve as a marker for identification of *Anthoxanthum* species (Drapikowska *et al.* 2013).

The basic aim of this study was to assess interspecific and intraspecific variation of three species of the genus *Anthoxanthum*, which differ in their geographical-historical status in Poland and environmental requirements. Analysing the natural and anthropogenic factors that condition the variation, special attention was given to:

- morphological and anatomical differences between natural and anthropogenic populations of the native species *A. odoratum*, which in Poland is at a phase of intensive ecological expansion;
- structural differences between populations of the alien species *A. aristatum*, which in Poland is at a phase of chorological expansion;
- verification of a hypothesis about potential hybridization of the native *A. odoratum* and the alien *A. aristatum*;
- determination of morphological differences between closely related altitudinal vicariants: *A. odoratum* and *A. alpinum*;
- verification of a hypothesis about potential hybridization of the vicariant species.

1.1. Distribution and environmental conditions of *Anthoxanthum odoratum*

This species is a perennial, flowering from April to June, sometimes to early July (Falkowski 1982). It forms separate tufts, which do not spread vegetatively. It is self-incompatible (Antonovics *et al.* 1987). This widely distributed Eurasian taxon (Hultén & Fries 1986; Fig. 2A) is classified as an invasive species in other parts of the world, e.g. in Australia, New Zealand, and since the late 18th century also in North America (Dwire 1983; Meusel *et al.* 1965; Grant & Antonovics 1978; Hultén & Fries 1986; Csurhes & Edwards 1998; Jesson *et al.* 2000; Mack 2000; Barker *et al.* 2005; Bostock & Holland 2007; Jacobs & Hastings 2007). On pastures in North America, it competes with other grasses, e.g. *Dactylis glomerata* or *Lolium perenne* (Remison & Snaydon 1978; Fowler 1982). Intensive research on the causes of expansion of this species has evidenced that *A. odoratum* reproduces most effectively on sites transformed by humans (Jesson *et al.* 2000). Populations grown in controlled conditions were also investigated intensively. Most spectacular experiments have been conducted for 150 years in Canada, where morphological variation, developmental biology, and recently genetic diversity of populations grown on plots varying in fertility have been analysed (Silvertown *et al.* 2006; Freeland *et al.* 2010), and phenotypic plasticity of populations was analysed in controlled conditions in various habitats on the basis of seedling and seed morphology (Platenkamp 1991). This grass species is competitive as compared to other species because of its early flowering period (Remison & Snaydon 1978) and allelopathic properties (Yamamoto 1995). Since the end of the 20th century, *A. odoratum* has been observed to colonize sites strongly transformed by human activity (e.g. Antonovics 1972).

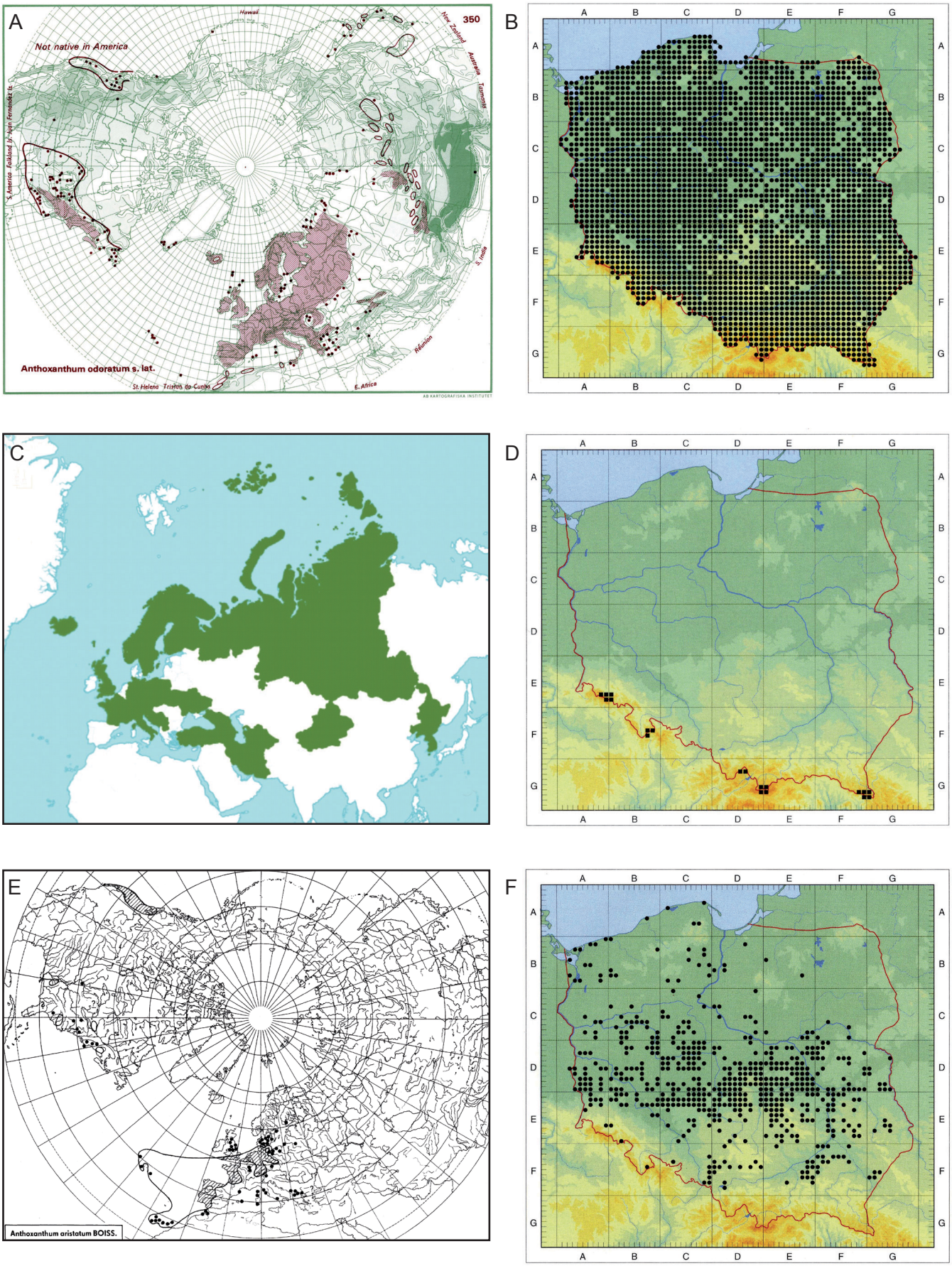

Fig. 2. Distribution of *Anthoxanthum odoratum* (A, B), *A. alpinum* (C, D), and *A. aristatum* (E, F) in the world and in Poland
Explanations: A – according to Hultén & Fries (1986); B, D, F – according to Zając & Zając (2001); C – according to http://build.e-monocot.org; E – according to Kästner *et al.* (2001)

In Europe, *A. odoratum* is found in a wide spectrum of habitats: from open deciduous and coniferous forests to moist and dry meadows and other dry grasslands, where it is most common, and to habitats strongly transformed by human activity: squares, roadsides, and wastelands (Dostál 1989; Matuszkiewicz 2001; Rothmaler *et al.* 2005; Rostański & Woźniak 2007; Rutkowski 2011). *A. odoratum* is widespread in Poland (Zając & Zając 2001; Fig. 2B), in mountains reaching to the upper montane zone, very rarely the subalpine zone (Mirek & Piękoś-Mirkowa 2003).

Anthoxanthum odoratum is an euapophyte, i.e. a native species that is well adapted to conditions of anthropogenic sites, created and maintained as a result of human activity. Populations of *A. odoratum* – according to the concept of 2-phase expansion (Jackowiak 1999) – were subject to the adaptation process while crossing the successive ecological barriers. This could have led to various differences, e.g. structural, biological, and cytogenetic. Knowledge of the course and effects of differentiation of populations of species during ecological expansion (i.e. within its natural range) may be crucial for understanding the mechanisms of chorological expansion of this species, i.e. the course of its spread outside the natural range (Jackowiak 1999).

1.2. Distribution and environmental conditions of *Anthoxanthum alpinum*

This species is a perennial, flowering from June to August. Distributed in mountainous regions in many Eurasian countries (http://build.e-monocot.org, Fig. 2C). Found in subalpine pastures, dry grasslands, slopes, and screes (Dostál 1989), in the Alps recorded also in open larch forests (Adler *et al.* 1994). Rare at anthropogenic sites (Mirek & Piękoś-Mirkowa 2005). This species is an old, Pleistocene component of the Polish flora (Zając & Zając 2007), found in our country only in the Sudetes and Carpathians (Zając & Zając 2001, Fig. 2D), mostly in the alpine zone, but also in the subalpine and rarely in the subnival zone (Mirek & Piękoś-Mirkowa 2003). *A. alpinum* and *A. odoratum* are altitudinal vicariants (Mirek & Piękoś-Mirkowa 2007). *Anthoxanthum alpinum* was distinguished in Poland on the basis of taxonomic and cytological research conducted by Rozmus (1960, 1963). *A. odoratum*, recorded below the forest line, is replaced by *A. alpinum* in the subalpine and alpine zones. These taxa differ also in ecological requirements (Stančić 2005).

1.3. Distribution and environmental conditions of *Anthoxanthum aristatum*

This species is an annual with sparse tufts, flowering from May to June, sometimes flowering again in summer and autumn (Falkowski 1982). *A. aristatum* is distributed naturally in West Europe in the Mediterranean and Atlantic regions (Hegi 1909; Kästner *et al.* 2001, Fig. 2E), occupying there a variety of habitats: from mountain grasslands to segetal and ruderal habitats. Accidentally introduced to Germany in the Napoleonic period, i.e. 1805-1813 (Hegi 1909), by the late 19th century it spread in the Netherlands and all over Germany (Kästner *et al.* 2001). It grows mostly on sandy sites, infertile fields, adjacent sandy grasslands and roadsides, rarely industrial wastelands (Falkowski 1982; Kästner *et al.* 2001; Rothmaler *et al.* 2005; Rostański & Woźniak 2007). In Poland it was first recorded near Kwidzyń by Klinggräff (1866). Since the late 19th century, it has colonized the present area of Poland from the west (Rola & Kuźniewski 1979; Tokarska-Guzik 2005; Latowski *et al*. 2010). In successive decades, it spread to Central Poland and towards the eastern border of Poland, and reached it in the 1990s (Ciosek & Skrzyczyńska 1997, Fig. 2F).

Anthoxanthum aristatum is regarded in Poland as a kenophyte (Tokarska-Guzik 2005) and invasive species (Tokarska-Guzik *et al.* 2007, 2011, 2012) with most records in western and central Poland (Warcholińska & Siciński 1996; Zając & Zając 2001; Skrzypczyńska *et al.* 2010). It is at a phase of chorological expansion in Poland (sensu Jackowiak 1999) and has achieved the status of epecophyte, i.e. an alien species occupying exclusively anthropogenic habitats, created and maintained by strong and continuous human activity (Korniak & Urbisz 2007). The spread of *A. aristatum* in our country and colonization of new sites poses an increasing threat to our crop fields. Its spread in Poland is due to its high seed yield, ability to germinate even after many years, and allelopathic properties in relation to seedlings of other species (Latowski 2005).

Unlike many model invasive species, *A. aristatum* has a narrow ecological spectrum, as it grows mostly on infertile fields, rarely sandy roadsides. The observed colonization of more fertile sites is a natural phenomenon, and the adaptive capacity of *A. aristatum* is probably within the limits of its plasticity. An additional cause of the spread of *A. aristatum* onto more fertile sites may result from global warming and extended dry spells (Soukupová *et al.* 2001; Skrzypczyńska *et al.* 2010).

2. Material and methods

2.1. Material

The collected material represents a broad range of morphological variation of the studied *Anthoxanthum* species in Poland. The material comes mostly from western and eastern parts of lowland Poland as well as from the Babia Góra massif, lying in the Western Carpathians. On Babia Góra, samples of *A. odoratum* and *A. alpinum* were collected along an altitudinal transect including the following zones: lower montane

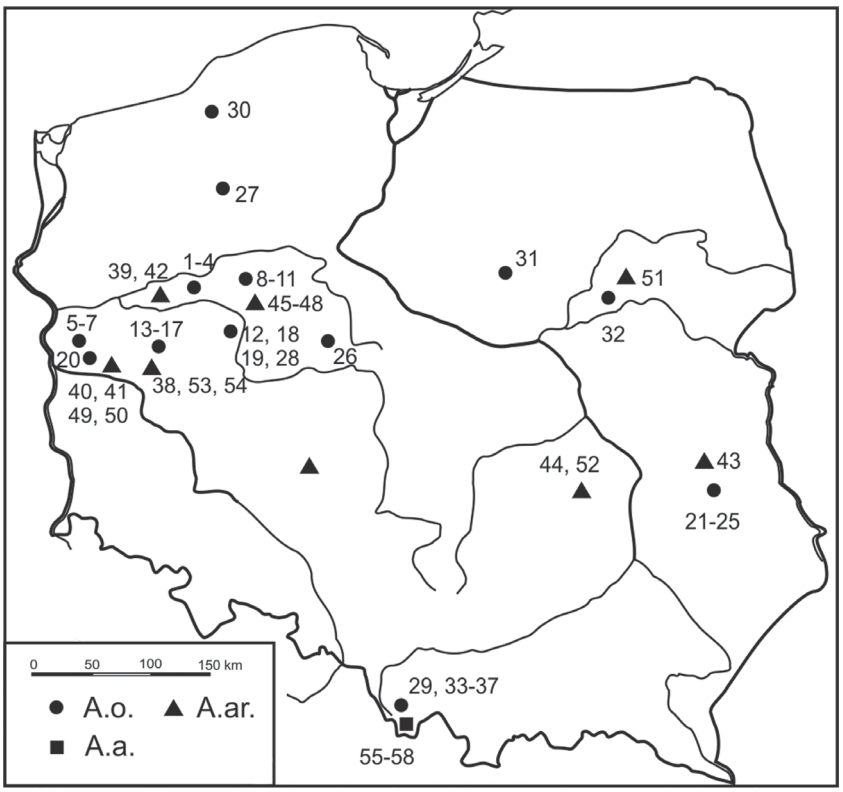

Fig. 3. Collection sites of *Anthoxanthum odoratum* (A.o.), *A. alpinum* (A.a.) and *A. aristatum* (A.ar.). Site numbers see Appendix 1

(700-1150 m), upper montane (1150-1350 m), subalpine (1350-1650 m), and alpine (1650-1725 m).

Plant material was collected in 2007-2011, when the studied grass species flowered and produced seeds. The study involved three species. In total, 58 populations (37 *A. odoratum*, 17 *A. aristatum* and 4 *A. alpinum*) were investigated that represented both natural, seminatural and synanthropic habitats (altogether 21 habitats) (see Appendix 1). From each of the selected populations of *A. alpinum*, *A. odoratum*, and *A. aristatum*, up to 35 plants were collected, spaced at least 5 m away from one another. In total, 1412 plants were collected, including 921 of *A. odoratum*, 396 of *A. aristatum*, and 95 of *A. alpinum*. After collection, individual plants were placed in separate paper bags. Next the material was described and dried. For morphological analyses, 30-35 panicles were selected from each population. Anatomical analyses of the stem (culm) and leaves involved 3-6 individuals of each species (26 individuals of *A. odoratum* representing the selected populations: 1PF, 7MM, 8AR, 13PP, 16EF, 29LM, 8 individuals of *A. alpinum* representing populations: 55AG, 56SM, 58UG, and 10 individuals of *A. aristatum* representing the selected populations: 38A, 40F, 42A) (see Appendix 1). Morphological examination was based on dried specimens, whereas material for anatomical observations was placed in containers with 70% ethanol.

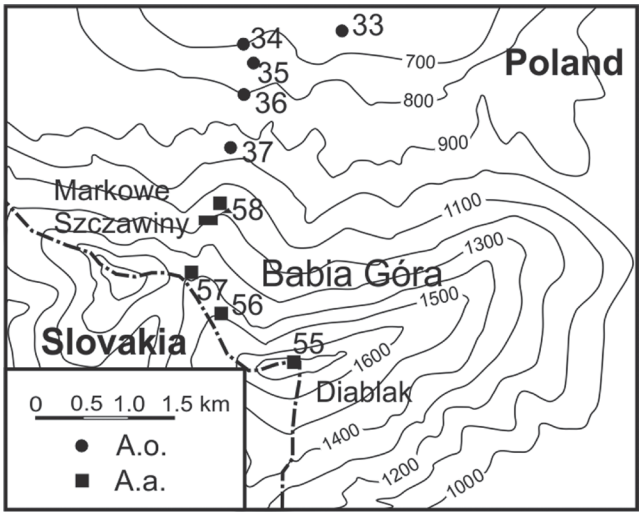

Fig. 4. Collection sites in the massif of Babia Góra (according to Drapikowska *et al.* 2012b modified)
Explanations: A.o. – *Anthoxanthum odoratum* (33-37), A.a. – *A. alpinum* (55-58), site numbers see Appendix 1

The collected seeds were also used to establish a plantation in the Botanic Garden of Adam Mickiewicz University in Poznań, Poland, to produce material for genetic analysis (see Drapikowska 2013). Seeds of *A. odoratum*, and *A. aristatum* were sown in pots filled with parboiled garden soil and kept in a greenhouse. Next the seedlings were transplanted, each to a separate pot. When the plants reached the 3-leaf

Table 1. List of analysed morphological characters of *Anthoxanthum odoratum*, *A. alpinum*, and *A. aristatum*

No.	Character
1	Panicle length
2	No. of panicle nodes
3	First panicle internode length
4	Second panicle internode length
5	Third panicle internode length
6	Fourth panicle internode length
7	Fifth panicle internode length
8	Spikelet length on second uppermost panicle branch
9	No. of spikelets on second uppermost panicle branch
10	Spikelet length on middle panicle branch
11	No. of spikelets on middle panicle branch
12	Spikelet length on lowermost panicle branch
13	No. of spikelets on lowermost panicle branch
14	Lower glume length
15	Lower glume width
16	Upper glume length
17	Upper glume width
18	Palea length in sterile floret
19	Palea awn length to knee in sterile floret
20	Palea awn length from knee in sterile floret
21	Lemma length in sterile floret
22	Lemma awn length in sterile floret
23	Lemma length in fertile floret
24	Palea length in fertile floret

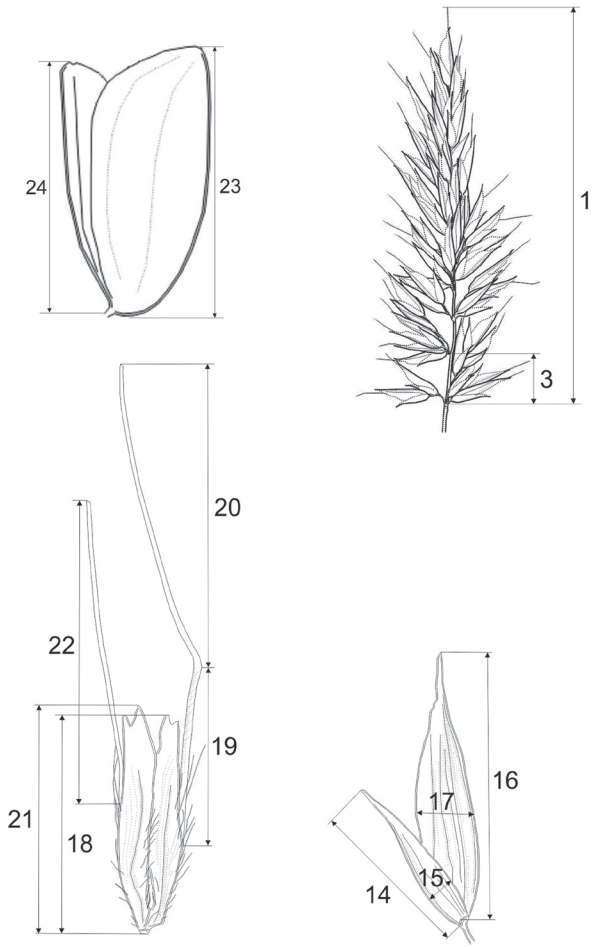

Fig. 5. Structure of the panicle and inflorescence elements of *Anthoxanthum* species. Number designations refer to the way the measurements of individual morphological characters were taken (drawing by P. Szkudlarz)
Explanations: characters no. see Table 1

stage, they were planted in the ground. Plots of the 2 species were spatially isolated to prevent interspecific hybridization.

2.2. Morphological and anatomical methods

The applied methods of structural analysis (morphological and anatomical) are routinely used to assess the level of variation of grass populations in selected habitats (Pimentel Pereira *et al.* 2007a; Szczepaniak 2009).

For morphological analyses, diagnostic features of the 3 studied species were selected on the basis of earlier studies of variation of *Anthoxanthum* species (Teppner 1969; Rostański 1996; Pimentel Pereira *et al.* 2007a, Drapikowska *et al.* 2008, 2012a, 2012b).

Table 2. Analysed soil parameters at sites of *Anthoxanthum odoratum*, *A. alpinum*, and *A. aristatum*

Parameter	Unit	Method
pH_{KCl}		potentiometer
Cation-exchange capacity (CEC)	mmol/100 g soil	titration
Conductivity (G)	mS/cm	conductivity meter
Phosphorus (P)	mg P/100 g soil	Egner-Rhim colorimetry
Potassium(K)	mg K/100 g soil	Egner-Rhim flame photometry
Nitrogen (N)	mg N/100 g soil	Kjeldahl distillation
N/P ratio	–	–
N/K ratio	–	–
C/N ratio	–	–
Organic carbon (C)	%	Tyurin method
Humus	%	58% of C

Individual plants (3-5 of each species) were examined in respect of 24 characters of inflorescences (Fig. 5, Table 1). Panicle length was measured with a ruler, to nearest 1 mm, whereas panicle internode length as well as parameters of spikelets and their parts were measured with a Nicon stereomicroscope, to nearest 0.1 mm.

Anatomical analyses were focused on the stem and leaves. The analysed parameters included: (*i*) in stems: number of vascular bundles and number of layers of sclerenchyma cells in the stem cross-section between the first and second node; and (*ii*) in leaves: number of vascular bundles, number of stomatal rows in the leaf cross-section in the adaxial and abaxial parts, presence of short cells, long and short hairs, and stomatal length, to nearest 0.1 μm. The selected characters were already earlier used in taxonomic studies of grasses, including *Anthoxanthum* species (Pimentel & Sahuquillo 2003).

2.3. Analysis of habitats

Soil samples were taken from sites representative of the habitat spectrum of individual species. In total, 108 soil samples were taken at 36 localities in 19 habitat types. For *A. odoratum*, samples were collected in 9 lowland habitats: pine forest (PF), dry meadow (DM), moist meadow (MM), sandy grassland (pG), roadside in pine forest (FR), moist edge of pine forest (EF), pine forest plantation (PP), agricultural wasteland (W), and reed-grass oak forest (OF). In the Babia Góra massif, soil samples were taken along the altitudinal transect, at the sites of *A. odoratum* representing 2 habitats: lower montane roadside (LR), lower montane meadow (LM) and *A. alpinum* representing 3 habitats: upper montane forest glade (UG), subalpine matgrass meadow (SM), and alpine grassland (AG). For *A. aristatum*, soil samples were taken from 6 habitats: cultivated arable field (A), fallow (F), sandy grassland near a pine forest plantation (pG), sandy grassland near pine forest (fG), sandy grassland near arable field margin (aG), and field roadside (AR).

From each site, three 150 ml samples were taken from the rooting zone (0.3 m), using the manual Edelman drill. Next the samples were dried and sieved through a sieve (mesh size 2 mm). Sampling and chemical analyses were performed according to the Polish standards (Ostrowska *et al.* 1991). Organic carbon content was analysed in samples ground using a mortar and pestle. The analysed soil parameters are listed in Table 2. Additionally, in all the distinguished habitats, phytosociological relevés were made according to the method of Braun-Blanquet (1964), to document the species composition of plant communities where *Anthoxanthum* species were found (see Appendix 2).

2.4. Statistical analysis

Results of the biometric analysis and soil analysis were analysed statistically. Mean, minimum, and maximum values, and standard deviation of individual features were calculated. Analysis of variance (ANOVA) was used to assess the significance of differences between populations and species. Principal component analysis (PCA) was employed to investigate relationships between individuals from different populations, without any *a priori* assumptions (Sneath & Sokal 1973). Next, the morphological variables most strongly correlated with the first two principal components were selected and introduced in canonical discriminant analysis (CDA, Sneath & Sokal 1973). The analysis was used to assess morphological differences between the distinguished groups (populations from various habitats) and to evaluate the discriminant power of the selected set of features. Mahalanobis distances were calculated and their significance was assessed by the *F* test. Then Euclidean distances were calculated and, on this basis, dendrograms were

Table 3. Analysis of variance of *Anthoxanthum odoratum* populations for 24 morphological characters (*F* values in bold are significant at $p < 0.05$

Character	*F*
1	**6.36**
2	**9.64**
3	**10.05**
4	**7.33**
5	**6.71**
6	**7.58**
7	**4.32**
8	**4.67**
9	**14.75**
10	**4.20**
11	3.59
12	**5.44**
13	**7.30**
14	3.93
15	**15.23**
16	**7.50**
17	**32.16**
18	**8.15**
19	**8.83**
20	**6.91**
21	**12.21**
22	**8.07**
23	**19.06**
24	**14.09**

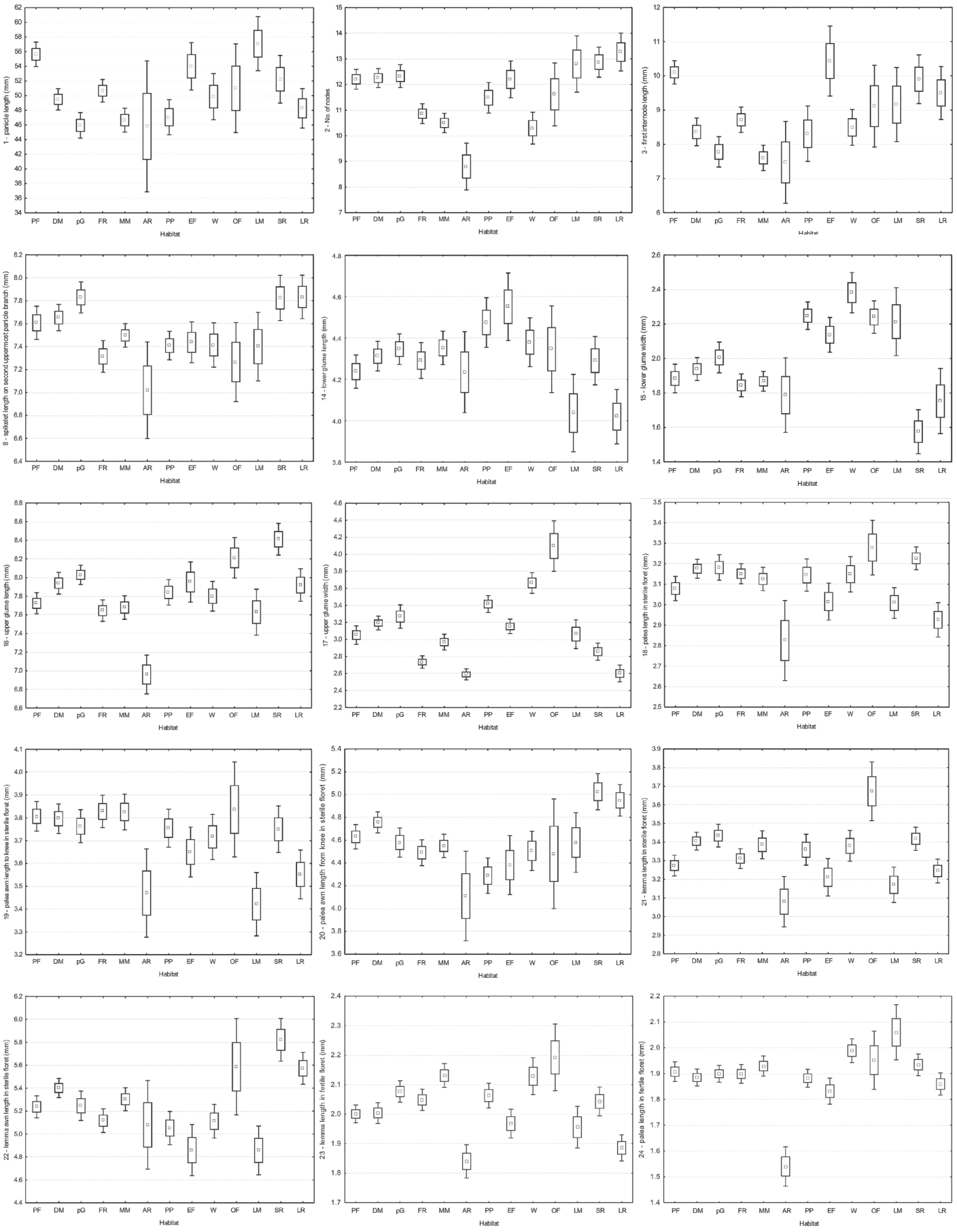

Fig. 6. Variability of selected morphological characters in *Anthoxanthum odoratum* populations in various habitats
Explanations: midpoint – mean, box – stand. dev., whiskers – 1.96 stand. dev.; PF – pine forest, DM – dry meadow, pG – sandy grassland near pine forest plantation, FR – roadside in pine forest, MM – moist meadow, AR – field roadside, PP – pine forest plantation, EF – edge of pine forest, W – wasteland, OF – red-grass oak forest, LM – lower montane meadow, SR – submontane ruderal roadside, LR – lower montane forest roadside

Table 4. Analysis of variance for 24 morphological characters for *Anthoxanthum odoratum* populations from different habitats (*F* values in bold are significant at $p < 0.05$)

Character	*F*	Character	*F*	Character	*F*
1	**8.92**	9	**13.12**	17	**23.41**
2	**14.20**	10	**5.35**	18	**4.55**
3	**10.81**	11	**2.16**	19	**2.83**
4	**10.30**	12	**7.18**	20	**6.00**
5	**8.97**	13	**6.09**	21	**4.59**
6	**8.07**	14	**5.12**	22	**7.38**
7	**4.76**	15	**14.17**	23	**8.64**
8	**4.65**	16	**8.04**	24	**4.92**

constructed using the complete linkage method and *k*-mean clustering. Statistical analyses were made using STATISTICA 8 for Windows software (Stat Soft, Inc. 2011).

To investigate relationships between morphometric data and soil parameters, redundancy analysis (RDA) was applied (Ter Braak 1986). This is an analysis of nonlinear correlations between 2 sets of variables. It was already earlier used e.g. in research on relationships between habitat parameters and morphological characters (see Borowiak *et al.* 2011). In this study, 2 sets of data were analysed: morphological data and soil parameters. Calculations were made by CANOCO software.

2.5. Identification of relative DNA content in *Anthoxanthum odoratum* and *A. alpinum*

The ploidy level in *Anthoxanthum* samples collected along the altitudinal transect in the Babia Góra massif was measured using flow cytometry (Śliwińska 2008; Kubešová *et al.* 2010), in the Kutno Sugar Beet Breeding Company in Staszkowo. Individuals of *A. odoratum*, identified on the basis of chromosomes number, were treated as a control sample (Drapikowska *et al.* 2013).

3. Results

3.1. Morphological and environmental variation of *Anthoxanthum odoratum*

3.1.1. Morphological variation related to environmental and phytocenotic conditions

Results of ANOVA show that mean values of nearly all characters vary significantly between populations (Appendix 3, Table 3). The only exceptions are: character 1 (number of spikelets on the middle panicle branch) and 14 (lower glume length). The analysis revealed also significant variation between population groups distinguished on the basis of habitat type (Table 4, Fig. 6).

Panicles are longest in populations from lower montane meadows (LM) and pine forests (PF), whereas the shortest in populations from sandy grasslands (pG), moist meadows (MM), pine forest plantations (PP), and

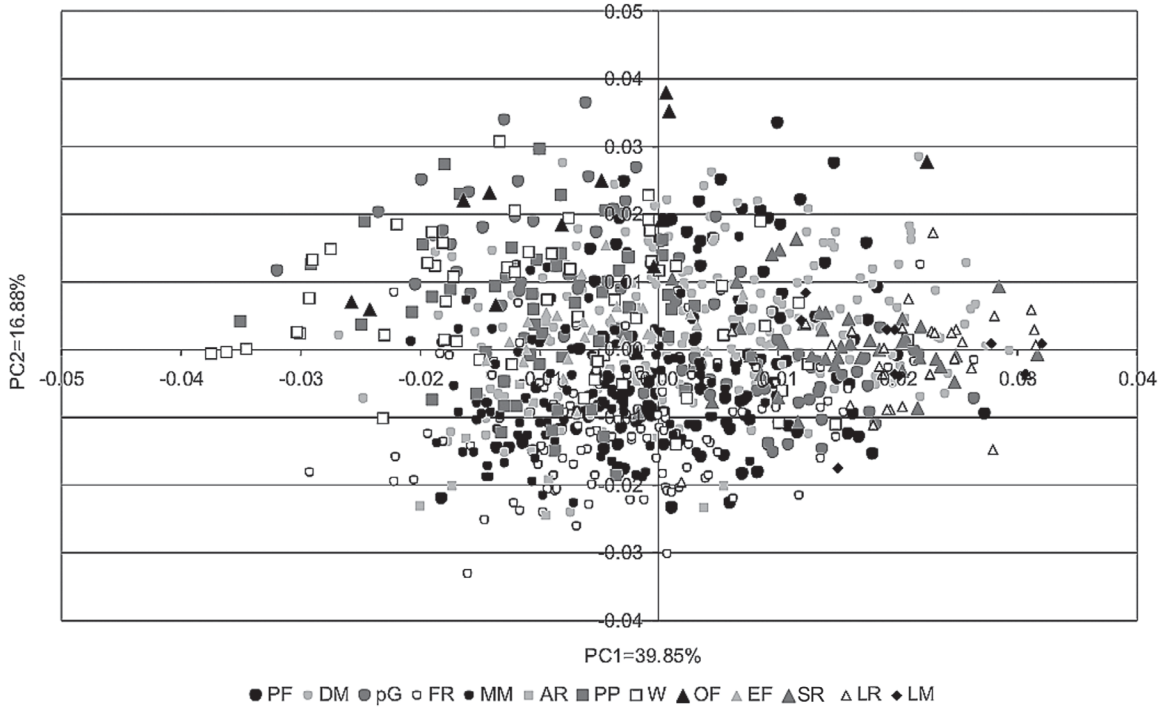

Fig. 7. Distribution of *Anthoxanthum odoratum* specimens in the system of the first two principal components (PC1 and PC2)
Explanations: see Fig. 6 and Appendix 1

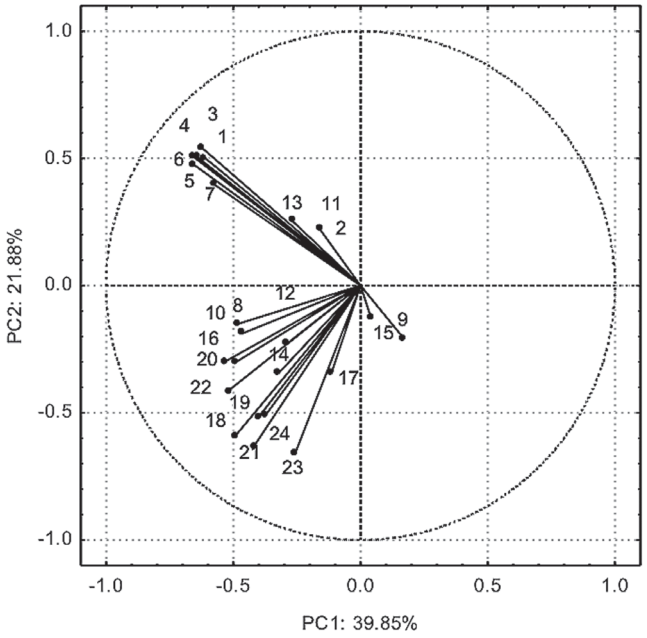

Fig. 8. Position of vector loads (characters 1-24) in relation to the first two principal components (PC1 and PC2) for *Anthoxanthum odoratum*

Table 5. Loadings of 24 morphological characters for the first two principal components PC1 and PC2 for *Anthoxanthum odoratum* (values in bold are for highly correlated characters, $r > 0.4$)

Character	PC1	PC2
1	**-0.629**	**0.515**
2	-0.165	0.221
3	**-0.606**	**0.512**
4	**-0.614**	**0.552**
5	**-0.649**	**0.514**
6	**-0.651**	**0.483**
7	**-0.570**	**0.404**
8	**-0.484**	0.144
9	0.175	0.204
10	**-0.465**	0.181
11	-0.206	0.178
12	-0.290	-0.223
13	-0.265	-0.259
14	-0.317	-0.336
15	0.026	-0.130
16	**-0.535**	-0.291
17	-0.137	-0.348
18	**-0.500**	**-0.586**
19	-0.394	**-0.506**
20	**-0.501**	-0.297
21	**-0.425**	**-0.624**
22	**-0.526**	-0.406
23	-0.263	**-0.657**
24	-0.387	**-0.508**

Table 6. Correlations between 24 morphological characters of *Anthoxanthum odoratum* and canonical variables CAN1 and CAN2

Character	CAN1	CAN2
1	0.21	-0.08
2	0.47	0.29
3	0.27	-0.03
4	0.16	-0.10
5	0.25	-0.11
6	0.24	-0.03
7	0.18	-0.04
8	0.21	0.18
9	-0.53	-0.14
10	0.10	0.27
11	-0.05	-0.08
12	-0.12	0.28
13	0.07	-0.05
14	-0.26	0.11
15	-0.37	0.63
16	0.15	0.36
17	-0.33	0.76
18	-0.08	0.15
19	-0.10	-0.06
20	0.32	0.07
21	-0.07	0.23
22	0.28	0.08
23	-0.31	0.07
24	-0.04	0.12

moist edge of pine forest (EF). Panicle node number is the lowest in populations from field roadsides (AR) and the highest in submontane and lower montane populations (LM, SR, and LR). Spikelets are longer in populations from sandy grasslands pG as well as the submontane roadside (SR) and the lower montane forest roadside (LR), while the shortest in populations from field roadsides (AR). Populations from the moist edge of pine forest (EF) and from pine plantations (PP) have longer lower glumes, whereas they are shortest in lower montane populations (LM and LR). Upper glume length clearly distinguishes roadside populations (AR), where its mean values are the lowest. Upper glumes are the widest in the population from reed-grass oak forest (OF). Palea lenght in sterile floret is the shortest in populations from field roadsides (AR). Lemma in sterile floret is the longest in the population from reed-grass oak forest (OF) and the shortest in populations from field roadsides (AR), where also lemmas in fertile florets are the shortest. The analysed characters show continuous variation, but the most distinct are populations collected on field roadsides (AR), which have the

Table 7. Discrimination power of 24 morphological characters of *Anthoxanthum odoratum* (values in bold are significant at $p \leq 0.001$). Partial lambdas range from 1.0 (no discrimination power) to 0.0 (complete discrimination against a particular model)

Character	Wilks' lambda	Partial Wilks' lambda
1	0.049	0.8315
2	0.052	0.7837
3	0.048	0.8508
4	0.044	0.9330
5	0.044	0.9376
6	0.045	0.9093
7	0.043	0.9409
8	0.045	0.9108
9	0.050	0.8101
10	0.044	0.9265
11	0.046	0.8798
12	0.048	0.8576
13	0.053	0.7685
14	0.046	0.8925
15	0.051	0.7953
16	0.050	0.8092
17	0.070	**0.3806**
18	0.044	0.9276
19	0.048	0.8537
20	0.046	0.8871
21	0.046	0.8922
22	0.047	0.8658
23	0.063	**0.6436**
24	0.065	**0.6251**

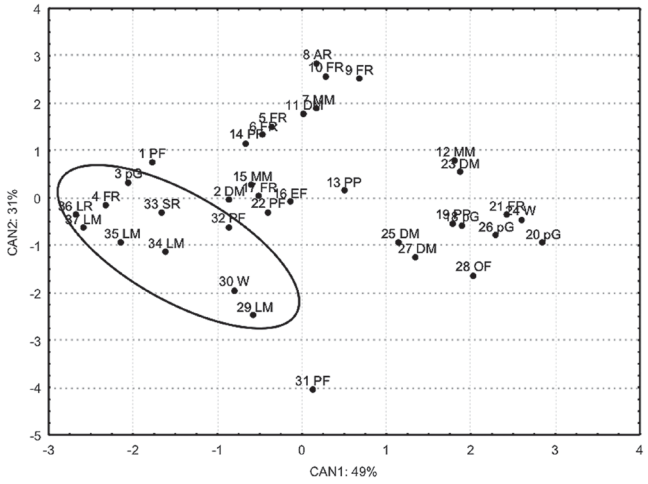

Fig. 9. Distribution of *Anthoxanthum odoratum* populations in the system of the first two canonical variables (CAN1 and CAN2) based on morphological characters
Explanations: see Appendix 1

lowest number of panicle nodes, shortest spikelet and palea awn in sterile floret, as well as the population from reed-grass oak forest (OF), which has the widest upper glume, longest lemma and palea in sterile floret, and lemma in fertile floret (Fig. 6).

In the PCA diagram (Fig. 7), populations of this species form a homogeneous group, and only single individuals from pine forest plantation PP, wasteland W, sandy grasslands (pG) and pine forests (PF) are distinguished form the others. Populations from the submontane zone (SR), lower montane grassland (LM), and lower montane roadside (LR) are group in the right part of diagram by positive values of PC1. The first two

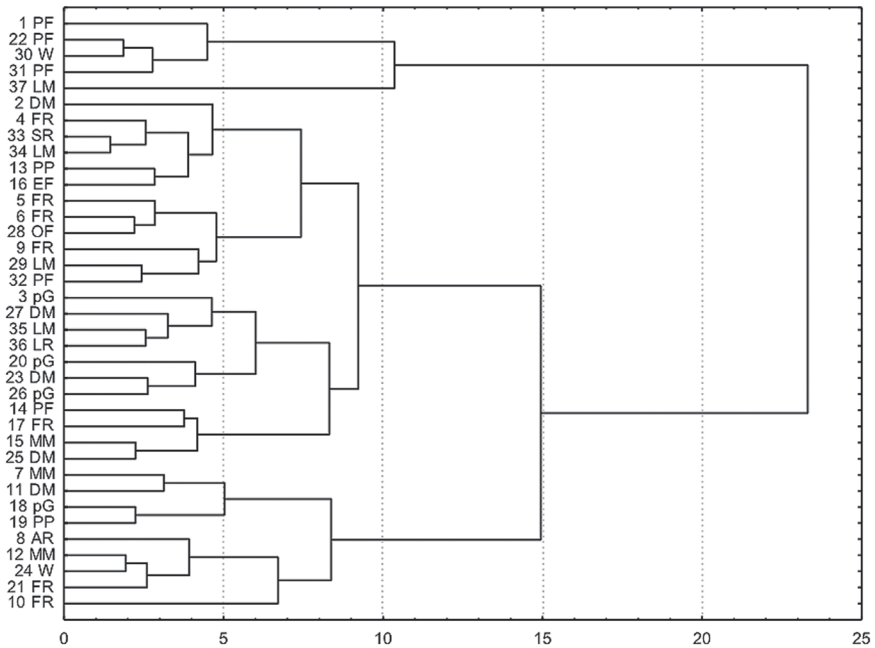

Fig. 10. Dendrogram of *Anthoxanthum odoratum* populations based on morphological characters (Euclidean distances)
Explanations: see Fig. 6

principal components explain a total of 56.73% of variation in primary data. Characters 1, 3, 4-8, 10, 16, 18, 20-22 are most strongly correlated with PC1, whereas characters 1, 4-7, 18, 19, 21, 23 and 24 are strongly correlated with PC2 (Fig. 8, Table 5).

Values of factor structure coefficients indicate that most of the analysed characters are poorly correlated with canonical functions; only characters 2 and 9 are slightly more strongly correlated with CAN1, and characters 15 and 17 with CAN2 (Table 6). Values of partial Wilks' lambda indicate that characters 17, 23, and 24 best discriminate between populations from various habitats (Table 7). In the diagram of population

Table 8. Analysis of variance for soil parameters in populations of *Anthoxanthum odoratum* (*F* values in bold are significant at $p < 0.05$)

Parameter	*F*
pH_{KCl}	**4.950**
Cation-exchange capacity (CEC)	**10.551**
Conductivity (G)	**12.407**
Phosphorus (P)	**4.654**
Potassium(K)	**8.294**
Nitrogen (N)	**5.192**
N/P ratio	**5.177**
N/K ratio	**9.572**
C/N ratio	**4.130**
Organic carbon (C)	**12.682**
Humus	**13.648**

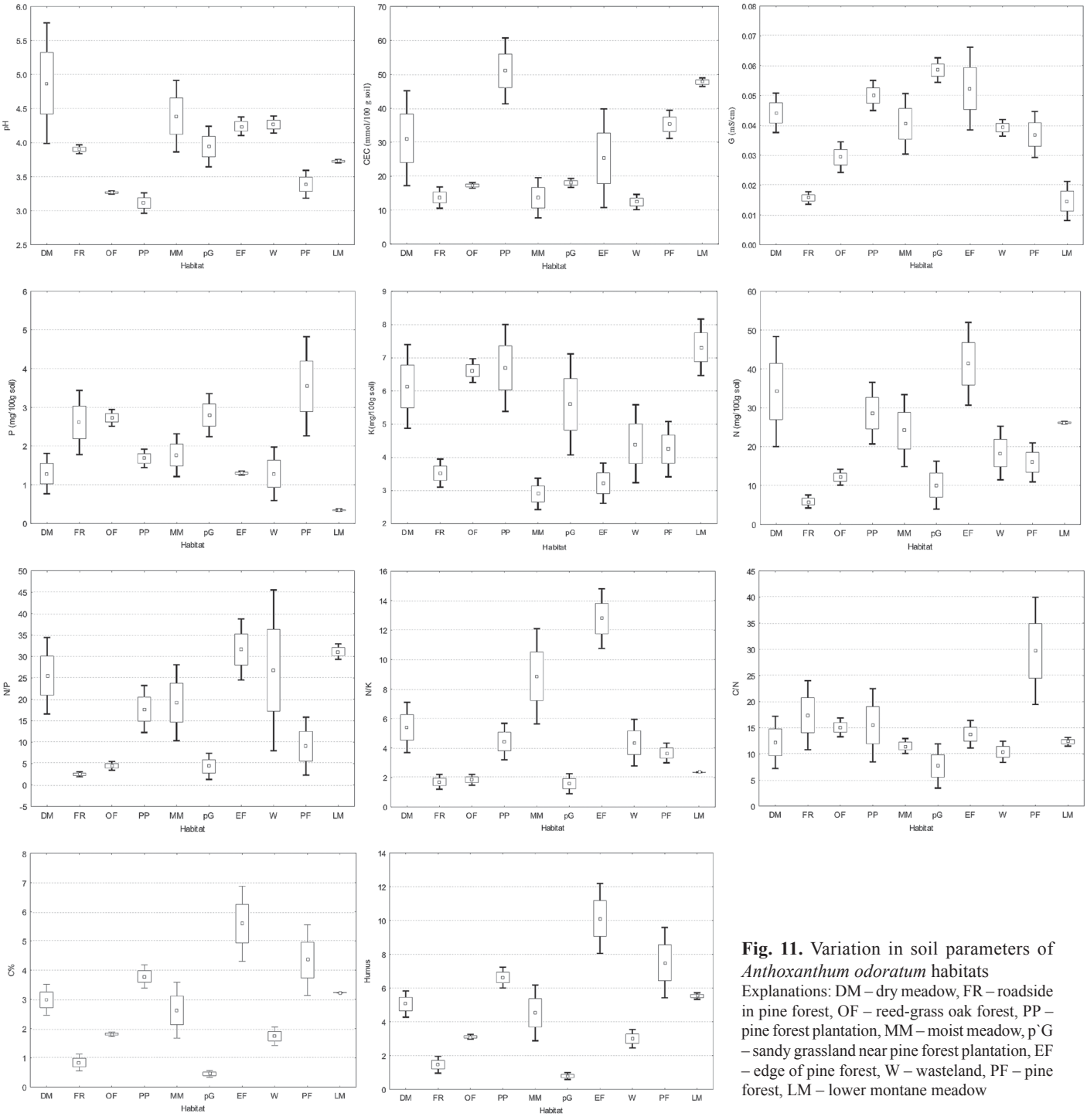

Fig. 11. Variation in soil parameters of *Anthoxanthum odoratum* habitats
Explanations: DM – dry meadow, FR – roadside in pine forest, OF – reed-grass oak forest, PP – pine forest plantation, MM – moist meadow, p`G – sandy grassland near pine forest plantation, EF – edge of pine forest, W – wasteland, PF – pine forest, LM – lower montane meadow

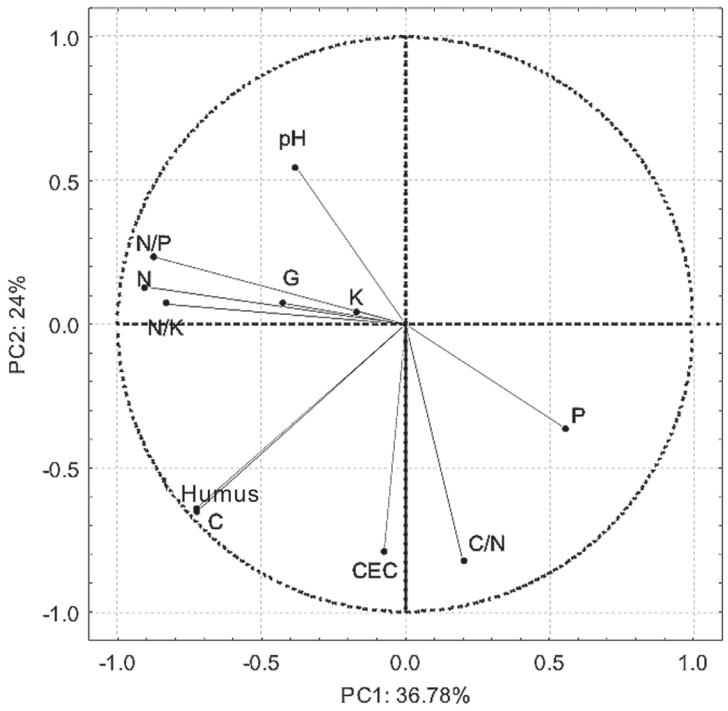

Fig. 12. Correlations between soil parameters (pH, P, N, K, C, N/P, N/K, C/N, conductivity G, cation exchange capacity CEC) of *Anthoxanthum odoratum* habitats and the first two principal components (PC1 and PC2)

distribution in the plot of the first two canonical variables (Fig. 9), the most distinct is a population from pine forest (31PF). Also populations from wasteland (30W) and lower montane grassland (29 LM) are located far away from the other populations. Negative values of the first canonical variable were also recorded for lower montane populations: 33SR, 34LM, 35LM, 37LM, 36LR, 3pG and 4FR. The other populations are scattered in the central and upper parts of plot.

Cluster analysis distinguished three groups (Fig. 10). The first group, most distant from the others, is composed of populations 1PF, 22PF and 31PF (pine forests), 30W (wasteland) and 37LM (lower montane meadow). The second group consists of 23 populations forming two subgroups: the first one including populations 2DM, 4FR, 33SR, 34LM, 13PP, 16EF, 5FR, 6FR, 28OF, 9FR, 29LM, 32PF, and the second one including populations 3PP, 27DM, 35LM, 36LR, 20pG, 23DM, 26pG, 14PF, 17FR, 15MM, and 25DM. The third group is composed of 9 populations: 7MM (moist meadow), 11DM (dry meadow), 18pG (sandy grassland), 19PP (pine plantation), 8AR (field roadside), 12MM (moist meadow), 24W (wasteland), 21FR, and 10FR (roadsides in pine forest).

Populations of *A. odoratum*, found in various habitats, are characterized by high morphological variation, which is only weakly correlated with habitat type. PCA and CDA show similar patterns of variation of submontane and upper montane populations.

Table 9. Correlation between soil parameters of *Anthoxanthum odoratum* sites and the first two principal components PC1 and PC2 (strongest correlations are marked in bold)

Parameter	PC1	PC2
pH_{KCl}	-0.347	0.615
Cation-exchange capacity (CEC)	-0.209	**-0.744**
Conductivity (G)	-0.422	0.083
Phosphorus (P)	0.555	-0.336
Potassium(K)	-0.186	-0.039
Nitrogen (N)	-0.904	0.161
N/P ratio	**-0.867**	0.242
N/K ratio	**-0.817**	0.173
C/N ratio	0.173	**-0.805**
Organic carbon (C)	**-0.744**	-0.611
Humus	**-0.752**	-0.604

3.1.2. Morphological variation in relation to soil conditions

One-way ANOVA with *F* statistic shows that all the studied soil properties significantly affected the morphological variation of *A. odoratum* found at individual sites (Table 8). Habitat parameters varied between the studied sites (Fig. 11). At all sites, soil pH was low, particularly in reed-grass oak forest (OF) – pH=3.25, pine forest plantations (PP) – pH=3.15, and pine forests (PF) – pH=3.45. Soil pH was higher in dry meadows (DM) - pH=4.58 and moist meadows (MM) – pH=4.40. Cation-exchange capacity (CEC) was the highest in pine forest

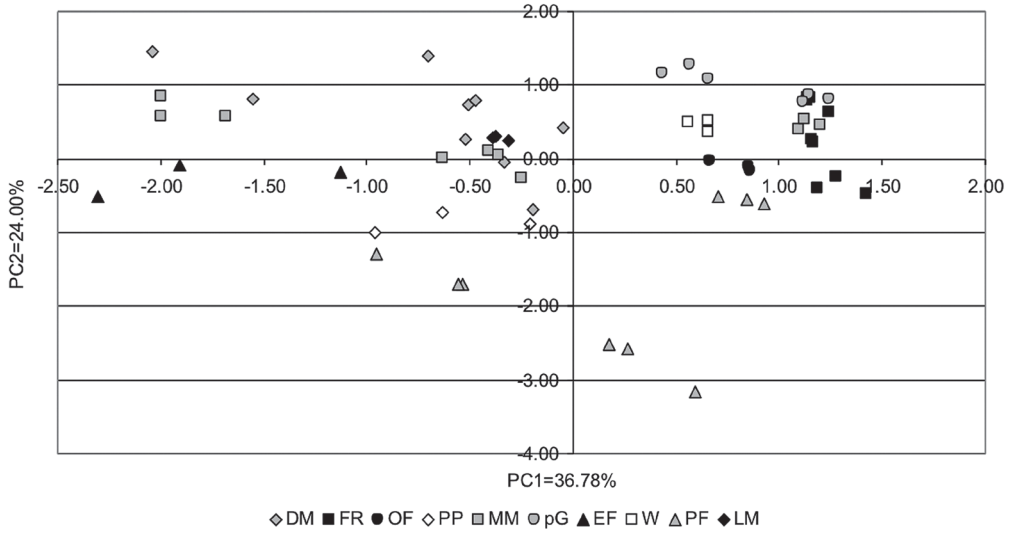

Fig. 13. Distribution of *Anthoxanthum odoratum* habitats in the system of the first two principal components (PC1 and PC2) based on soil parameters
Explanations: see Fig. 11

plantations (PP) and lower montane grasslands (LM). Conductivity (G) varied from 0.015 for lower montane grasslands (LM) to 0.059 at the sandy grassland near pine forest plantation (pG). Bioavailable (assimilable) phosphorus (P) content at the studied sites was low, varying from 0.5 mgP/100g soil in lower montane grasslands (LM) to 3.5 mgP/100g soil in pine forests (PF). Mean level of bioavailable potassium (K) was the lowest on

Table 10. Redundancy analysis (RDA) based on morphological characters and soil parameters in populations of *Anthoxanthum odoratum* (permutation test $p = 0.039$)

	RDA1	RDA2
Cumulative % of variance	0.229	0.037
Morphological data	22.9	26.6
Soil parameters	75.1	87.2

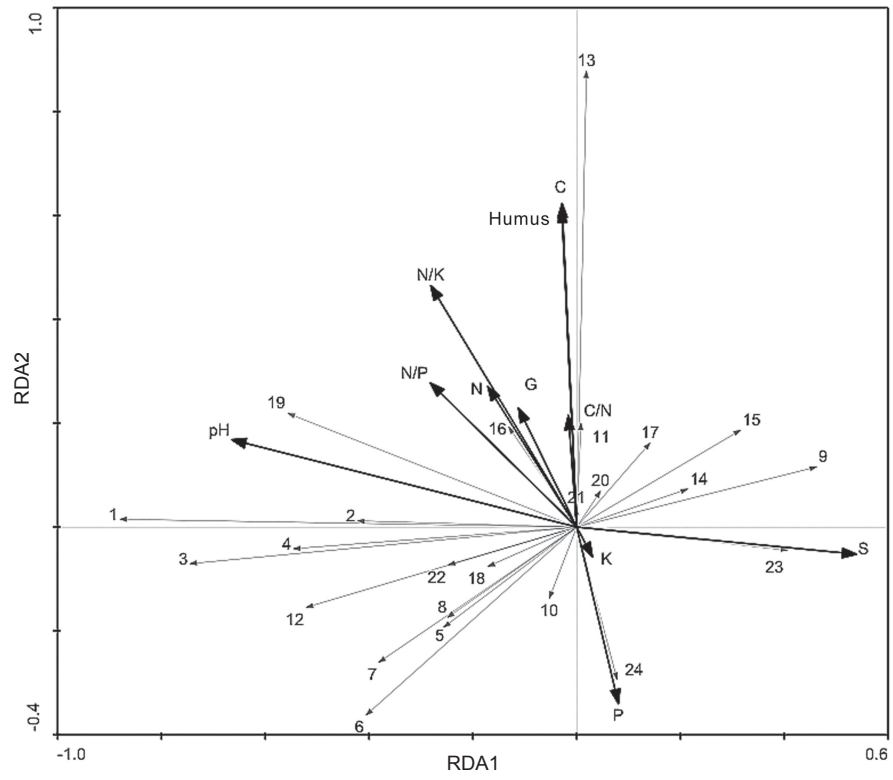

Fig. 14. Redundancy analysis axes (RDA1 and RDA2) showing the impact of selected soil parameters (black arrows: pH, P, N, C, N/P, C/N, conductivity G, cation-exchange capacity CEC) on *Anthoxanthum odoratum* morphological characters (gray arrows: 1-24)
Explanations – see Tables 1 and 2

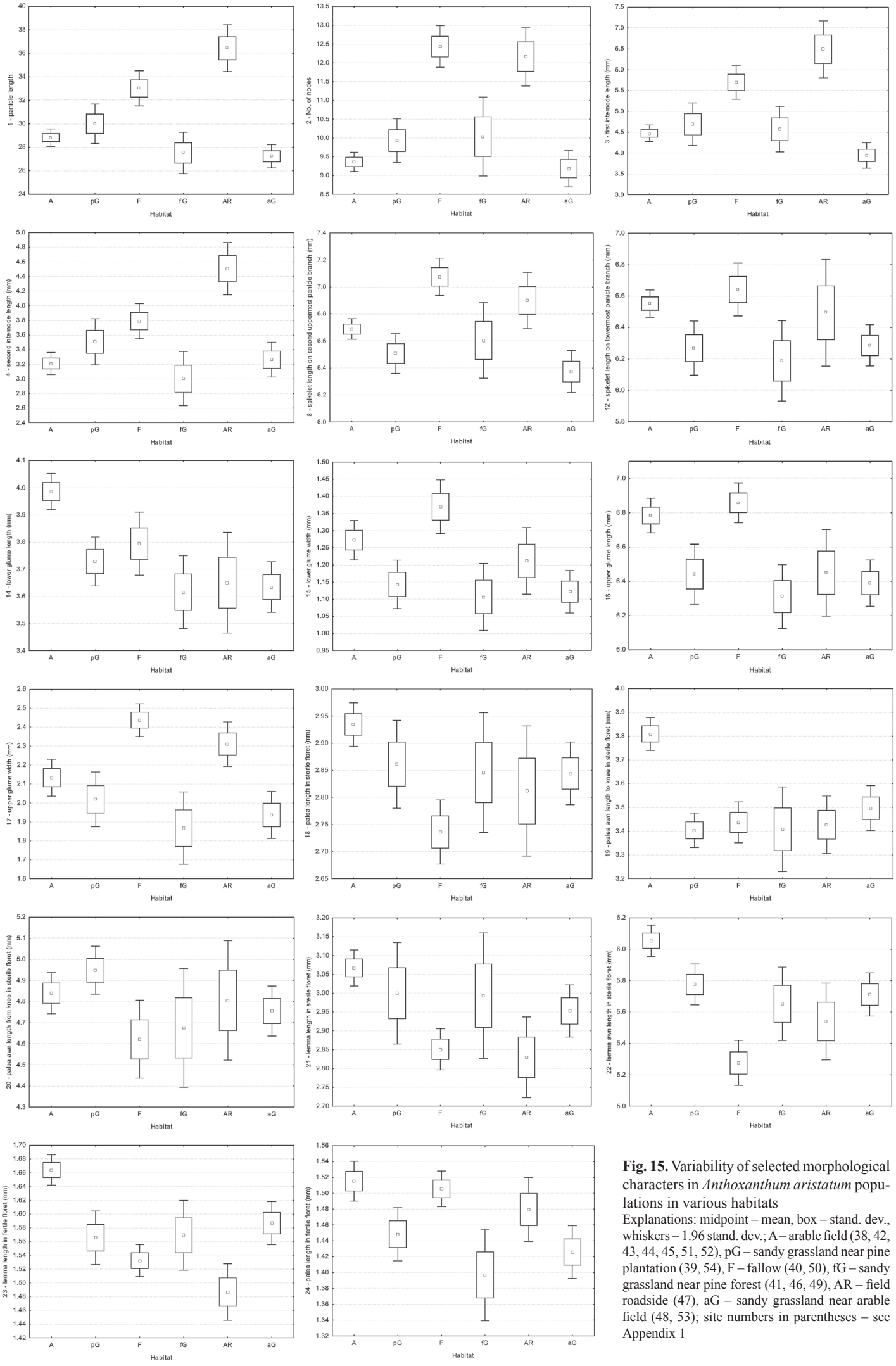

Fig. 15. Variability of selected morphological characters in *Anthoxanthum aristatum* populations in various habitats

Explanations: midpoint – mean, box – stand. dev., whiskers – 1.96 stand. dev.; A – arable field (38, 42, 43, 44, 45, 51, 52), pG – sandy grassland near pine plantation (39, 54), F – fallow (40, 50), fG – sandy grassland near pine forest (41, 46, 49), AR – field roadside (47), aG – sandy grassland near arable field (48, 53); site numbers in parentheses – see Appendix 1

moist meadows (MM, only 2.9 mgK/100g soil), whereas the highest (7.3), in lower montane grasslands (LM). Total nitrogen (N) content varied from 6 mgN/100g soil on roadsides in pine forests (FR) to 42 mgN/100g soil at the moist edge of pine forest (EF). Organic carbon content was the highest in the soil from the moist edge of pine forest (EF, 55%) and the lowest in the soil from sandy grasslands (pG), (0.5%). N/K and N/P ratios were the highest in the soil from the moist edge of pine forest (EF.), whereas C/N ratio was the highest (30), in the soil from pine forests (PF).

PCA was based on all soil parameters. The first principal component (PCA1) is correlated with total nitrogen content N, N/P, N/K, organic carbon content (C), and humus content, whereas the second principal component (PCA2) is most strongly correlated with cation-exchange capacity (CEC) and C/N (Fig. 12, Table 9).

An analysis of all soil parameters jointly indicates that samples from pine forests (PF) are distinguished primarily by higher phosphorus content and C/N ratio. They form a loose group, with negative values of PC2. However, 2 of them are located in the group of samples with positive values of PC1 and PC2, from roadsides in pine forests (FR), reed-grass oak forest (OF), wastelands (W), and sandy grasslands pG. Samples from dry meadows (DM), and moist meadow (MM) have the highest pH values and are distinguished by negative values of PC1 and positive of PC2 (Fig. 13).

Results of redundancy analysis (RDA) show that bioavailable phosphorus (P) content is correlated with

Table 11. Analysis of variance for 24 morphological characters for *Anthoxanthum aristatum* populations from different habitats (*F* values in bold are significant at $p < 0.01$)

Character	*F*
1	**19.68**
2	25.12
3	18.19
4	15.36
5	12.56
6	8.66
7	9.85
8	10.34
9	20.06
10	14.48
11	8.51
12	5.92
13	6.29
14	15.08
15	20.46
16	12.91
17	38.98
18	9.76
19	14.18
20	4.02
21	8.80
22	14.50
23	20.28
24	14.55

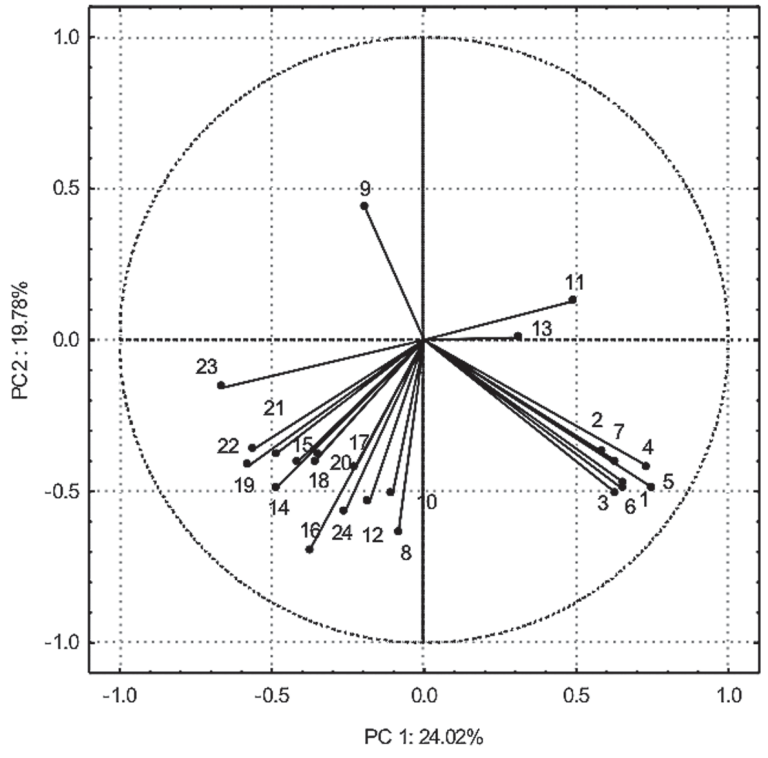

Fig. 16. Correlations between the first two principal components (PC1 and PC2) and morphological characters of *Anthoxanthum aristatum*

Table 12. Correlation between 24 morphological characters of *Anthoxanthum aristatum* populations and the first two principal components PC1 and PC2 (strongest correlations are marked in bold)

Character	PC1	PC2
1	0.69	-0.47
2	0.60	-0.34
3	0.67	-0.49
4	**0.76**	-0.39
5	**0.77**	-0.44
6	0.67	-0.42
7	0.63	-0.34
8	-0.08	-0.61
9	-0.21	0.41
10	-0.10	-0.49
11	0.49	0.15
12	-0.17	-0.52
13	0.32	0.01
14	-0.44	-0.54
15	-0.34	-0.41
16	-0.32	**-0.73**
17	-0.23	-0.40
18	-0.39	-0.44
19	-0.55	-0.45
20	-0.32	-0.40
21	-0.46	-0.40
22	-0.53	-0.40
23	-0.66	-0.19
24	-0.21	-0.60

palea length (character 24) and less strongly with spikelet length (character 10), whereas cation-exchange capacity (CEC), with lemma length (23). C/N ratio, organic carbon and humus content are correlated with number of spikelets on the middle panicle branch (11), palea awn length (20), and lemma length (21). Upper glume length (character 16) is correlated with conductivity, total nitrogen content, as well as N/K and N/P ratios, whereas number of panicle nodes (2) and palea awn length to knee in sterile floret (19) are correlated with pH (Fig. 14, Table 10).

3.2. Morphological and environmental variation of *Anthoxanthum aristatum*

3.2.1. Morphological variation related to environmental and phytocenotic conditions

Results of one-way ANOVA show that mean values of nearly all the studied characters vary significantly between populations (Table 11). Panicles as well as first and second panicle internodes are the longest in plants from field roadsides (AR). The highest number of panicle nodes and longest spikelets on second uppermost panicle branch are also distinguishing features of populations (AR) and populations on fallows (F). Spikelet length on lowermost panicle branch partly distinguishes populations from fallows (F). Lower glumes are longest in plants from arable fields (A), whereas widest, in plants from fallows (F). Upper glumes are longest in plants from fallows (F) and arable fields (A), whereas widest, in plants from fallows (F).

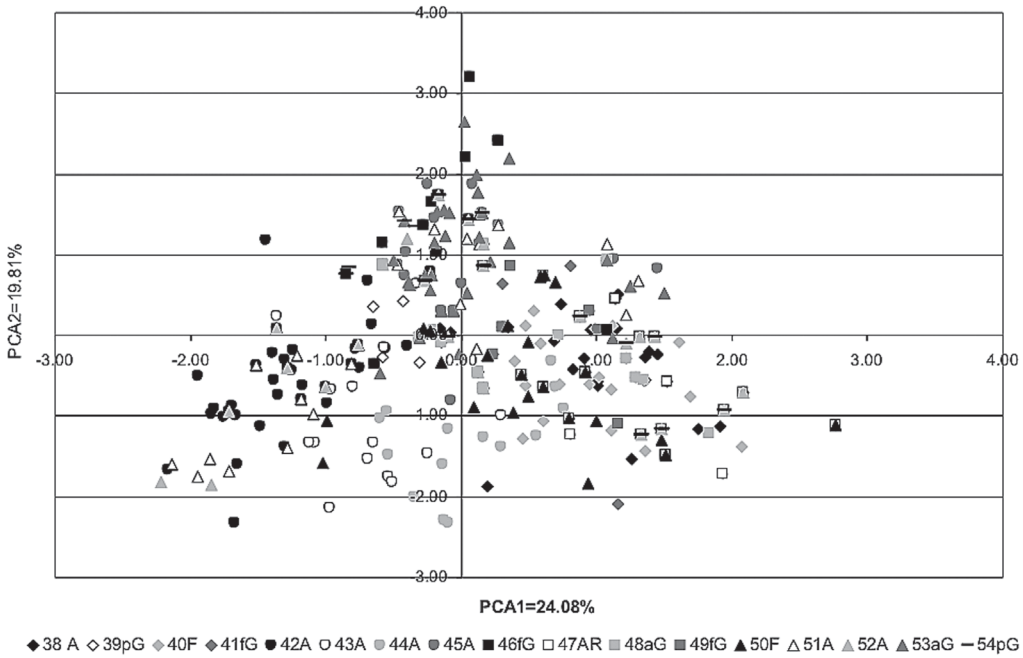

Fig. 17. Distribution of *Anthoxanthum aristatum* specimens in the system of the first two principal components (PC1 and PC2)
Explanations: western Poland – Noteć Forest (45A, 46fG, 47AR, 48aG, 39pG, 42A), Nowy Tomyśl Sandur (38A, 49fG, 53aG, 54pG), Rzepin Forest (40F, 41fG, 50F); mid-eastern Poland – Kozienice Forest (44A, 52A), Wandzin (43A), Przytoka (51A). Site numbers – see Appendix 1

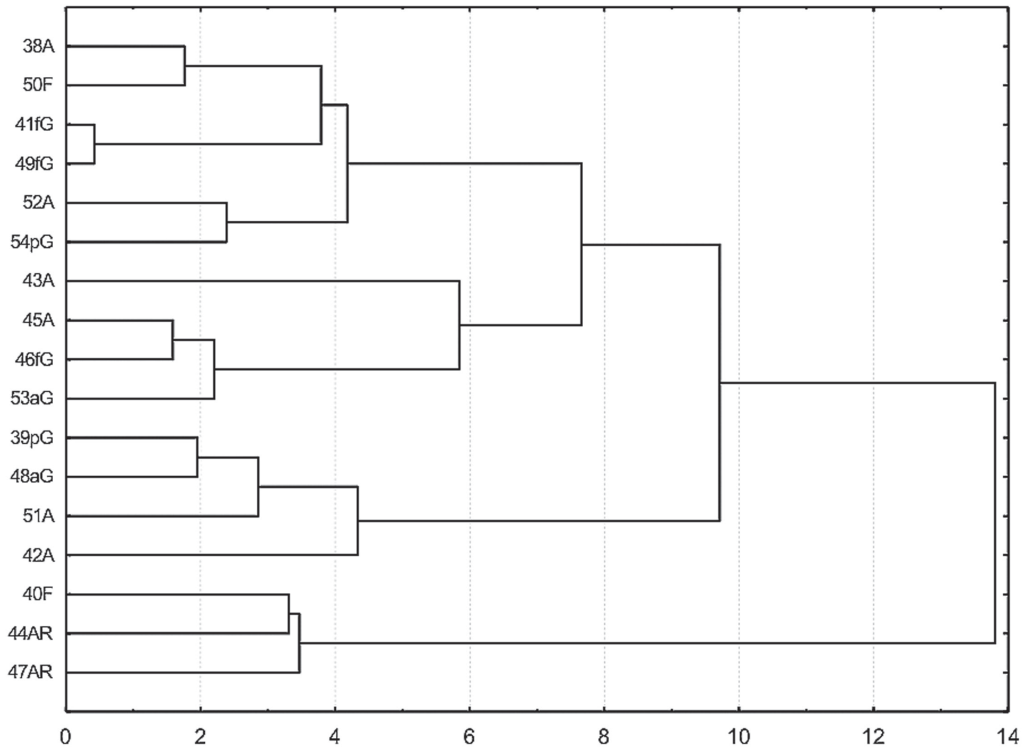

Fig. 18. Dendrogram of *Anthoxanthum aristatum* populations based on morphological characters (Euclidean distances)
Explanations: A – arable field, AR – field roadside, F – fallow, aG – sandy grassland near arable field, pG – sandy grassland near pine forest plantation, fG – sandy grassland near pine forest; site numbers – see Appendix 1

Individuals from arable fields (A) are distinguished by longest palea in sterile floret, palea awn, lemma and lemma awn in sterile floret, and lemma in fertile floret (Fig. 15).

PCA was based on all the studied morphological characters. PC1 explains 24.02% of the observed variation and is significantly correlated with second and third panicle internode length (characters 4 and 5), whereas

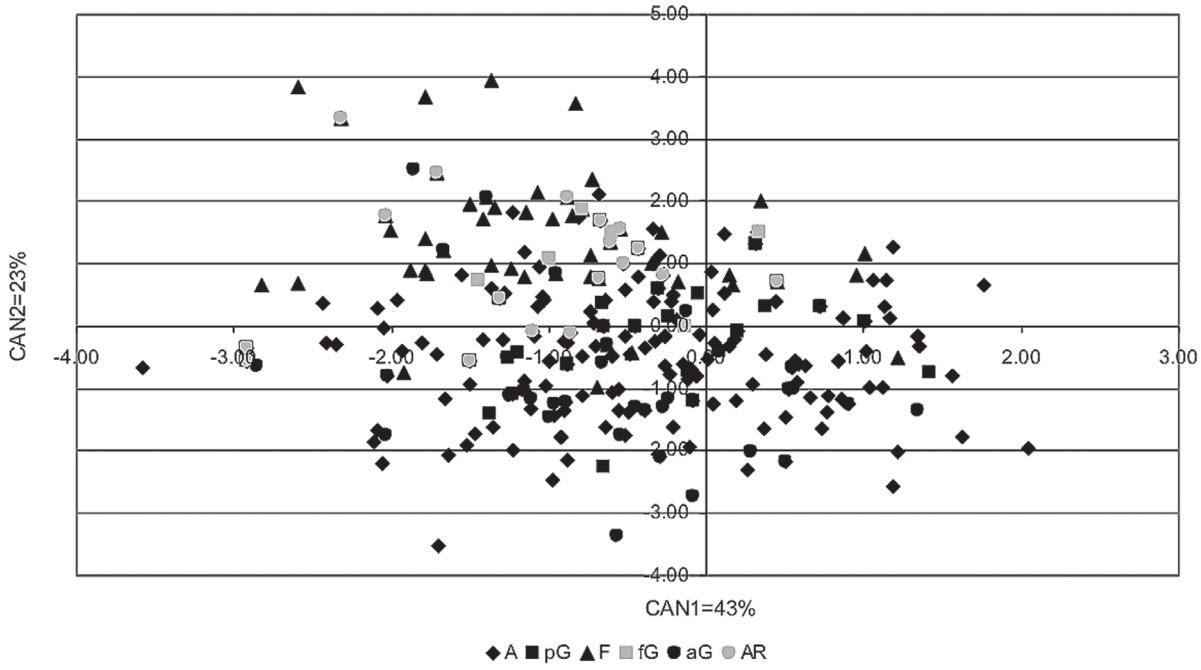

Fig. 19. Distribution of *Anthoxanthum aristatum* specimens from various habitats in the system of the first two canonical variables (CAN1 and CAN2) based on morphological characters
Explanations: A – arable field, pG – sandy grassland near pine forest plantation, F – fallow, fG – sandy grassland near pine forest, aG – sandy grassland near arable field, AR – field roadside

Table 13. Discrimination power of 24 morphological characters of *Anthoxanthum aristatum* (values in bold are significant at $p \leq 0.001$)

Character	Wilks' lambda	Partial Wilks' lambda
1	**0.060**	**0.906**
2	**0.068**	**0.799**
3	**0.064**	**0.848**
4	**0.057**	**0.943**
5	0.055	0.975
6	**0.057**	**0.950**
7	**0.058**	**0.926**
8	**0.058**	**0.933**
9	**0.066**	**0.812**
10	**0.057**	**0.941**
11	**0.056**	**0.964**
12	0.055	0.973
13	**0.057**	**0.944**
14	**0.056**	**0.960**
15	**0.057**	**0.954**
16	**0.064**	**0.844**
17	**0.062**	**0.868**
18	**0.058**	**0.927**
19	**0.058**	**0.937**
20	**0.058**	**0.937**
21	**0.057**	**0.942**
22	**0.057**	**0.943**
23	**0.066**	**0.813**
24	**0.066**	**0.812**

Table 14. Correlations between 24 morphological characters of *Anthoxanthum aristatum* and the first two canonical variables CAN1 and CAN2

Character	CAN1	CAN2
1	-0.39	0.33
2	-0.27	0.49
3	-0.40	0.16
4	-0.31	0.16
5	-0.20	0.29
6	-0.13	0.34
7	-0.03	0.40
8	0.15	0.12
9	0.12	-0.03
10	0.16	0.22
11	-0.17	0.20
12	0.16	0.06
13	-0.14	0.20
14	-0.04	-0.26
15	0.05	0.03
16	-0.15	-0.21
17	0.21	0.13
18	0.03	-0.37
19	0.14	-0.45
20	0.05	-0.24
21	0.13	-0.30
22	0.11	-0.46
23	0.28	-0.30
24	-0.15	-0.02

PC2 explains 19.78% and is significantly correlated with upper glume length (character 16) (Fig. 16, Table 12). In the diagram, populations form scattered groups in the plot of the first two principal components. Individuals from populations 51A and 52A are partly distinguished by negative values of PC1. This group in the lower part of the diagram, with negative values of PC2, includes also individuals from populations 43A and 44A. All the listed populations were found on arable fields in mid-eastern Poland. The central part of the diagram and positive values of PC1 are typical of populations from western Poland (Fig. 17). Cluster analysis divides populations into two groups. The first one consists of three subgroups: (1) populations 38A from Chlebowo, 50F from Połęcko, 41fG and 49fG from the Rzepin Forest, 52A from Morasko, and 54pG from Nowy Tomyśl Sandur; (2) populations 43A, 45A, 46fG, and 53aG; and (3) populations 39pG, 48aG, 51A, and 42A. The second group includes populations 40F, 44A, and 47AR (Fig. 18).

Table 15. Analysis of variance for soil parameters at sites of *Anthoxanthum aristatum* (*F* values in bold are significant at $p < 0.05$)

Parameter	*F*
pH_{KCl}	**12.144**
Cation-exchange capacity (CEC)	**64.145**
Conductivity (G)	**4.188**
Phosphorus (P)	**31.254**
Potassium(K)	**11.741**
Nitrogen (N)	**43.512**
N/P ratio	**23.623**
N/K ratio	**5.624**
C/N ratio	**11.842**
Organic carbon (C)	**24.107**
Humus	**24.102**

In the scatter plot of the first two canonical variables, populations form overlapping groups, scattered in respect of positive and negative values of CAN1, whereas CAN2 separates individuals from a population on fallow land in the upper part of the plot (Fig. 19). Values of discriminant power of most of the used traits discriminate well between the separated groups (habitats) (Table 13), whereas values of factor structure

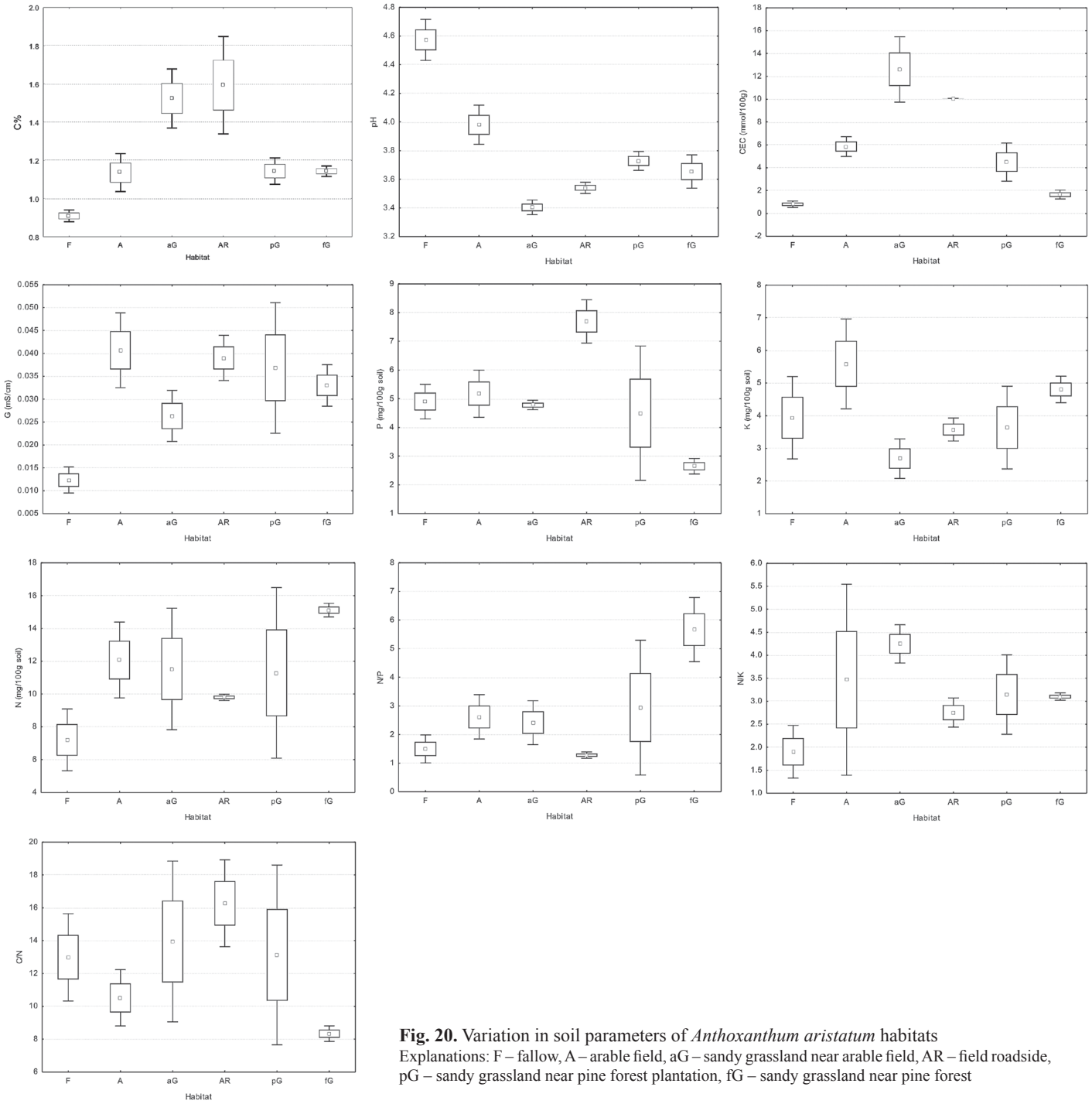

Fig. 20. Variation in soil parameters of *Anthoxanthum aristatum* habitats
Explanations: F – fallow, A – arable field, aG – sandy grassland near arable field, AR – field roadside, pG – sandy grassland near pine forest plantation, fG – sandy grassland near pine forest

coefficients indicate that all the characters are poorly correlated with discriminant functions (Table 14).

3.2.2. Morphological variation related to soil conditions

ANOVA shows that mean values of all the studied soil parameters vary significantly among the habitats (Table 15). The highest value of pH (4.6) was recorded on fallow land (F), second highest (4.0) on arable field (A), while values of this parameter in the other habitats were low. Cation-exchange capacity (CEC) was the highest in sandy grassland near arable field (aG), 13 mmol/100g soil, and the lowest, on fallow land (F), 1 mmol/100g soil. Conductivity (G) was also the lowest on fallow land (F), 0.013 mS/cm, but at the other sites, mean values varied from 0.27 to 0.41 mS/cm. Phosphorus (P) content reached the highest values in field roadsides (AR), ca. 7.8 mgP/100g soil, while the lowest in fG, ca. 2.8 mgP/100g soil, but in the other types of habitats phosphorus content was also low. Potassium (K) content was low in all habitats, varying on average from 2.8 mgK/100g soil in aG to 5.5 mgK/100g soil in arable field (A). Nitrogen (N) content was the highest in sandy grassland near pine forest (fG), ca. 15 mgN/100g soil, and the lowest 7.5 in fallow land

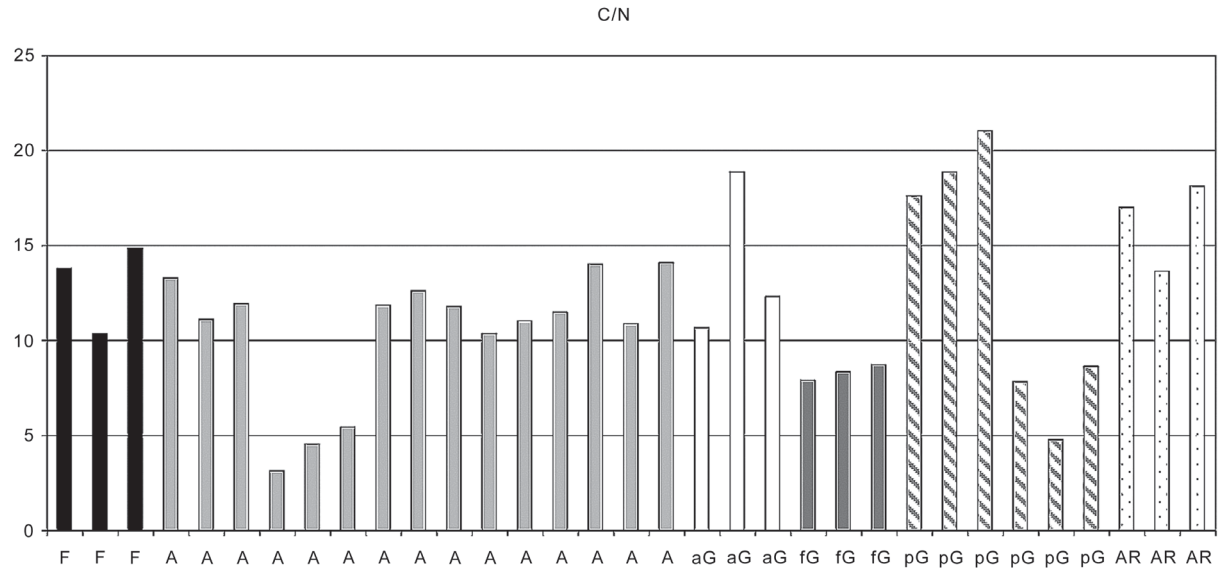

Fig. 21. Variation in C/N ratio between *Anthoxanthum aristatum* habitats
Explanations: F – fallow, A – arable field, aG – sandy grassland near arable field, fG – sandy grassland near pine forest, pG – sandy grassland near pine forest plantation, AR – field roadside

(F). Organic carbon content ranged from 0.9% on fallow land (F) to 1.6 on a field roadside (AR) (Fig. 20). Values of C/N ratio usually amounted to 10-15 and to 20 in sandy grassland in arable field (aG) and sandy grassland forest pine plantation (pG, Fig. 21).

The first two principal components jointly explain 70.35% of the observed variation. PC1 is most strongly correlated with the level of N, C, and humus content, C/N ratio, and P content. PC2 is most strongly correlated with K content and N/K ratio. Carbon and humus content are correlated with N content and the N/P ratio (Fig. 22, Table 16).

In the scatter plot of the first two principal components, samples from sandy grassland near pine forests pG form a distinct group, with positive values of PC1 and negative of PC2. Negative values of PC1 and PC2

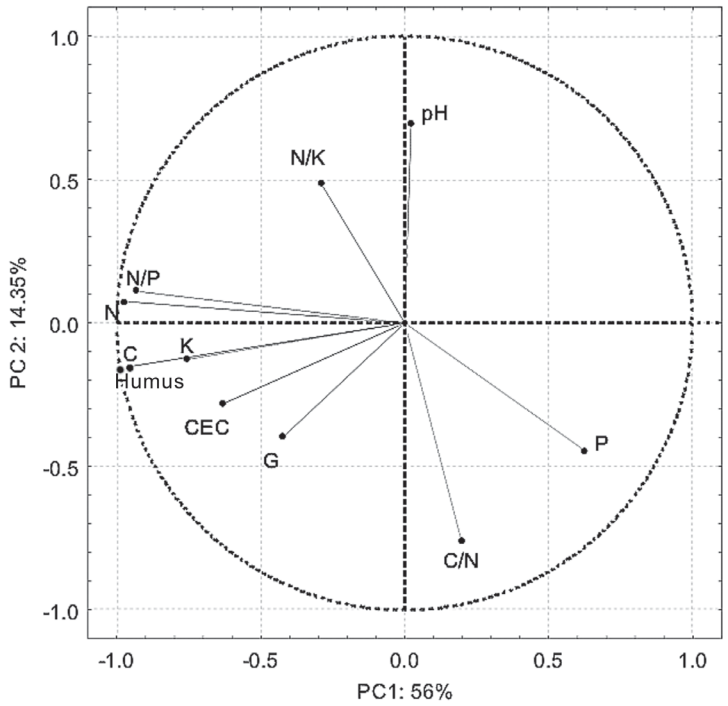

Fig. 22. Correlations between soil parameters (pH, P, N, K, C, N/P, N/K, C/N, conductivity G, cation exchange capacity CEC) of *Anthoxanthum aristatum* habitats and the first two principal components (PC1 and PC2)

Table 16. Correlation between 24 morphological characters of *Anthoxanthum aristatum* and the first two principal components PC1 and PC2 (strongest correlations are marked in bold)

Parameter	PC1	PC2
pH_{KCl}	-0.143	**0.789**
Cation-exchange capacity (CEC)	-0.099	**-0.758**
Conductivity (G)	-0.514	0.105
Phosphorus (P)	0.681	-0.306
Potassium(K)	-0.670	0.504
Nitrogen (N)	**-0.957**	-0.176
N/P ratio	**-0.973**	-0.071
N/K ratio	-0.196	-0.611
C/N ratio	0.213	-0.099
Organic carbon (C)	**-0.943**	-0.160
Humus	**-0.943**	-0.160

Table 17. Redundancy analysis (RDA) based on morphological characters and soil parameters in populations of *Anthoxanthum aristatum* (permutation test $p = 0.04$)

	RDA1	RDA2
Cumulative % of variance	0.387	0.043
Morphological data	95.3	44.3
Soil parameters	85.8	95.3

are recorded for populations located on field roadsides (AR) and on sandy grasslands near pine forest plantations (aG), which are distinguished by higher values of organic carbon (C) and humus content as well as cation-exchange capacity (CEC). The central part of the diagram contains

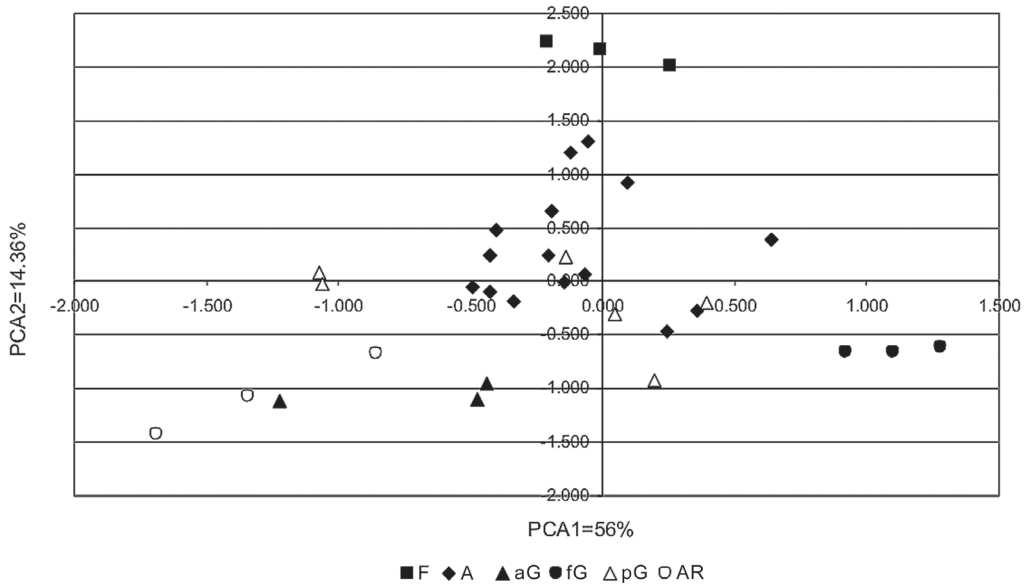

Fig. 23. Distribution of *Anthoxanthum aristatum* habitats in the system of the first two principal components (PCA1 and PCA2)
Explanations: F – fallow, A – arable field, aG – sandy grassland near arable field, fG – sandy grassland near pine forest, pG – sandy grassland near pine forest plantation, AR – field roadside

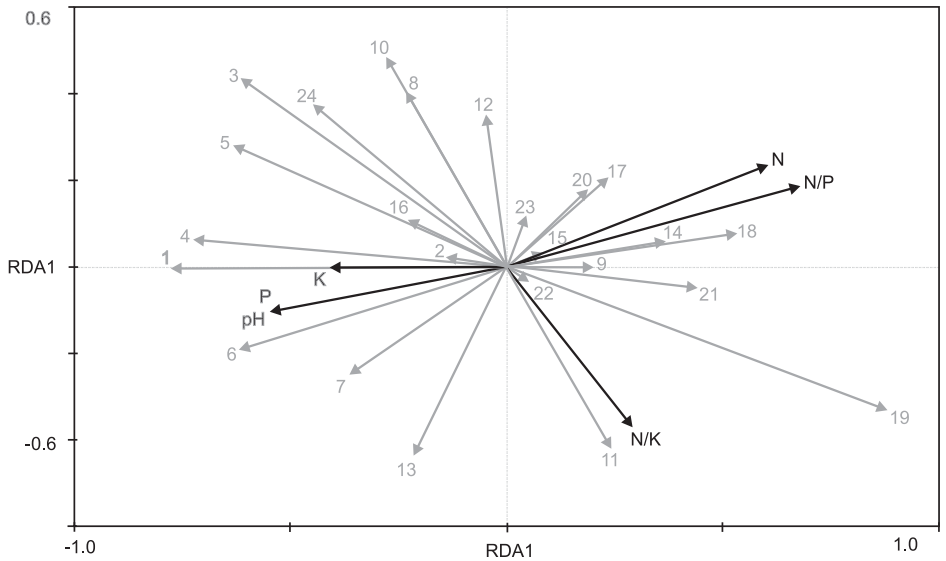

Fig. 24. Redundancy analysis axes (RDA1 and RDA2) showing the impact of selected soil parameters (black arrows: pH, P, N, K, N/P, N/K) on *Anthoxanthum aristatum* morphological characters (gray arrows: 1-24)
Explanations – see Tables 1 and 2

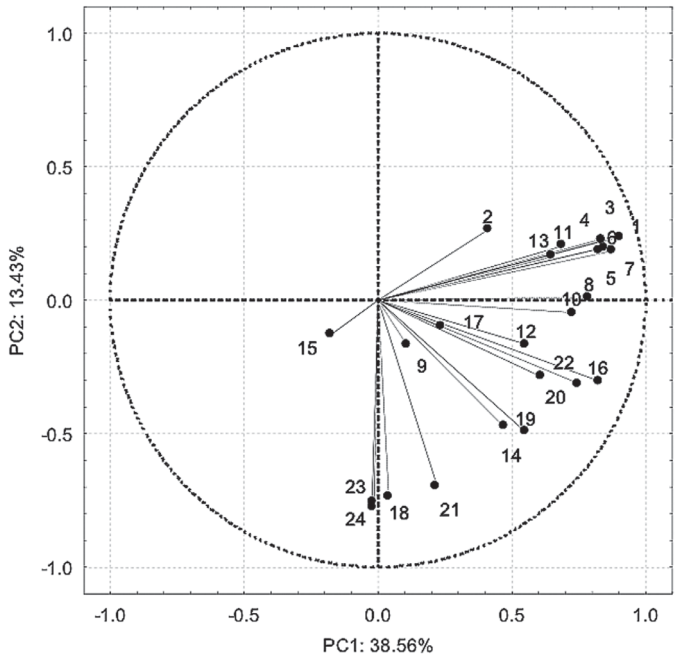

Fig. 25. Correlations between morphological characters (1-24) of *Anthoxanthum odoratum* and *A. alpinum* and the first two principal components (PC1 and PC2)
Explanations: see Table 1

Table 18. Correlation between 24 morphological characters of *Anthoxanthum odoratum* and *A. alpinum* and the first two principal components PC1 and PC2 (strongest correlations are marked in bold)

Character	PC1	PC2
1	**0.903**	0.237
2	0.414	0.264
3	**0.837**	0.230
4	**0.831**	0.221
5	**0.820**	0.190
6	**0.877**	0.184
7	**0.844**	0.197
8	**0.795**	0.011
9	0.109	-0.166
10	**0.725**	-0.047
11	0.689	0.204
12	0.545	-0.166
13	0.653	0.162
14	0.457	-0.474
15	-0.193	-0.130
16	**0.819**	-0.303
17	0.238	-0.103
18	0.045	**-0.737**
19	0.549	-0.495
20	0.603	-0.286
21	0.228	-0.695
22	**0.743**	-0.312
23	-0.013	**-0.758**
24	-0.024	**-0.780**

Table 19. Analysis of variance for 24 morphological characters of *Anthoxanthum odoratum* and *A. alpinum* (*F* values in bold are significant at $p < 0.05$)

Character	*F*
1	**58.224**
2	**10.319**
3	**34.093**
4	**26.499**
5	**30.426**
6	**50.449**
7	**38.976**
8	**41.649**
9	**1.915**
10	**21.170**
11	**23.229**
12	**12.021**
13	**17.162**
14	**7.681**
15	**8.959**
16	**40.759**
17	**6.556**
18	**10.133**
19	**13.046**
20	**8.718**
21	**5.416**
22	**23.523**
23	**8.122**
24	**6.856**

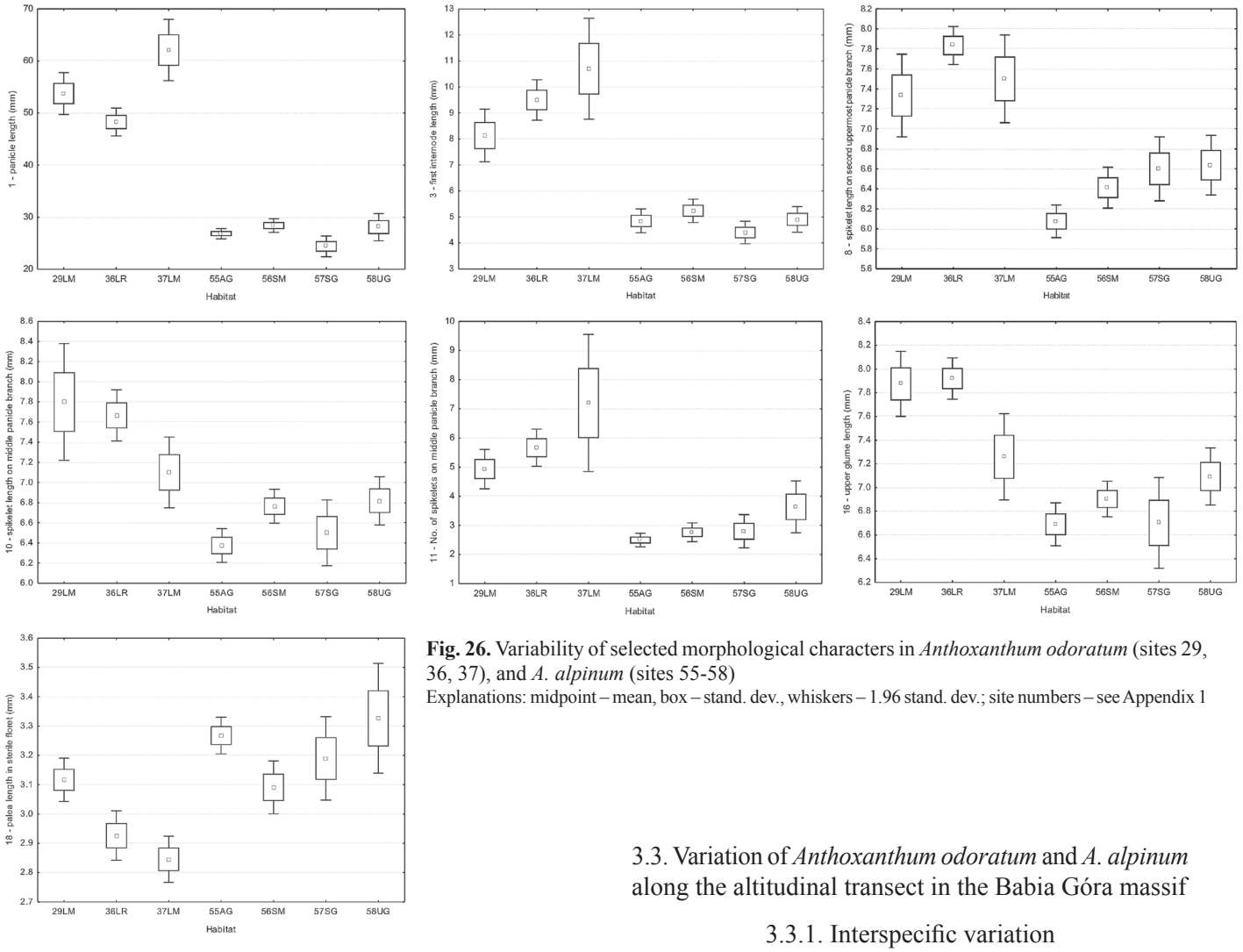

Fig. 26. Variability of selected morphological characters in *Anthoxanthum odoratum* (sites 29, 36, 37), and *A. alpinum* (sites 55-58)
Explanations: midpoint – mean, box – stand. dev., whiskers – 1.96 stand. dev.; site numbers – see Appendix 1

scattered samples from arable fields (A) and sandy grasslands near arable fields pG. The upper part of the diagram contains samples from fallows (F), distinguished by the lowest concentrations of organic carbon, humus, total nitrogen, conductivity, cation-exchange capacity, and highest pH values (Fig. 23).

Graphic representation of RDA results shows a scatter plot of data along the first two axes (RDA1 and RDA2), divided into two groups: soil parameters (black arrows) and morphological characters (gray arrows) (Fig. 24). Total nitrogen (N) content and N/P ratio affects lower glume width (15), palea awn length from knee in sterile floret (20), upper glume width (17), number of spikelets on second uppermost panicle branch (9), lower glume length (14), and palea length in sterile floret (18). Potassium (K) content affects panicle length (1) and the number of panicle nodes (2) and the second panicle internode length (4). Bioavailable phosphorus (P) content partly affects fourth and fifth panicle internode length (6 and 7). Permutation test ($P = 0.04$) shows that the result is statistically significant (Table 17).

3.3. Variation of *Anthoxanthum odoratum* and *A. alpinum* along the altitudinal transect in the Babia Góra massif

3.3.1. Interspecific variation

Populations of *A. odoratum* and *A. alpinum* from Baba Góra were compared in respect of variation of 24 morphological characters of panicles. In total, 73 individuals from *A. odoratum* representing 3 sites were analysed: lower montane meadow (29LM and 35LM) and lower montane forest roadside (36LR), 95 individuals from *A. alpinum* 4 sites in the Babia Góra massif were analysed: alpine grassland (55AG), Diablak, 1697 m; subalpine grassland near a trail (57SG), 1432 m; subalpine matgrass meadow, Przełęcz Brona, 1413 m (56SM); upper montane forest glade (58UG), 1166 m. PCA for all samples coming from this massif made it possible to identify 15 characters that discriminate best between individual taxa. PC1 (which explains 38.56% of the total variance) is correlated with characters 1, 3, 8, 10, 16, and 22, while PC2 (13.43%) is correlated with characters 18, 23, and 24 (Table 18, Fig. 25).

ANOVA assessed effects of individual traits on the pattern of variation within individual samples and between them. The results show that all the characters affect significantly the pattern of variation of populations of *A. odoratum* and *A. alpinum* (Table 19). The best discriminating characters of *A. odoratum* and *A. alpinum* (1, 3, 8, 10, 11, 16) are shown in Fig. 26. Most of the

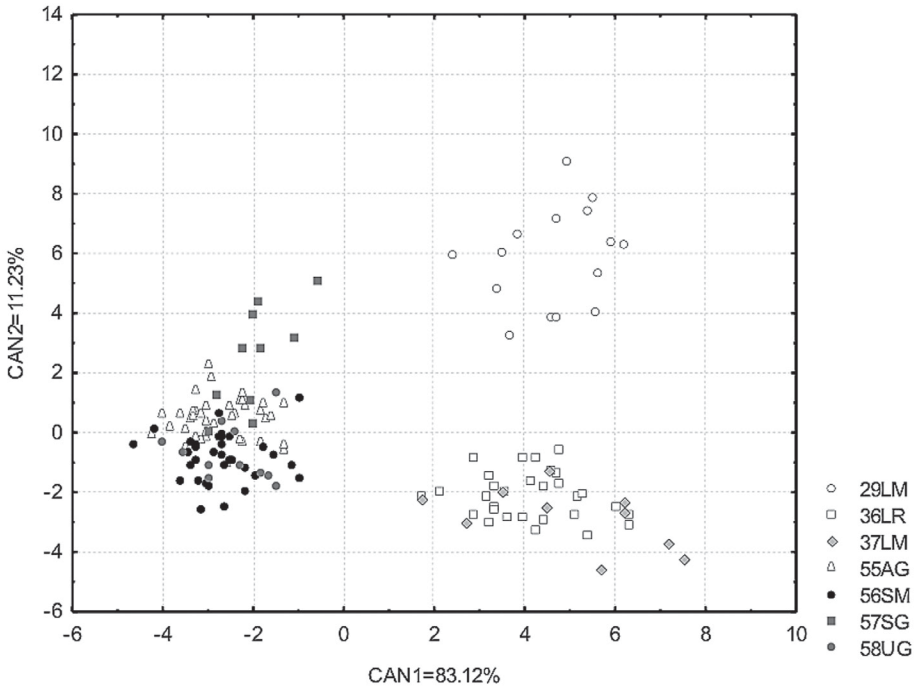

Fig. 27. Distribution of *Anthoxanthum odoratum* (sites 29, 36, 37), and *A. alpinum* (sites 55-58) specimens from the Babia Góra massif in the system of the first two canonical variables (CAN1 and CAN2) based on morphological characters
Explanations: site numbers – see Appendix 1

Table 20. Discrimination power of 24 morphological characters of *Anthoxanthum odoratum* and *A. alpinum* (values in bold are significant at $p \leq 0.001$)

Character	Wilks' lambda	Partial Wilks' lambda	CAN1	CAN2
1	**0.112**	0.908	-0.166	-0.090
2	**0.114**	**0.895**	-0.223	-0.258
3	0.110	0.930	-0.261	-0.149
4	0.105	0.971	-0.197	-0.100
5	0.106	0.959	-0.201	-0.092
6	**0.113**	0.899	-0.192	-0.154
7	0.106	0.964	-0.094	-0.090
8	**0.121**	**0.841**	-0.354	-0.130
9	0.107	0.955	0.385	0.281
10	0.107	0.953	0.013	-0.157
11	**0.111**	0.920	0.078	0.063
12	**0.116**	**0.881**	0.106	-0.060
13	0.108	0.946	-0.035	0.046
14	**0.111**	0.917	0.136	-0.028
15	**0.133**	**0.765**	0.278	-0.345
16	**0.122**	**0.834**	-0.046	-0.222
17	**0.118**	**0.862**	0.083	-0.235
18	**0.132**	**0.773**	0.301	**-0.662**
19	**0.126**	**0.812**	0.165	0.081
20	0.106	0.961	-0.085	-0.129
21	**0.112**	0.908	0.244	-0.089
22	**0.119**	**0.855**	-0.270	-0.051
23	**0.130**	**0.783**	**0.440**	-0.045
24	**0.130**	**0.765**	**0.709**	-0.322

characters divided the studied samples into 2 groups. The first group is composed of samples 29LM, 36LR, and 37LM, which represent *A. odoratum,* whereas the second group consists of samples 55AG-58UG, representing *A. alpinum*.

CDA confirmed the selection of 16 quantitative characters on the basis of PCA, distinguishing between *A. odoratum* and *A. alpinum*. Values of canonical structure coefficients indicate that the first canonical variable is linked with characters 23 and 24, whereas the second canonical variable is linked with character 18. Values of partial Wilks' lambda indicate that the most useful for discrimination are characters 1, 2, 6, 8, 11, 12, 14-19, and 21-24 (Table 20).

In the scatter plot the first two canonical variables, samples 55AG-58UG classified as *A. alpinum* are clearly distinct in respect of CAN1. The other individuals, classified as *A. odoratum*, form 2 groups: populations 36LR and 37LM in the lower right corner of the plot and a group of individuals from sample 29LM in the upper right part of the plot (Fig. 27).

To test if the studied populations were properly identified to species on the basis of morphological variation, DNA content was assessed in samples collected in the alpine, lower montane, and upper montane zones. DNA content in specimens from the alpine zone, classified morphologically as *A. alpinum* ($2n$=10), is half as high as in lower montane specimens, identified as *A. odoratum* ($2n$=20). DNA content in specimens from population 58UG, located in the upper montane

zone, where both species can occur, corresponded to that characteristic of *A. alpinum* (Fig. 28).

3.3.2. Morphological variation of *Anthoxanthum alpinum*

Results of measurements of individuals identified as *A. alpinum* were subjected to statistical analysis to assess the level of intra- and interspecific variation. In total, 95 individuals from 4 sites in the Babia Góra massif were analysed: alpine grassland (55AG), Diablak, 1697 m, subalpine matgrass meadow, Przełęcz Brona, 1413 m, (56SM); subalpine grassland near a trail (57SG), 1432 m; upper montane forest glade (58UG), 1166 m.

ANOVA shows that mean values of some characters (1, 8, 14-19, 21-24) differ significantly in populations

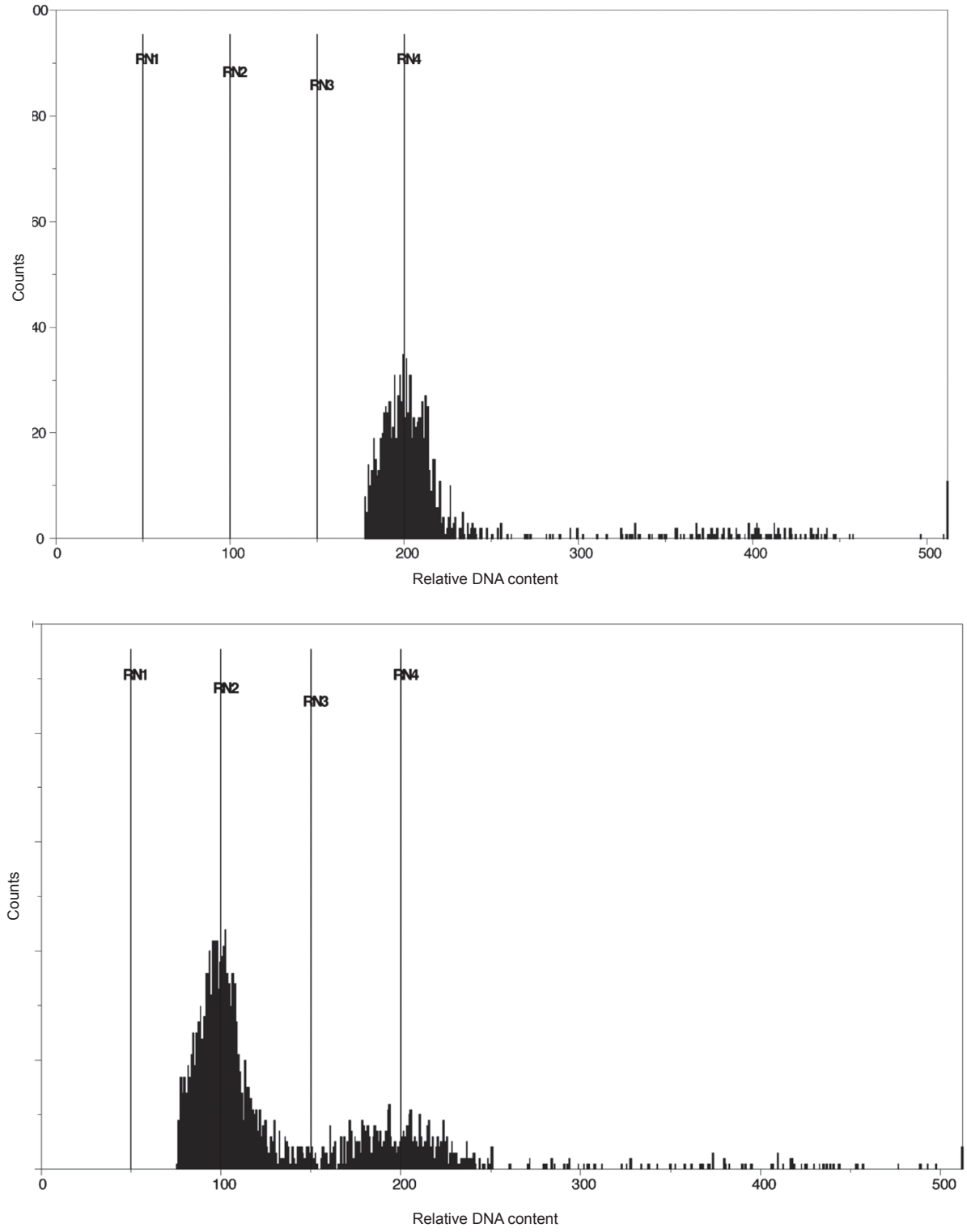

Fig. 28. DNA content in *Anthoxanthum alpinum* (bottom) and *A. odoratum* (top), determined by flow cytometry

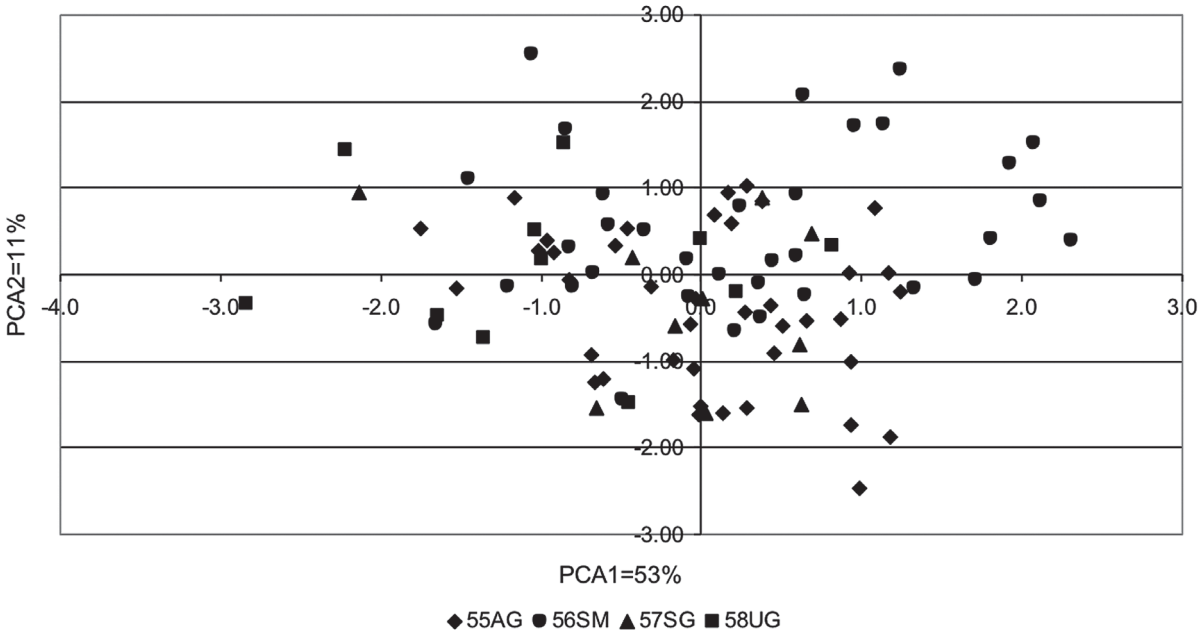

Fig. 29. Distribution of *Anthoxanthum alpinum* specimens in the system of the first two principal components (PC1 and PC2) based on morphological characters
Explanations: site numbers – see Appendix 1

Table 21. Analysis of variance for 24 morphological characters of *Anthoxanthum alpinum* populations (*F* values in bold are significant at $p < 0.05$)

Character	*F*
1	**3.539**
2	0.586
3	1.203
4	0.896
5	0.611
6	0.551
7	0.525
8	**4.959**
9	2.114
10	4.530
11	4.118
12	6.781
13	2.753
14	0.854
15	**6.666**
16	**2.286**
17	**4.676**
18	**4.274**
19	**11.745**
20	1.192
21	**5.111**
22	**6.866**
23	**6.212**
24	**11.612**

Table 22. Correlations between 24 morphological characters of *Anthoxanthum alpinum* and the first two principal components PC1 and PC2 (strongest correlations are marked in bold)

Character	PC1	PC2
1	-0.137	0.641
2	-0.071	-0.085
3	-0.013	0.524
4	-0.023	0.677
5	0.157	0.624
6	0.101	0.281
7	0.189	0.453
8	-0.387	0.278
9	-0.350	0.038
10	-0.293	0.450
11	-0.202	0.161
12	-0.382	0.421
13	-0.444	0.116
14	-0.636	0.019
15	-0.229	0.349
16	**-0.704**	0.214
17	-0.166	0.370
18	**-0.791**	-0.203
19	-0.660	0.145
20	-0.443	0.031
21	**-0.729**	-0.309
22	-0.585	-0.302
23	**-0.765**	-0.177
24	**-0.716**	-0.258

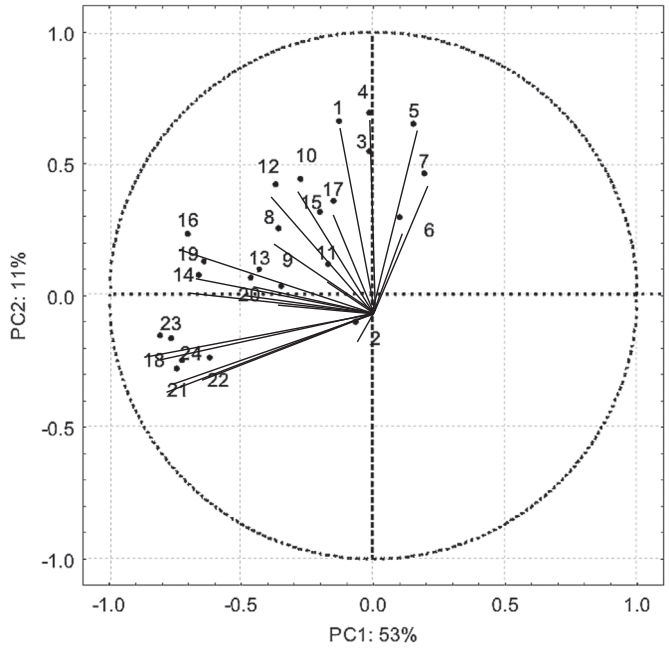

Fig. 30. Correlations between morphological characters (1-24) of *Anthoxanthum alpinum* and the first two principal components (PC1 and PC2)
Explanations: see Table 1

of *A. alpinum* (Table 21). The populations form one group in the central part of the plot, whereas several individuals from subalpine matgrass meadow (56SM) differ from the others by positive values of PC1 and PC2. Moreover, some plants from Diablak (55AG) were separated because of negative values of PC1 (Fig. 29).

Characters 16, 18, 23, and 24 are most strongly correlated with PC1 (Fig. 30, Table 22). The studied characters are weakly correlated with PC2. Mutually positively correlated characters form 2 groups: one composed of characters 18 and 21-23, whereas the other composed of characters 9, 13, 14, 16, 19, and 20.

Cluster analysis based on Euclidean distances for individuals of *A. alpinum* (Fig. 31, Table 23), separates two groups, which include individuals from all 4 populations. Values of partial Wilks' lambda indicate that the analysed characters only to a small extent discriminate between populations of *A. alpinum* (Table 24). Values of canonical structure coefficients suggest that some characters (5, 11, 12, 15, 18, 19) are slightly more strongly correlated with CAN1 (Table 25). CAN2 is more strongly correlated only with character 21. In the plot of the first two canonical variables (Fig. 32), individuals from population 56SM and 58UG form a loose group in the central part of the plot, whereas individuals from population 55 have positive values of CAN1. Individuals from lower montane population 57 differ from the others by positive values of CAN1 and negative of CAN2.

3.3.3. Environmental variation of *Anthoxanthum odoratum* and *A. alpinum* along the altitudinal transect

Soil samples collected along the altitudinal transect were analysed in respect of basic parameters (Table 2). Mean pH at alpine, subalpine, upper montane, and lower montane grassland sites varied from 3.1 to 4.8.

Table 23. Individuals from mountain populations of *Anthoxanthum alpinum* (55AG-58UG), arranged in the order of connections to particular groups in cluster analysis – see Fig. 31

Group	Specimens of populations no. 55, 56, 57, 58
I	57SG, 56SM, 58UG, 57SG, 56SM, 56SM, 57SG, 55AG, 55AG, 57SG, 58UG, 56SM, 56SM, 56SM, 57SG, 55AG, 56SM, 55AG, 56SM, 57SG, 55AG, 55AG, 55AG, 56SM, 56SM, 55AG, 55AG, 56SM, 56SM, 55AG, 56SM, 55AG, 57SG, 55AG, 58UG, 56SM, 58UG, 55AG
II	58UG, 57SG, 55AG, 56SM, 56SM, 55AG, 56SM, 55AG, 55AG, 56SM, 56SM, 56SM, 58UG, 56SM, 56SM, 57SG, 57SG, 57SG, 55AG, 55AG, 58UG, 58UG, 57SG, 56SM, 56SM, 55AG, 55AG, 56SM, 56SM, 56SM, 55AG, 55AG, 55AG, 55AG, 56SM, 56SM, 56SM, 55AG, 56SM, 58UG, 55AG, 57SG, 55AG, 56SM, 55AG, 55AG, 55AG, 55AG, 55AG, 55AG, 55AG, 58UG, 57SG, 56SM, 58UG, 56SM, 55AG

Table 24. Discrimination power of 24 morphological characters of *Anthoxanthum alpinum* (values in bold are significant at $p \leq 0.001$)

Character	Wilks' lambda	Partial Wilks' lambda
1	0.044	0.968
2	0.044	0.985
3	0.043	0.989
4	0.044	0.971
5	0.047	0.913
6	0.044	0.969
7	0.044	0.971
8	0.046	0.939
9	0.044	0.972
10	0.045	0.964
11	**0.048**	**0.890**
12	**0.052**	**0.831**
13	0.046	0.932
14	0.044	0.980
15	0.048	0.894
16	0.046	0.938
17	**0.045**	**0.960**
18	**0.056**	**0.771**
19	0.064	0.667
20	0.046	0.929
21	0.045	0.953
22	0.047	0.910
23	**0.091**	**0.471**
24	**0.102**	**0.421**

Table 25. Correlations between 24 morphological characters of *Anthoxanthum alpinum* and the first two canonical variables CAN1 and CAN2

Character	CAN1	CAN2
1	-0.238	0.254
2	-0.101	-0.142
3	-0.004	-0.178
4	0.104	0.261
5	0.**402**	0.292
6	0.011	0.040
7	-0.285	-0.117
8	-0.254	-0.268
9	-0.162	0.018
10	0.073	-0.287
11	**-0.383**	-0.260
12	**-0.551**	-0.210
13	0.361	0.082
14	0.355	0.026
15	-0.**403**	-0.203
16	**-0.517**	0.089
17	-0.037	-0.176
18	**0.556**	0.095
19	**-0.480**	-0.258
20	0.299	0.277
21	-0.209	**-0.416**
22	0.382	0.163
23	-0.301	1.753
24	0.320	-0.122

Mean conductivity (G) ranged from 0.02 mS/cm at site 29LM and 37LM to 0.15 at site 58UG. Cation-exchange capacity (CEC) varied on average from 5 mmol/100g at 37LM to 29 mmol/100g soil at 55AG, while bioavailable phosphorus (P) content, from 0.3 mgP/100g at site 29LM to 2.7 mgP/100g at site 56SM. The lowest K content, 6.1 mgK/100g soil, was at site 58UG, whereas the highest, 11.1 mgK/100g soil, at site 36LR. Total nitrogen (N) and organic carbon (C) content in higher montane samples were lower than in samples from the sites located at higher altitudes (Fig. 33).

The first principal component (PC1) is correlated most strongly with pH, CEC, N, N/K, C, and humus content, whereas the second (PC2), with P, K, and C/N (Table 26). Lower montane samples have negative

Table 26. Correlation between 24 morphological characters of *Anthoxanthum alpinum* and the first two principal components PC1 and PC2 (strongest correlations are marked in bold)

Parameter	PC1	PC2
pH_{KCl}	**0.896**	-0.299
Cation-exchange capacity (CEC)	**0.878**	0.008
Conductivity (G)	-0.225	0.008
Phosphorus (P)	-0.166	**0.959**
Potassium(K)	0.366	**0.926**
Nitrogen (N)	**-0.919**	-0.376
N/P ratio	0.119	**-0.980**
N/K ratio	**-0.740**	-0.648
C/N ratio	-0.543	**0.717**
Organic carbon (C)	**-0.978**	-0.015
Humus	**-0.979**	-0.018

Table 27. Redundancy analysis (RDA) based on morphological characters and soil parameters in samples of *Anthoxanthum odoratum* and *A. alpinum* from Babia Góra massif (permutation test $p = 0.043$)

	RDA1	RDA2
Cumulative % of vriance	0.898	0.102
Morphological data	89.8	100.0
Soil parameters	89.8	100.0

values of PC1. This is associated e.g. with lower total nitrogen and organic carbon content at those sites. In contrast, site 56SM is distinguished by higher bioavailable phosphorus content and C/N ratio. Lower montane samples have positive values of PC1 but they vary. Site 29LM is characterized by the highest pH and N/P ratio, whereas site 36LR is distinguished mostly by a high level of bioavailable potassium (Fig. 34).

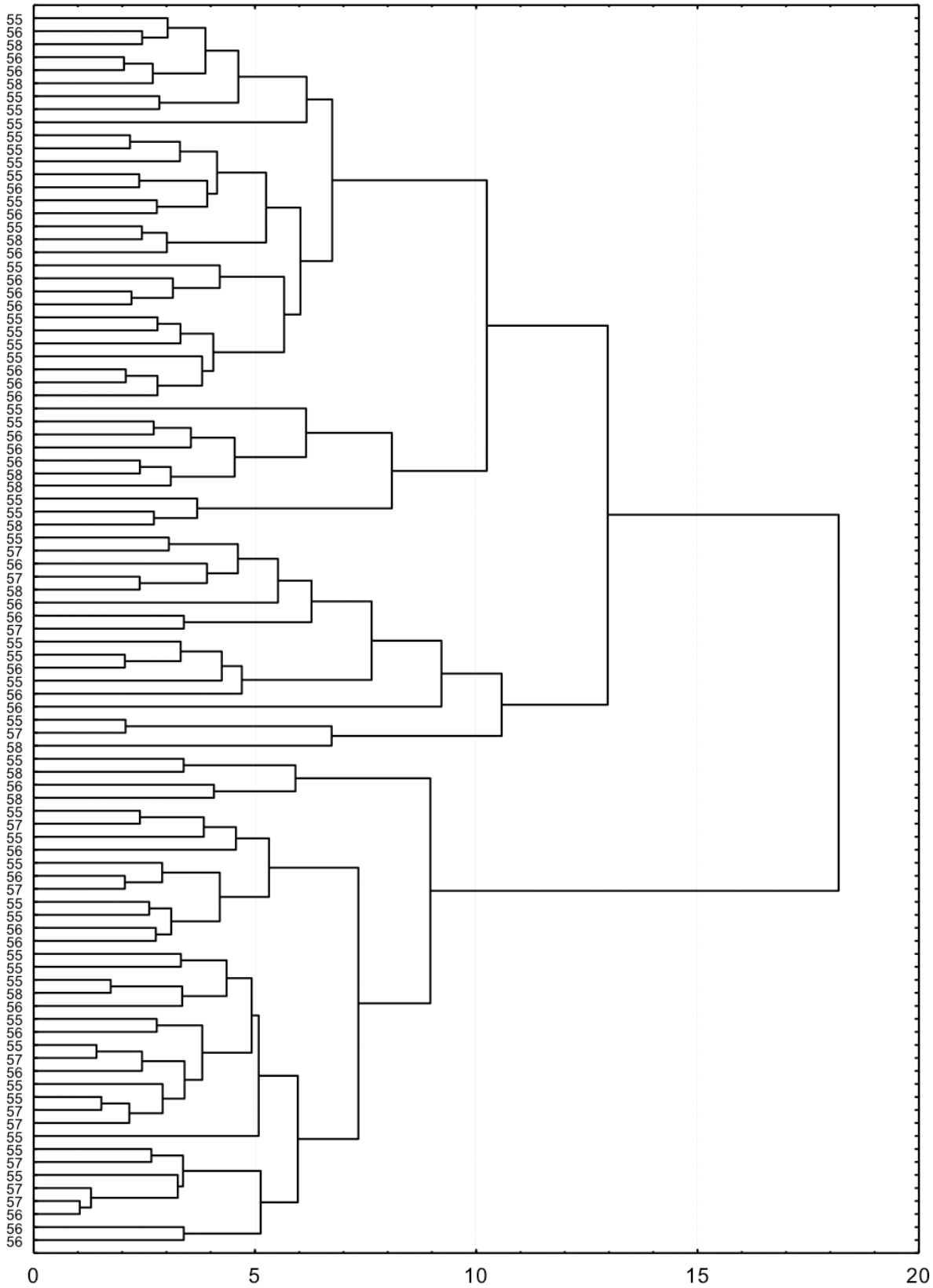

Fig. 31. Dendrogram of *Anthoxanthum alpinum* specimens based on morphological characters (Euclidean distances)
Explanations: site numbers – see Appendix 1

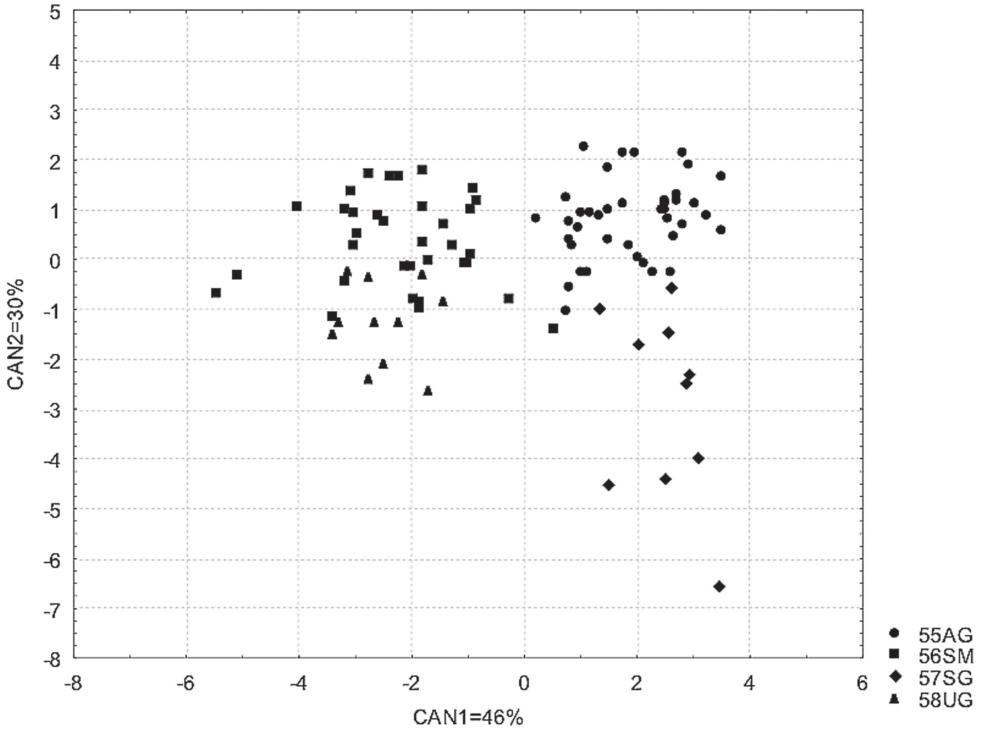

Fig. 32. Distribution of *Anthoxanthum alpinum* specimens in the system of the first two canonical variables (CAN1 and CAN2) based on morphological characters
Explanations: site numbers – see Appendix 1

Graphic representation of RDA results (Fig. 35, Table 27), shows a scatter plot of data along the first twoaxes (RDA1 and RDA2), divided into two groups: soil parameters (black arrows) and morphological characters (gray arrows). Most of morphological characters are not correlated with soil parameters, except character 18 correlated with potassium content of soil, character 21 correlated with total nitrogen (N) content, and N/K ratio, character 9 correlated with potassium (K), as well as characters 7, 11 and 23 are correlated with pH and N/P ratio.

3.4. Interspecific variation in stem and leaf anatomy of *Anthoxanthum odoratum*, *A. alpinum*, and *A. aristatum*

Anatomical variation of stems and leaves of the three studied species is presented on the basis of an analysis of 44 individuals, including 26 of *A. odoratum,* 10 of *A. aristatum*, and 8 of *A. alpinum*.

3.4.1. Anatomical stem structure

Anthoxanthum odoratum, *A. alpinum*, and *A. aristatum* have a similar internal structure of stems. It is composed of a ring of alternating larger and smaller collateral vascular bundles, arranged more or less regularly, with sclerenchyma cells located between larger vascular bundles and epidermal cells (Fig. 36). The range of variation in number of vascular bundles is similar in individual species: 8-14 in *A. odoratum*, 8-12 in *A. aristatum*, and 11-14 in *A. alpinum* (Fig. 36a). Sclerenchyma cells in *A. odoratum* form 4-7 layers (Fig. 36b), whereas in *A. aristatum* usually in 4-5 layers, but in some plants, only 3 layers of sclerenchyma cells are present. In *A. alpinum*, sclerenchyma cells form 4-5 layers.

3.4.2. Anatomical leaf structure

Anatomical structure of leaves of the three studied *Anthoxanthum* species is very similar. In cross-sections, several to about a dozen collateral vascular bundles are visible (Fig. 37A). The bundles vary in size. The larger bundles are on both sides connected with sclerenchyma cells. On the adaxial side of the leaf blade, among the vascular bundles, bulb-shaped epidermal cells can be seen. In the same place on the abaxial side, high cells are visible (Fig. 37A). Epidermal cells between veins are short. Veins on both sides of the leaf are covered with short and long hairs (Fig. 37B).

In the leaf cross-section of *A. odoratum*, 11-20 collateral vascular bundles of various size are present. In the leaf epidermis of the adaxial side, between the veins, 3-4 stomatal rows are visible, while on the abaxial side, 2-4 rows. Stomatal length ranges from 36 μm to 51 μm. In the leaf cross-section of *A. alpinum*, 12-23 collateral vascular bundles can be seen. In the leaf epidermis of the adaxial side, 4-6 stomatal rows are visible between the veins, compared to 3-4 rows on the abaxial side. Stomatal length in this species varies from 32.2 μm to 36.4 μm.

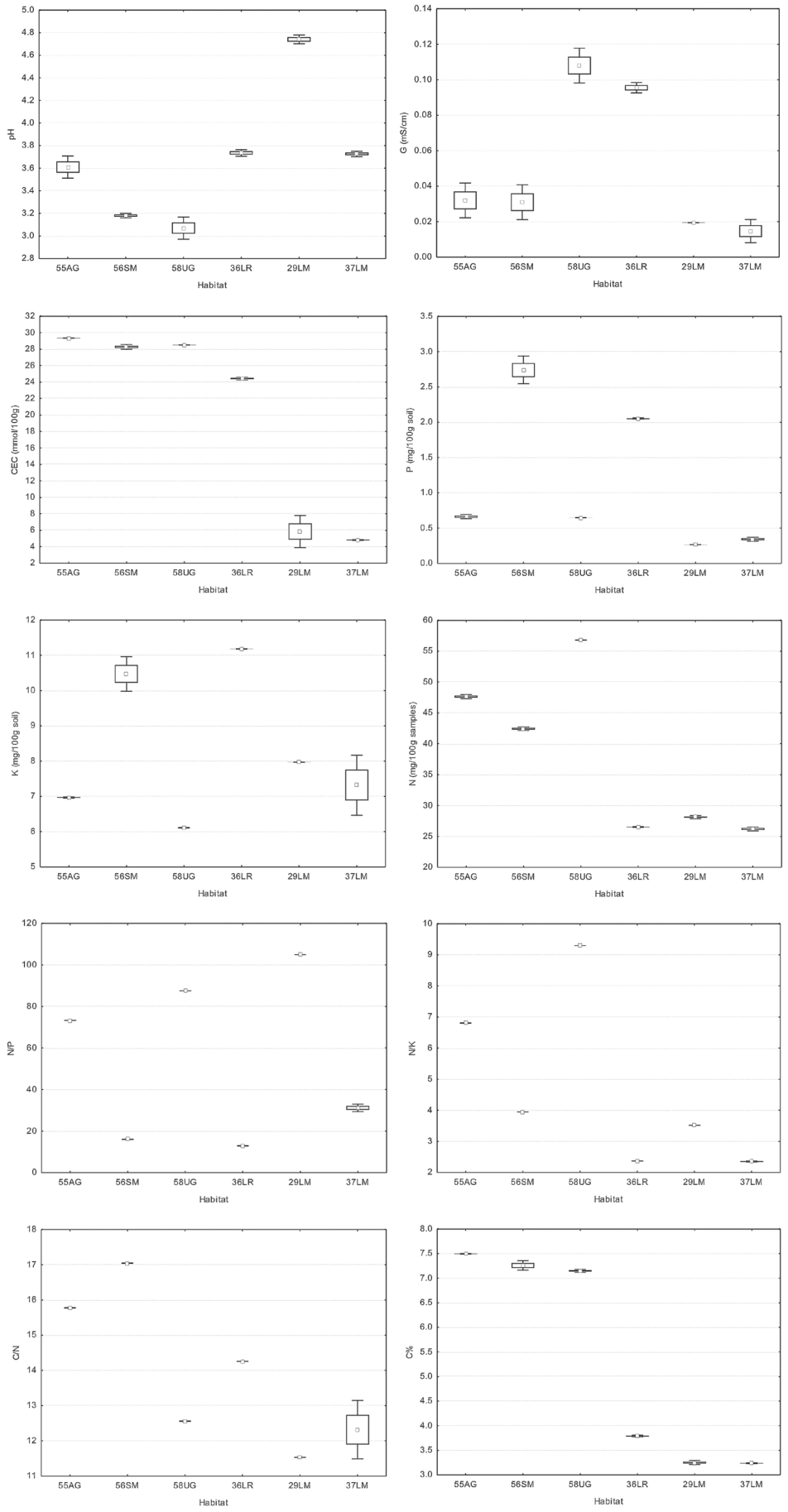

Fig. 33. Variation in soil parameters of habitats of *Anthoxanthum alpinum* (sites: 55AG, 56SM, 58UG) and *A. odoratum* (sites: 36LR, 29LM, 37LM) along the longitudinal transect
Explanations: site numbers – see Appendix 1

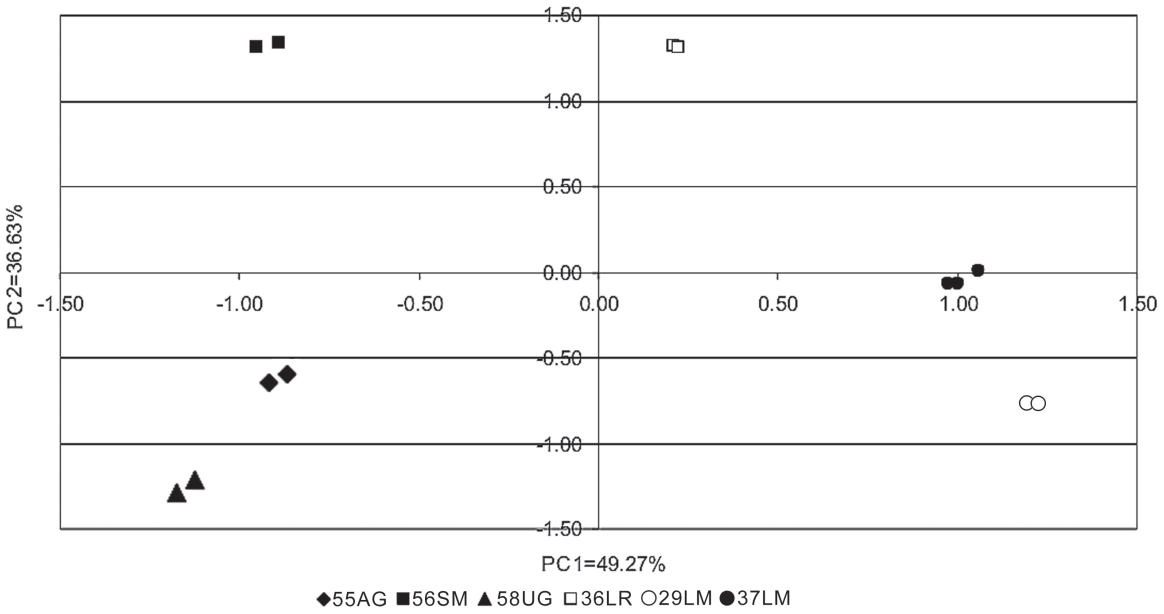

Fig. 34. Distribution of habitats of *Anthoxanthum alpinum* (sites: 55, 56, 58) and *A. odoratum* (sites: 36, 29, 37) from the Babia Góra massif in the system of the first two principal components (PCA1 and PCA2) based on soil parameters
Explanations: site numbers – see Appendix 1

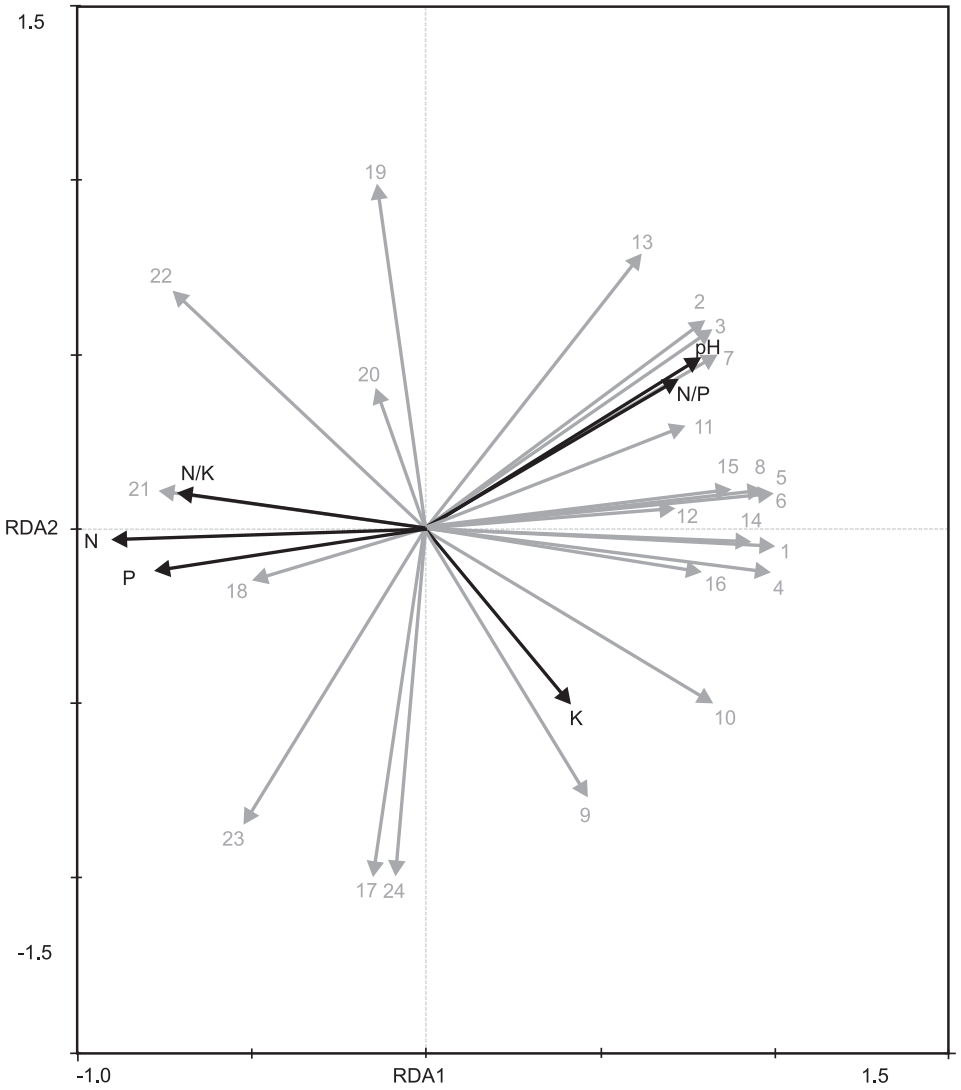

Fig. 35. Redundancy analysis axes (RDA1 and RDA2) showing the impact of selected soil parameters (black arrows: P, N, N/K, N/P, pH, K) on *Anthoxanthum odoratum* and *A. alpinum* morphological characters (gray arrows: 1-24)
Explanations: see Tables 1 and 2

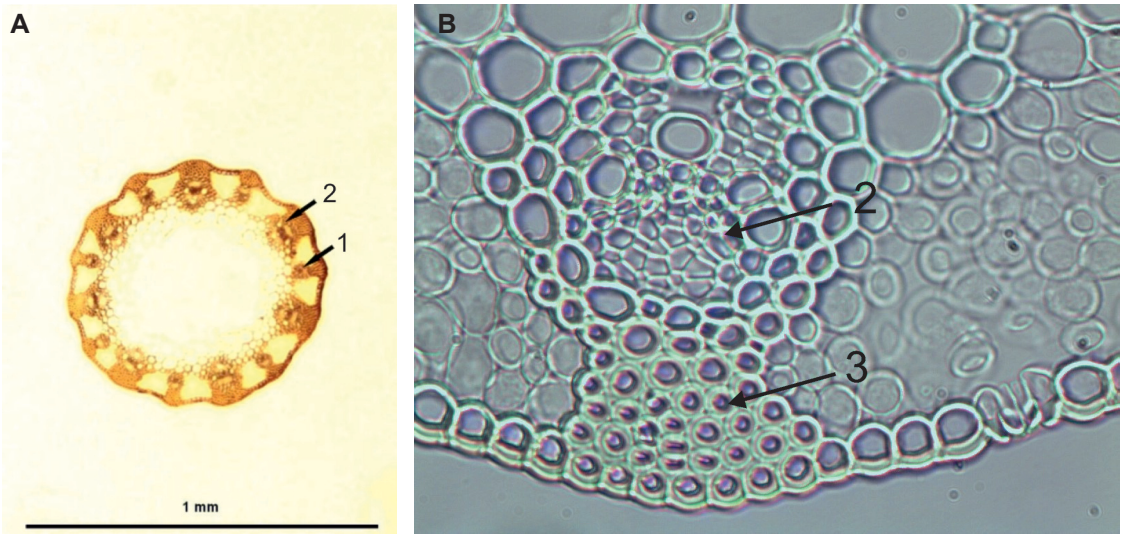

Fig. 36. Transverse section of the stem of *Anthoxanthum alpinum* (A) and *A. odoratum* (B)
Explanations: 1 – small vascular bundles, 2 – large vascular bundles, 3 – sclerenchyma cells

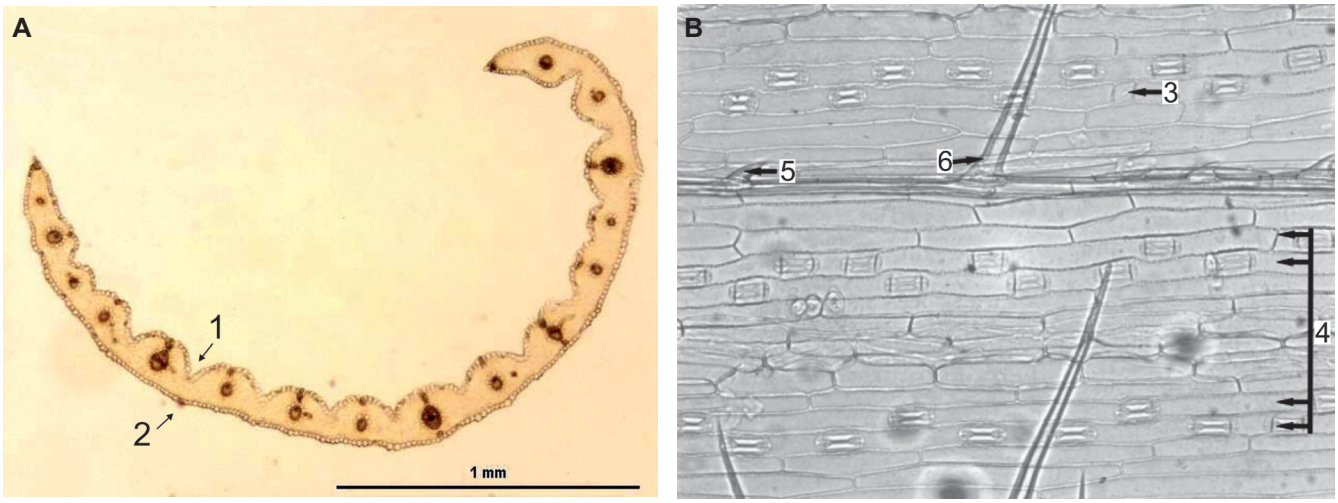

Fig. 37. Transverse section of the leaf of *Anthoxanthum alpinum* (A) and *A. odoratum* (B)
Explanations: 1 – bulliform cells, 2 – high cells, 3 – short cell, 4 – stomatal rows on adaxial leaf surface, 5 – short hair, 6 – long hair

In the leaf cross-section of *A. aristatum*, 15-16 collateral vascular bundles can be seen. In the leaf epidermis of the adaxial side, 4 stomatal rows are located between the veins, whereas on the abaxial side, only 2 stomatal rows are found between them. Stomatal length on both sides of the leaf ranges from 32.7 µm to 37.3 µm.

4. Discussion

Anthoxanthum odoratum grows in a great variety of habitats, from eutrophic wetlands, moist and dry meadows, to open forests, both deciduous and coniferous (Snaydon & Davies 1972, 1976; Grant & Antonovics 1978). In recent years, *A. odoratum* has been observed to invade habitats strongly transformed by human activity (Antonovics 1972). In such habitats, *A. odoratum* has very different soil conditions than in its original habitats. The process of adaptation to different soil parameters could contribute to genetic and morphological differentiation within this taxon. Potassium, phosphorus, and nitrogen content in soil are known to affect morphological variation of plants, e.g. of *Trifolium repens* (Snaydon & Bradshaw 1969), *Agrostis stolonifera*, *Scirpus sylvaticus* (Crick & Grime 2006), and *Doronicum austriacum* (Stachurska-Swakoń & Kuź 2011). Also controlled experiments were conducted to investigate relationships between soil fertility and morphological variation in *Holcus lanatus*, *Deschampsia cespitosa* (Ławniczak *et al.* 2009), and physiological variation in *Anthoxanthum odoratum* (Davies 1975). Results of the present study indicate that sites of *A. odoratum* differ in soil parameters. The most distinct soil conditions were found in pine forests (PF), mostly

due to high organic matter content and slightly higher bioavailable phosphorus content. Meadows (DM and MM) were also outliers, because of higher pH values. Moreover, nitrogen content varied widely between the occupied habitats, as observed already in a preliminary study (Ławniczak *et al.* 2011). In grasses of the genus *Anthoxanthum*, morphological characters are correlated with soil parameters, such as pH (Pimentel & Sahuquillo 2003). Results of this study indicate that number of panicle nodes (character 2) and palea awn length to knee in sterile floret (character 19) are related to pH. Phosphorus content is also related to palea length (character 24), while N content, N/K and N/P ratio, organic carbon, humus content, and the C/N ratio are related to the no. of spikelets on middle panicle branch (11), upper glume length (16), palea awn length from knee in sterile floret (20), and lemma length in sterile floret (21) (Fig. 14). Besides, as reported by other authors, N/K and N/P are good indicators of soil fertility (Roem & Berendse 2000; Grüsewell & Koerselman 2002; Ławniczak *et al.* 2011).

Morphological variation observed in populations of wild plants is conditioned by genetic as well as environmental factors. Relationships between environmental factors and structural variation have been studied e.g. in *Phalaris arundinacea* (Gifford *et al.* 2002), *Elymus repens* (Szczepaniak 2002), *Calamagrostis epigejos* (Drapikowska *et. al.* 2007a; Krzakowa & Celka 2007), and *Phragmites australis* (Drapikowska & Krzakowa 2009). Phenotypic variability was found to be correlated with habitat diversity in e.g. *Anthoxanthum armarum* (Pimentel & Sahuquillo 2007) and *A. odoratum* (Antonovics *et al.* 1987; Platenkamp 1991). Phenotypic variation observed in the present study confirms results of preliminary studies of populations of *A. odoratum* from Poland (Drapikowska *et al.* 2011) and West Europe (Pimentel *et al.* 2010) Ranges of variation in the studied characters were compared with those reported for *A. odoratum* by Pimentel Pereira *et al.* (2007a, 2007b). The high observed variation in morphological forms of *A. odoratum* only weakly correlated with habitat type. No significant differences were found between populations from natural, seminatural, and synanthropic sites. Only populations from field roadsides (AR) are distinguished from the others by lower number of panicle nodes (2), shortest spikelets on second uppermost panicle branch (8), higher number of spikelets on second uppermost panicle branch (9), shorter spikelets on lowermost panicle branch (12), shorter upper glumes (16), shorter palea in sterile floret (18), shorter palea awn length from knee in sterile floret (20), shorter lemma in sterile floret (21), and shorter lemma and palea in fertile floret (23 and 24). Additionally, some individuals from field roadsides (AR) have a higher number of vascular bundles in leaves. Submontane and lower montane populations numerously represented in structural analyses, partly differ in morphology from lowland populations, e.g. they have more panicle nodes (character 2) (Figs. 6 and 9).

Within its natural distribution range, *A. aristatum* is highly variable morphologically (Pimentel Pereira *et. al* 2007a; Pimentel *et al.* 2010). Morphological variation of *A. aristatum* within its secondary distribution range is reflected mostly in differences in panicle length (1), number of panicle nodes (2), length of panicle internodes, length of spikelets, length and width of glumes, palea and lemma in sterile floret, and their awns. These characters distinguish between populations from fields (A), fallows (F), and field roadsides (AR). Extreme values of these characters in many populations overlap, so on their basis it is impossible to distinguish morphotypes characteristic of individual habitats. Similar results were reported in an earlier study (Drapikowska *et al.* 2012a).

A. aristatum is classified in Poland as an invasive species (Latowski 2005; Tokarska-Guzik 2005). One theory assumes that invasive species are characterized by high genetic variability, higher in the colonized areas than in populations from the natural range (Lavergne & Molofsky 2007). This is associated with selection pressure, which conditions the evolution of competitive features, allowing them to outcompete native plants. Many models have been developed to investigate the causes of success of invasive plants (e.g. Blossey & Nötzold 1995). The evolution of increased competitive ability (EICA) hypothesis suggests that the competitiveness of invasive species is stimulated by contact with native species. Skrajna and Skrzypczyńska (2007) reported that variation in reproductive characters (e.g. panicle length) of *A. aristatum* is correlated with habitat type. Results of the present study show that panicle length is variable and the longest panicles were found in populations on field roadsides (AR). Besides, populations from arable fields were distinct morphologically, mostly because of the presence of many competing species in rye fields (Skrajna & Skrzypczyńska 2007). As reported by Latowski (2005), these populations are characterized by a higher viability of seeds, which are able to germinate even after 18 years.

The pattern of variation of *A. aristatum* could be also affected by the fact that it has been accidentally introduced to Poland from 2 sources: northern and southern (Tokarska-Guzik 2005). This type of variation has been observed also in *Hordeum murinum* (Mizianty 2006). PCA (Fig. 17) and cluster analysis (Fig. 18) for individual populations did not reveal any tendency to form groups of geographically close populations. Within its natural range, *A. aristatum* occupies habitats varying in fertility from oligotrophic to mesotrophic (Djebaili 1990; Fernández-Moya *et al.* 2010; Pimentel *et al.* 2010), from ruderal and segetal sites to mountain grasslands at 600 m (original observations). Within its

secondary range, *A. aristatum* grows on oligotrophic fields but also on sandy grasslands, roadsides, fallows, and wastelands (Ryves *et al.* 1996; Niemann & Zwerger 2006). In Poland it is found mostly on poor arable fields (class 6, poor rye complex; and class 7, very poor rye complex) (Latowski 2005), sandy grasslands, and roadsides (Korniak 1992; Skrajna & Skrzypczyńska 2007). It is rarer in open pine, birch, and pine-oak forests, on former arable fields, at the forest-field border, and on sandy forest roads and their sides (Woziwoda 2006).

The analysed habitats of *A. aristatum* differ in soil parameters. PCA shows distinct properties of soils on fallows (F), sandy grasslands near pine forests (fG), and partly also on field roadsides (AR) (see Fig. 23). Taking into account detailed data, it should be noted that soils were very acidic in fields, field roadsides, and grasslands (pG, fG, and aG), whereas fallows were slightly acidic. Phosphorus, potassium, and total nitrogen content of the studied soils were low in all samples, as compared with their threshold values reported by Ostrowska et al. (1991). Values of C/N ratio varied, mostly between 10 and 20 (Fig. 21). According to Thompson and Troeh (1978), C/N ratio in a majority of soils in the humus horizon ranges from 8 to 15, most often 10-12. Presence of nutrients in the soil affects vegetative characters (Crick & Grime 2006; Ławniczak *et al.* 2009, 2011). Results of this study show a correlation between some soil parameters and reproductive characters. Total nitrogen content is positively correlated with 6 characters: the no. of spikelets on second uppermost panicle branch (9), lower glume length (14), lower glume width (15), upper glume width (17), palea length in sterile floret (18), and palea awn length from knee in sterile floret (20), assimilable potassium content affects the number of panicle nodes (2) and panicle length (1) whereas pH and assimilable phosphorus content partly affects fourth and fifth panicle internode length (6 and 7) (see Fig. 24). *Anthoxanthum aristatum* outside natural ecosystems (primary range of distribution) shows an ability to colonize various secondary habitats, markedly deviating from those occupied by the species originally. This probably results from the high polymorphism observed in this study within populations of *A. aristatum*, which attests to a high plasticity of the species. It may be a cause of its expansion onto new anthropogenic sites, e.g. more fertile fields (Kapeluszny & Haliniarz 2010; Skrzypczyńska *et al.* 2010). The process of expansion of *A. aristatum* and colonization of new ecological niches has been observed in Poland for only several decades, so it cannot be expected that microevolutionary processes within such a short time would allow selection of stable genotypes characteristic of different ecological niches.

Anthoxanthum odoratum is a tetraploid (2n = 20) species recorded in lowlands, in the submontane zone, and in the lower montane zone. By contrast, *A. alpinum* is a diploid (2n = 10), found in the alpine and subalpine zone, very rare in lower parts of mountains, in the upper montane zone (Filipová & Krahulec 2006; Drapikowska *et al.* 2012b). Relationships between these 2 species have been discussed for many years. Allopolyploid origin of *A. odoratum*, probably deriving from *A. alpinum* and *A. ovatum* was reported already long ago by Jones (1964) and Hedberg (1986). The existence of a contact zone between *A. odoratum* and *A. alpinum* results from the spread of *A. odoratum* and *A. alpinum* due to global warming after the last glaciation. A contact zone of both species may be created also currently as a result of human interference, e.g. deforestation and expansion of pastures (Felber-Girard *et al.* 1996). Biometric analysis of samples collected along the altitudinal transect confirmed the existence of 2 morphological types classified as 2 species: *A. odoratum* and *A. alpinum*. They differ primarily in panicle length, as reported also by Bogenrieder *et al.* (1993), but also in upper glume length and palea length in sterile floret, whereas values of the other characters show continuous variation in both morphological species. A morphological study of populations of both species from the Iberian Peninsula and Scandinavia (Pimentel & Sahuquillo 2008), has also revealed continuous variation of morphological characters in the *A. odoratum-A. alpinum* complex. Diagnostic characters given by some authors, e.g. plant height, leaf colour, hairs on palea and lemma in sterile floret, or caryopsis length (Teppner 1969; Felber 1993; Rostański 1996), after the analysis of a large number of specimens have proved to be highly variable, so they are not useful for identification of both taxa.

This study shows continuous variation in anatomical features of stems and leaves in the 2 taxa. They differ only in stomatal length, which is correlated with their ploidy (Drapikowska *et al.* 2013). In the Babia Góra massif the contact zone between *A. odoratum* and *A. alpinum* is very narrow. In the upper montane zone, which is the potential contact zone of both species, the collected sample included exclusively individuals classified as *A. alpinum* on the basis of morphological characters of panicles and isoenzymatic markers (Drapikowska 2013) and comparative analyses of genome size of individual plants by flow cytometry (see Fig. 28). Flow cytometry is successfully used to assess ploidy level, e.g. in *Dactylis glomerata* (Vilhar *et al.* 2002). However, earlier research revealed coexistence of both vicariants at this altitude (Drapikowska *et al.* 2012b). The retreat of *A. odoratum* from this altitude probably results from reconstruction of the tourist trail, which caused removal of infrequent individuals of *A. odoratum* growing along the tourist trail. Altitudinal ranges of both species only slightly overlap (Mirek & Piękoś-Mirkowa 2005, 2007). This is due to e.g. different environmental requirements of these 2 taxa

(Thompson & Lumaret 1992; Felber-Girard *et al*. 1996). *A. alpinum* tolerates low temperatures under the long-lasting snow cover. Within the altitudinal range of *A. odoratum* in lower parts of mountains, *A. alpinum* does not survive, as a result of strong competition from *A. odoratum* as well as other lower montane species. In contrast, *A. odoratum* does not flower in higher parts of mountains, so it does not produce seeds and thus is not capable of generative reproduction, which dominates in this species (Flegerová & Krahulec 1999; Stančić 2005).

Studies conducted by Borrill (1963) and Jones (1964) showed that triploid hybrids between these species in the wild are probable but unlikely. In the French and Swiss Alps, some tetraploid cytotypes were found in populations of *A. alpinum* and triploid ones in populations of *A. odoratum* (Hedberg 1986; Felber *et al*. 1996). Among plants analysed in respect of morphology and isoenzymes (Drapikowska 2013), no individuals were of hybrid origin. This is linked primarily with the existence of barriers to gene flow and differences in flowering time between these species (Felber 1988).

A. alpinum is more abundant on southern slopes, but is less dependent on slope orientation than *A. odoratum* (Filipová & Krahulec 2006). However, *A. odoratum* has a wider ecological amplitude than its diploid relative (Felber-Girard *et al.* 1996). The analysis of soils from sites along the altitudinal transect in the Babia Góra massif on the northern slope revealed variation between populations in respect of the analysed parameters. Soils from the altitude of 806 and 883 m, within the lower montane zone, differed from upper montane, subalpine, and alpine samples in cation-exchange capacity (CEC), pH, total nitrogen (N), humus content, and organic carbon (C). On Przełęcz Brona (a mountain pass), in grassland at 1413 m, phosphorus content (P) and total potassium (K) were higher than at the other sites. Subalpine meadows dominated by matgrass (*Nardus stricta*), with deeply leached soils, are an optimum habitat type for *A. alpinum* (Stančić 2005). Besides, the latter species prefers moderately moist to moderately dry soils, well aerated, poor in nutrients, with a high humus content. In an earlier study of upper montane soils in the Babia Góra massif at 1350 m (Stachurska-Swakoń & Kuź 2011), values higher than in this study were recorded: organic carbon (C) 30.4 g/100g, humus 52%, potassium (K) 32.2 mg/100g, and phosphorus (P) 17.6 mg/100g. In the present study in the upper montane zone (1166 m), the level of phosphorus (P) was moderate, 0.6 mg/100g, and bioavailable potassium (K) reached 6.1 mg/100g, whereas values of pH and cation-exchange capacity were similar. The observed differences in soil conditions of *A. odoratum* and *A. alpinum* along the transect partly determined the occurrence of both species. However, other factors played a decisive role, e.g. climate, slope exposure, and interspecific competition (Filipova & Krahulec 2006). Felber-Girard *et al.* (1996) reported that both cytotypes can successfully grow on sites occupied by the other taxon. Climate change can influence changes in altitudinal ranges of mountain plants. This process is caused by global warming. Changes of this type were also observed in *A. alpinum*, which during the last 100 years expanded its altitudinal range in the Alps by 190 m (Frei *et al.* 2010).

5. Conclusions

- *Anthoxanthum odoratum* is characterized by high morphological and anatomical variation of lowland populations in natural habitats as well as in those transformed by human activity. The phase of ecological expansion of this species is not correlated with the observed morphological variation.
- Most distinct morphologically were the populations of *Anthoxanthum odoratum* collected on field roadsides (AR).
- Montane populations of *Anthoxanthum odoratum* have a larger number of panicle nodes than lowland populations.
- *Anthoxanthum aristatum* is characterized by morphological and anatomical variation, which is only weakly correlated with the phase of chorological expansion.
- The native *Anthoxanthum odoratum* and the alien *A. aristatum* differ morphologically in panicle length, length of panicle internodes, length and wih of upper and lower glumes, lemma awn length in sterile floret, as well as palea and lemma length.
- In sympatric populations of *Anthoxanthum odoratum* and *A. aristatum*, on the basis of structural characters, no potential interspecific hybrids were found.
- *Anthoxanthum alpinum* varies morphologically along the altitudinal transect, with marked differences between upper montane populations and both alpine and subalpine populations.
- *Anthoxanthum alpinum* and *A. odoratum* – altitudinal vicariants – differ morphologically in panicle length, first panicle internode length, spikelet length on second uppermost panicle branch, and number of spikelets on the middle panicle branch.
- In the contact zone of both species, no potential interspecific hybrids were found on the basis of morphological characters.
- Anatomical features of stems and leaves are characterized by continuous variation in these 2 taxa.
- *Anthoxanthum odoratum* has longer stomata than *A. alpinum* and *A. aristatum*.

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Appendix 1. Collection sites of *Anthoxanthum odoratum*, *A. alpinum*, and *A. aristatum* samples

Site no.	Locality, part of Poland	Geographical location (GPS)	Habitat type (relevé no. – see Appendix 2)	Habitat abbr.	Collection date
		Anthoxanthum odoratum			
1	Jasionna I, Noteć Forest, W Poland	52°46'42.6"N 16°27'05.5"E	pine forest (6)	PF	21.05.2008
2	Jasionna II, Noteć Forest, W Poland	52°46'05.6"N 16°27'59.3"E	dry meadow (7)	DM	21.05.2008
3	Jasionna III, Noteć Forest, W Poland	52°46'39.6"N 16°26'35.8"E	sandy grassland near pine forest plantation (8)	pG	21.05.2008
4	Jasionna IV, Noteć Forest, W Poland	52°46'39.8"N 16°26'35.3"E	roadside in pine forest	FR	21.05.2008
5	Torzym I, Rzepin Forest, W Poland	52°15'52.7"N 15°03'36.7"E	roadside in pine forest (10)	FR	29.05.2008
6	Torzym II, Rzepin Forest, W Poland	52°15'51.2"N 15°03'43.1"E	roadside in pine forest (11)	FR	29.05.2008
7	Debrznica I, Rzepin Forest, W Poland	52°14'27.6"N 15°02'28.4"E	moist meadow (13)	MM	29.05.2008
8	Chlebowo I, Noteć Forest, W Poland	52°44'39.5"N 16°45'59.3"E	field roadside	AR	17.05.2007
9	Chlebowo II, Noteć Forest, W Poland	52°44'17.8"N 16°46'50.6"E	roadside in pine forest	FR	17.05.2007
10	Chlebowo III, Noteć Forest, W Poland	52°44'01.3"N 16°46'43.3"E	roadside in pine forest	FR	17.05.2007
11	Chlebowo IV, Noteć Forest, W Poland	52°43'45.2"N 16°46'37.8"E	dry meadow	DM	17.05.2007
12	Campus Morasko I, Poznań, W Poland	52°28'11.0"N 16°55'12.4"E	moist meadow (25)	MM	12.05.2008
13	Nowa Tuchorza, Nowy Tomyśl Sandur, W Poland	52°12'29.2"N 16°04'31.9"E	pine forest plantation (1)	PP	14.05.2008
14	NW of Ruchocki Młyn, Nowy Tomyśl Sandur, W Poland	52°10'58.9"N 16°05'05.1"E	pine forest (2)	PF	14.05.2008
15	Ruchocki Młyn I, Nowy Tomyśl Sandur, W Poland	52°09'22.8"N 16°06'28.1"E	moist meadow (3)	MM	14.05.2008
16	Ruchocki Młyn II, Nowy Tomyśl Sandur, W Poland	52°09'22.0"N 16°06'25.5"E	moist edge of pine forest (4)	EF	14.05.2008
17	Chorzemin, Nowy Tomyśl Sandur, W Poland	52°09'10.7"N 16°06'49.9"E	roadside in pine forest	FR	14.05.2008
18	Campus Morasko II, Poznań, W Poland	52°28'03.8"N 16°55'36.4"E	sandy grassland near pine forest plantation (26)	pG	07.05.2008
19	Campus Morasko III, Poznań, W Poland	52°28'08.0"N 16°55'33.8"E	pine forest plantation (27)	PP	12.05.2008
20	Debrznica II, Rzepin Forest, W Poland	52°14'28.9"N 15°02'27.3"E	sandy grassland near pine forest plantation (14)	pG	29.05.2008
21	Leszkowice I, E Poland	51°33'34.0"N 22°37'15.7"E	roadside in pine forest (24)	FR	29.05.2009
22	Leszkowice II, E Poland	51°33'31.5"N 22°37'20.6"E	pine forest	PF	29.05.2009
23	Siemień, E Poland	51°37'28.8"N 22°44'46.2"E	dry meadow (25)	DM	29.05.2009
24	Wandzin I, E Poland	51°23'53.0"N 22°38'04.0"E	wasteland (21)	W	29.05.2009
25	Wandzin II, E Poland	51°23'53.7"N 22°38'01.2"E	dry meadow (22)	DM	29.05.2009
26	Sokolniki Powidzkie, W Poland	51°23'53.7"N 22°38'01.2"E	sandy grassland near pine forest plantation (30)	pG	01.06.2010
27	Piła, W Poland	53°09'11.0"N 16°40'55.7"E	dry meadow (29)	DM	25.05.2011
28	Campus Morasko IV, Poznań, W Poland	52°28'04.8"N 16°55'36.8"E	reed-grass oak forest	OF	20.05.2011
29	Babia Góra IV, S Poland	49°36'33.5"N 19°29'51.2"E	lower montane meadow	LM	10.06.2011

Site no.	Locality, part of Poland	Geographical location (GPS)	Habitat type (relevé no. – see Appendix 2)	Habitat abbr.	Collection date
30	Storkowo, NW Poland	53°46'09.2"N 16°29'23.3"E	wasteland (28)	W	25.09.2010
31	Jasiony, E Poland	53°02'56.7"N 19°43'21.8"E	pine forest (34)	PF	06.07.2011
32	Borucza, E Poland	52°19'55.5"N 21°34'18.2"E	pine forest (33)	PF	06.07.2011
33	Zawoja I, Babia Góra, S Poland	49°36'46.9"N 19°31'05.1"E	submontane ruderal roadside	SR	02.06.2008
34	Zawoja II, Babia Góra, S Poland	49°37'06.6"N 19°30'49.0"E	lower montane meadow (15)	ML	02.06.2008
35	Zawoja III, Babia Góra, S Poland	49°36'33.5"N 19°29'51.2"E	lower montane meadow (16)	LM	02.06.2008
36	Babia Góra I, S Poland	49°36'23.9"N 19°29'31.5"E	lower montane forest roadside	LR	02.06.2008
37	Babia Góra II, S Poland	49°35'49.6"N 19°29'12.7"E	lower montane meadow	LM	02.06.2008
		Anthoxanthum aristatum			
38	Nowa Tuchorza I, Nowy Tomyśl Sandur, W Poland	52°12'24.2"N 16°04'38.3"E	arable field	A	14.05.2008
39	Wrzeszczyna II, Noteć Forest, W Poland	52°52'16.9"N 16°14'48.2"E	sandy grassland near pine forest plantation	pG	21.05.2008
40	Gęstowice I, Rzepin Forest, W Poland	52°09'32.3"N 14°53'20.7"E	fallow (12)	F	29.05.2008
41	Gęstowice II, Rzepin Forest, W Poland	52°09'38.8"N 14°53'29.5"E	sandy grassland near pine forest	fG	29.05.2008
42	Wrzeszczyna I, Noteć Forest, W Poland	52°52'08.6"N 16°14'41.3"E	arable field (9)	A	21.05.2008
43	Wandzin III, E Poland	51°23'52.8"N 22°38'04.8"E	arable field (23)	A	29.05.2009
44	Antoniówka I, Kozienice Forest, E Poland	51°25'54.3"N 21°17'33.0"E	arable field	A	28.05.2009
45	Chlebowo V, Noteć Forest, W Poland	52°44'51.4"N 16°45'59.8"E	arable field	A	17.05.2007
46	Chlebowo VI, Noteć Forest, W Poland	52°44'51.4"N 16°45'59.8"E	sandy grassland near pine forest	fG	17.05.2007
47	Chlebowo VII, Noteć Forest, W Poland	52°44'51.4"N 16°45'59.8"E	field roadside	AR	17.05.2007
48	Chlebowo VIII, Noteć Forest, W Poland	52°44'51.4"N 16°45'59.8"E	sandy grassland near arable field	aG	17.05.2007
49	Gęstowice II, Rzepin Forest, W Poland	52°09'38.8"N 14°53'29.5"E	sandy grassland near pine forest	fG	29.05.2008
50	Połęcko, Rzepin Forest, W Poland	52°03'27.8"N 14°53'56.4"E	fallow (31)	F	08.06.2011
51	Przytoka, E Poland	52°11'52.1"N 21°45'06.9"E	arable field (32)	A	05.07.2011
52	Antoniówka II, Kozienice Forest, E Poland	51°25'59.9"N 21°17'26.0"E	arable field (20)	A	28.05.2009
53	Barłożnia, Nowy Tomyśl Sandur, W Poland	52°09'27.0"N 16°07'30.7"E	sandy grassland near arable field (5)	aG	14.05.2008
54	Nowa Tuchorza II, Nowy Tomyśl Sandur, W Poland	52°12'28.0"N 16°04'33.5"E	sandy grassland near pine forest plantation	pG	14.05.2008
		Anthoxanthum alpinum			
55	Diablak (1697 m), Babia Góra, S Poland	49°34'19.3"N 19°31'48.4"E	alpine grassland (17)	AG	03.06.2008
56	Przełęcz Brona (1413 m), Babia Góra, S Poland	49°34'53.1"N 19°30'36.3"E	subalpine matgrass meadow (18)	SM	03.06.2008
57	Babia Góra III (1432 m), S Poland	49°34'49.0"N 19°30'43.4"E	subalpine grassland near trail	SG	03.06.2008
58	Markowe Szczawiny (1166 m), Babia Góra, S Poland	49°35'21.6"N 19°31'06.9"E	upper montane forest glade (19)	UG	03.06.2008

Appendix 2. Phytosociological relevés

Relevé 1. (Z.C., P.Sz. 14.05.2008 r.). Density of layer a – 60%, layer b<5%, coverage of layer c – 70%, layer d – 50%; the relevé area – 100 m^2; number of species – 16. *Pinus sylvestris* a 3.3, *Betula pendula* a 2.2; *Acer pseudoplatanus* b +, *Frangula alnus* b +, *Padus serotina* b +, *Quercus robur* b +, *Sorbus aucuparia* b +; ***Anthoxanthum odoratum* c 3.3**, *Carex digitata* c +, *Rumex acetosella* c +, *Dryopteris carthusiana* c +, *Hieracium murorum* c +, *Hieracium pilosella* c +, *Brachypodium sylvaticum* c r, *Melampyrum pratense* c r, *Veronica officinalis* c r; *Musci* d 5.5.

Relevé 2. (Z.C., P.Sz. 14.05.2008 r.). Density of layer a 50%, layer b 10%, coverage of layer c 80%, layer d 80%; the relevé area 100 m^2; number of species – 18. *Pinus sylvestris* a 4.4; *Frangula alnus* b 1.1, *Betula pendula* b +, *Pinus sylvestris* b +; *Vaccinium myrtillus* c 3.3, *Festuca ovina* c 2.2, *Pteridium aquilinum* c 2.2, ***Anthoxanthum odoratum* c 1.1**, *Deschampsia flexuosa* c 1.1, *Calluna vulgaris* c +, *Hieracium pilosella* c +, *Melampyrum pratense* c +, *Rumex acetosella* c +, *Vaccinium vitis-idaea* c +, *Padus serotina* c r, *Quercus robur* c r, *Scorzonera humilis* c r, *Sorbus aucuparia* c r; *Musci* d 5.5.

Relevé 3. (Z.C., P.Sz. 14.05.2008 r.). Coverage of layer c 75%, layer d 60%; the relevé area 50 m^2; number of species – 15. ***Anthoxanthum odoratum* c 3.3**, *Hydrocotyle vulgaris* c 2.2, *Ranunculus flamula* c 2.2, *Agrostis stolonifera* c 1.1, *Alnus glutinosa* c +, *Caltha palustris* c+, *Carex fusca* c +, *Carex rostrata* c +, *Equisetum fluviatile* c +, *Galium palustre* c +, *Ranunculus acris* c +, *Ranunculus repens* c +, *Betula pubescens* c r, *Cardamine pratensis* c r; *Musci* d 4.4.

Relevé 4. (Z.C., P.Sz. 14.05.2008 r.). Coverage of layer c 80%, layer d>1%; the relevé area 50 m^2; number of species – 24. *Holcus lanatus* c 3.3, ***Anthoxanthum odoratum* c 2.2**, *Avenastrum pubescens* c 1.1, *Cirisum palustre* c 1.1, *Filipendula ulmaria* c 1.1, *Ranunculus acris* c 1.1, *Ajuga genevensis* c +, *Carex hirta* c +, *Geum rivale* c +, *Hydrocotyle vulgaris* c +, *Lotus uliginosus* c +, *Poa pratensis* c +, *Rumex acetosa* c +, *Veronica chamaedrys* c +, *Bromus hordaceus* c r, *Cardamine pratensis* c r, *Cerastium holosteoides* c r, *Fragaria vesca* c r, *Galium mollugo* c r, *Luzula pilosa* c r., *Plantago lanceolata* c r, *Taraxacum officinale* c r, *Urtica dioica* c r, *Viola canina* c r; *Musci* d +.

Relevé 5. (Z.C., P.Sz. 14.05.2008 r.). Coverage of layer c 50%, layer d>1%; the relevé area 5 m^2; number of species – 11. *Hieracium pilosella* c 3.3, *Agrostis capillaris* c 1.1, *Elymus repens* c 1.1., *Festuca rubra* c 1.1, ***Anthoxanthum aristatum* c +**, ***Anthoxanthum odoratum* c +**, *Cerastium holosteoides* c r, *Quercus robur* c r, *Spergula morisonii* c r, *Teesdalea nudicaulis* c r; *Musci* d r.

Relevé 6. (Z.C., P.Sz. 21.05.2008 r.). Density of layer a 60%, layer b 20%, coverage of layer c 20%, layer d 100%; the relevé area 100 m^2; number of species – 20. *Pinus sylvestris* a 4.5; *Juniperus communis* b 2.2, *Frangula alnus* b +, *Padus serotina* c r, *Sorbus aucuparia* c r; *Deschampsia flexuosa* c 2.3, ***Anthoxanthum odoratum* c 1.1**, *Calluna vulgaris* c +, *Dryopteris carthusiana* c +, *Dryopteris filix-mas* c +, *Fragaria vesca* c +, *Hieracium pilosella* c +, *Orthilia secunda* c +, *Trientalis europaea* c +, *Vaccinium myrtillus* c +, *Vaccinium vitis-idaea* c +, *Pinus sylvestris* c r, *Quercus robur* c r, *Scorzonera humilis* c r, *Veronica officinalis* c r; *Musci* d 5.5.

Relevé 7. (Z.C., P.Sz. 21.05.2008 r.). Coverage of layer c 85%, layer d>1%; the relevé area 100 m^2; number of species – 20. ***Anthoxanthum odoratum* c 2.3**, *Holcus lanatus* c 2.3, *Deschampsia caespitosa* c 2.2, *Potentilla anserina* c 2.2, *Poa pratensis* c 2.2, *Alopecurus pratensis* c 1.1, *Cardamine pratensis* c 1.1, *Potentilla reptans* c 1.1, *Carex hirta* c +, *Cerastium holosteoides* c +, *Ranunculus acris* c +, *Rumex acetosa* c +, *Stellaria graminea* c +, *Cirsium arvense* c r, *Cirsium palustre* c r, *Festuca rubra* c r, *Lychnis flos-cuculi* c r, *Veronica chamaedrys* c r, *Vicia cracca* c r, *Viola palustris* c r; *Musci* d +.

Relevé 8. (Z.C., P.Sz. 21.05.2008 r.). Coverage of layer c 60%, layer d 80%; the relevé area 40 m^2; number of species – 10. ***Anthoxanthum odoratum* c 3.3**, *Veronica officinalis* c 2.1, *Teesdalea nudicaulis* c 1.1, *Festuca ovina* c +, *Hieracium pilosella* c +, *Pinus sylvestris* c +, *Rumex acetosella* c +, *Betula pendula* c r, *Carex pilulifera* c r, *Vincetoxicum officinale* c r; *Musci* d 4.5.

Relevé 9. (Z.C., P.Sz. 21.05.2008 r.). *Secale cereale* c 4.4. Coverage of layer c 50%; the relevé area 10 m^2; number of species – 13. ***Anthoxanthum aristatum* c 3.3**, *Scleranthus annus* c 2.2, *Arabidopsis thaliana* c 1.1, *Teesdalea nudicaulis* c 1.1, *Erophila verna* c +, *Myosotis stricta* c +, *Spergula morisonii* c +, *Viola arvensis* c +, *Aphanes arvensis* c r, *Centaurea cyanus* c r, *Cirsium arvense* c r, *Papaver argemone* c r, *Veronica triphyllos* c r.

Relevé 10. (Z.C., P.Sz. 29.05.2008 r.). Density of layer b>5%, coverage of layer c 40%, layer d 95%; the relevé area 20 m^2; number of species – 21. *Pinus sylvestris* b 1.1; ***Anthoxanthum odoratum* c 2.2**, *Deschampsia flexuosa* c 2.3, *Festuca ovina* c 2.2, *Hieracium pilosella* c 1.1, *Achillea millefolium* c +, *Calamagrsotis epigejos* c +, *Helichrysum arenarium* c +, *Poa pratensis* c +, *Rumex acetosella* c +, *Vaccinium myrtillus* c +, *Vaccinium vitis-idaea* c +, *Carex hirta* c r, *Cirsium arvense* c r, *Cerastium holosteoides* c r, *Euphorbia cyparissians* c r, *Lotus corniculatus* c r, *Plantago major* c r, *Taraxacum officinale* c r, *Veronica officinalis* c r, *Viola tricolor* c r; *Musci* d 5.5.

Relevé 11. (Z.C., P.Sz. 29.05.2008 r.). Density of layer b 5%, coverage of layer c 70%; the relevé area 20 m^2; number of species – 25. *Padus serotina* b 1.1; ***Anthoxanthum odoratum* c 2.2**, *Dactylis glomerata* c 2.2, *Deschampsia flexuosa* c 2.2, *Achillea millefolium* c 1.1, *Elymus repens* c 1.1, *Veronica chamaedrys* c 1.1, *Agrostis capillaris* c +, *Carex hirta* c +, *Cerastium holosteoides* c +, *Festuca ovina* c +, *Hieracium pilosella* c +, *Knautia arvensis* c +, *Luzula pilosa* c +, *Poa pratensis* c +, *Rumex acetosella* c +, *Arenaria serpyllifolia* c r, *Corynephorus canescens* c r, *Plantago major* c r, *Potentilla argentea* c r, *Rubus caesius* c r, *Senecio sylvaticus* c r, *Stellaria graminea* c r, *Viola canina* c r, *Viola tricolor* c r.

Relevé 12. (Z.C., P.Sz. 29.05.2008 r.). Coverage of layer c 80%; the relevé area 25 m^2; number of species – 15. ***Anthoxanthum aristatum* c 3.3**, *Rumex acetosella* c 3.3, *Conyza canadensis* c 1.1, *Secale cereale* c 1.1, *Myosotis stricta* c 1.1, *Arabidopsis thaliana* c +, *Papaver argemone* c +, *Senecio vernalis* c +, *Viola arvensis* c +, *Agrostemma githago* c r, *Hypericum perforatum* c r, *Hypochoeris radicata* c r, *Matricaria maritima* subsp *inodora* c r, *Raphanus raphanistrum* c r, *Vicia angustifolia* c r.

Relevé 13. (Z.C., P.Sz. 29.05.2008 r.). Coverage of layer c 100%, layer d 5%; %; the relevé area 100 m^2; number of species – 23. *Geum rivale* c 3.3, *Avenula pubescens* c 2.2, *Carex nigra* c 2.2, *Juncus effuses* c 2.2, *Ranunculus acris* c 2.2, *Holcus lanatus* c 1.2, ***Anthoxanthum odoratum* c 1.1**, *Carex gracilis* c 1.1, *Filipendula ulmaria* c 1.1, *Poa trivialis* c 1.1, *Rumex acetosa* c 1.1, *Angelica sylvestris* c +, *Cerastium holosteoides* c +, *Cirsium oleraceum* c +, *Equisetum palustre* c +, *Festuca rubra* c +, *Lotus uliginosus* c +, *Lychnis flos-cuculi* c +, *Veronica chamaedrys* c +, *Cardamine pratensis* c r, *Cirsium palustre* c r, *Galium uliginosum* c r, *Plantago media* c r; *Musci* d 1.1.

Relevé 14. (Z.C., P.Sz. 29.05.2008 r.). Coverage of layer c 100%; the relevé area 25 m^2; number of species – 18. *Helichrysum arenarium* c 3.3, ***Anthoxanthum odoratum* c 2.2**, *Hieracium pilosella* c 2.2, *Poa angustifolia* c 2.2, *Rumex acetosa* c 2.2, *Veronica chamaedrys* c 1.1, *Achillea millefolium* c +, *Arrhenatherum elatius* c +, *Cerastium semidecandrum* c +, *Festuca rubra* c +, *Holcus lanatus* c +, *Armeria martima* subsp. *elongata* c r, *Luzula campestris* c r, *Plantago lanceolata* c r, *Potentilla argentea* c +, *Rumex acetosella* c r, *Vicia angustifolia* c r, *Vicia hirsuta* c r.

Relevé 15. (Z.C., P.Sz. 2.06.2008 r.). 653 m a.s.l. Coverage of layer c 90%, layer d>1%; the relevé area 25 m^2; number of species – 21. *Alopecurus pratensis* c 2.2, ***Anthoxanthum odoratum* c 2.2**, *Dactylis glomerata* c 2.2, *Ranunculus acris* c 2.2., *Veronica chamaedrys* c 2.1, *Alchemilla* sp. 1.1, *Hypericum maculatum* c 1.1, *Ranunculus repens* c 1.1, *Plantago lanceolata* c +.2, *Aegopodium podagraria* c +, *Cerastium holosteoides* c +, *Cruciata glabra* c +, *Festuca rubra* c +, *Poa pratensis* c +, *Rhinanthus serotinus* c +, *Trifolium pratense* c +, *Rumex acetosa* c r, *Leondodon hispidus* c r, *Poa trivialis* c r, *Taraxacum officinale* c r, *Viola arvensis* c r; *Musci* d +.

Relevé 16. (Z.C., P.Sz. 2.06.2008 r.). 692 m a.s.l. Coverage of layer c 90%, layer d>1%; the relevé area 25 m^2; number of species – 15. ***Anthoxanthum odoratum* c 2.2**, *Poa pratensis* 2.2, *Ranunculus acris* c 2.2., *Veronica chamaedrys* c 2.2, *Festuca pratensis* c 1.1, *Rumex acetosa* c 1.1, *Alchemilla* sp. +, *Hypericum maculatum* c +, *Leondodon hispidus* c +, *Luzula campestris* c +, *Dactylis glomerata* c +, *Plantago lanceolata* c +, *Pimpinella saxifraga* c r, *Taraxacum officinale* c r, *Trisetum flavescens* c r; *Musci* d +.

Relevé 17. (Z.C., P.Sz. 3.06.2008 r.). 1697 m a.s.l. Coverage of layer c 90%, layer warstwy d <5%; the relevé area 12 m^2; number of species – 9. *Deschampsia flexuosa* c 4.4, *Nardus stricta* c 2.3, *Potentilla aurea* c 2.2, *Vaccinium vitis-idaea* c 2.1., *Vaccinium myrtillus* c 1.2, ***Anthoxanthum alpinum* c 1.1**, *Mutellina purpurea* c 1.1, *Campanula rotundifolia* c +.2, *Solidago alpestris* c +; *Musci* d 1.1.

Relevé 18. (Z.C., P.Sz., 3.06.2008 r.). 1413 m a.s.l. Coverage of layer c 100%, layer d <1%; the relevé area 16 m^2; number of species – 8. *Nardus stricta* c 5.5, *Deschampsia flexuosa* c 1.3, *Homogyne alpina* 1.1, *Luzula alpino-pilosa* c 1.1, *Polygonum bistorta* c 1.1, *Vaccinium myrtillus* c 1.1, ***Anthoxanthum alpinum* c +**, *Carex nigra* c +; *Musci* d +.

Relevé 19. (Z.C., P.Sz. 3.06.2008 r.). 1166 m a.s.l. Coverage of layer c 90%, layer d <1%; the relevé area 10 m^2; number of species – 12. *Festuca rubra* c 3.3, *Vaccinium myrtillus* c 3.3, ***Anthoxanthum alpinum* c 1.1**, *Athyrium alpestre* c +, *Cruciata glabra* c +, *Homogyne alpina* c +, *Luzula campestris* c +, *Luzula luzulina* c +, *Picea abies* juv. c +, *Gentiana asclepiadea* c r, *Rumex alpinus* c r, *Veratrum lobelianum* c r; *Musci* d +.

Relevé 20. (Z.C., P.Sz. 28.05.2009 r.). *Secale cereale* c 3.3. Coverage of layer c 90%; the relevé area 9 m^2; number of species – 4. ***Anthoxanthum aristatum* c 5.5**, *Scleranthus annus* c 1.1, *Anthemis arvensis* c r, *Arnoseris minima* c r.

Relevé 21. (Z.C., P.Sz. 29.05.2009 r.). Coverage of layer c 100%, layer d<1%; the relevé area 9 m^2; number of species – 16. *Hieracium pilosella* c 5.5, ***Anthoxanthum odoratum* c 2.2**, *Luzula campestris* c +, *Poa pratensis* c +, *Artemisia campestris* c r, *Campanula patula* c r, *Equisetum arvense* c r, *Holcus lanatus* c r, *Hypericum perforatum* c r, *Pimpinella saxifaga* c r, *Pinus sylvestris* juv. c r, *Solidago canadensis* c r, *Stellaria graminea* c r, *Veronica officinalis* c r, *Vicia angustifolia* c r; *Musci* d +.

Relevé 22. (Z.C., P.Sz. 29.05.2009 r.). Coverage of layer c 100%; the relevé area 16 m^2; number of species – 19. *Holcus lanatus* c 3.3, *Poa pratensis* c 3.3, *Trifolium repens* c 3.3, ***Anthoxanthum odoratum* c 2.2**, *Arrhenatherum elatius* c 1.1, *Achillea millefolium* c +, *Cerastium holosteoides* c +, *Leucanthemum vulgare* c +, *Plantago lanceolata* c +, *Rumex acetosa* c +, *Trifolium dubium* c +. *Trifolium pratense* c +, *Campanula patula* c r, *Cardaminopsis arenosa* c r, *Dactylis glomerata* c r, *Galium verum* c r, *Medicago lupulina* c r, *Ranunculus acris* c r, *Taraxacum officinale* c r.

Relevé 23. (Z.C., P.Sz. 29.05.2009 r.). *Secale cereale* c 4.4. Coverage of layer c 80%; the relevé area 10 m^2; number of species – 8. ***Anthoxanthum aristatum* c 4.4**, *Viola arvensis* c 2.2, *Convolvulus arvensis* c 1.1, *Centaurea cyanus* c +, *Galium aparine* c +, *Anthemis arvensis* c r, *Veronica arvensis* c r, *Vicia angustifolia* c r.

Relevé 24. (Z.C., P.Sz. 29.05.2009 r.). Coverage of layer c 40%, layer d 50%; the relevé area 9 m^2; number of species – 10. ***Anthoxanthum odoratum* c 3.3**, *Melampyrum pratense* c 1.1, *Festuca ovina* c 1.1, *Luzula campestris* c 1.1, *Hieracium pilosella* c +, *Poa pratensis* c +, *Juniperus communis* juv. c r, *Pinus sylvestris* juv. c r, *Quercus robur* juv. c r, Musci d 4.4.

Relevé 25. (Z.C., P.Sz. 29.05.2009 r.). Coverage of layer c 100%; the relevé area 10 m^2; number of species – 15. *Poa pratensis* c 3.3, *Holcus lanatus* c 2.2, ***Anthoxanthum odoratum* c 2.2**, *Dactylis glomerata* c 2.2, *Achillea millefolium* c +, *Carex hirta* c +, *Cerastium holosteoides* c +, *Deschampsia caespitosa* c +, *Glechoma hederacea* c +, *Stellaria graminea* c +, *Ranunculus repens* c +, *Luzula campestris* c r, *Taraxacum officinale* c r, *Veronica arvensis* c r, *Veronica chamaedrys* c r.

Relevé 25. (Z.C., P.Sz. 07.07.2009 r.). Coverage of layer c 100%; the relevé area 8 m^2; number of species – 15. *Deschampsia caespitosa* c 3.3, *Potentilla anserina* c 3.3, *Poa pratensis* c 2.2, *Potentilla reptans* c 2.2, ***Anthoxanthum odoratum* c 1.1**, *Holcus lanatus* c 1.1, *Ranunculus acris* c 1.1, *Achillea millefolium* c +, *Dactylis glomerata* c +, *Festuca pratensis* c +, *Agrostis gigantea* c r, *Cirsium arvense* c r, *Heracleum sibiricum* c r, *Medicago lupulina* c r, *Rumex acetosa* c r.

Relevé 26. (Z.C., P.Sz. 07.07.2009 r.). Density of layer b<1%, coverage of layer c 50%, layer d 50%; the relevé area 9 m^2; number of species – 23. *Betula pendula* b +, *Pinus sylvestris* b r, *Populus tremula* b r, *Salix caprea* c +, *S. purpurea* b +; *Achillea millefolium* c 2.2, ***Anthoxanthum odoratum* c 2.2**, *Festuca rubra* c 1.1, *Hieracium pilosella* c 1.1, *Lolium perenne* c 1.1, *Medicago lupulina* c 1.1, *Tussilago farfara* c 1.1, *Corynephorus canescens* c +, *Hypochoeris radicata* c +, *Picris hieracioides* c +, *Rumex acetosella* c +, *Equisetum arvense* c r, *Oenothera biennis* c r, *Potentilla argentea* c r, *Taraxacum officinale* c r, *Trifolium arvense* c r, *Vicia hirsuta* c r; *Musci* d 3.3.

Relevé 27. (Z.C., P.Sz. 07.07.2009 r.). Density of layer a 80%, layer b 10%, coverage of layer c 60%, layer d 80%; the relevé area 25 m^2; number of species – 10. *Pinus sylvestris* a 5.5; *Padus serotina* b 2.1, *Sorbus aucuparia* b +; *Calamagrostis epigejos* c 4.4, *Mycelis muralis* c 1.1, ***Anthoxanthum odoratum* c +**, *Moehringia trinervia* c r, *Rumex acetosella* c +, *Quercus robur* juv. c r; *Musci* 5.4.

Relevé 28. (Z.C. 25.08.2009 r.). Coverage of layer c 100%; layer d 5%; the relevé area 16 m^2; number of species – 10. *Achillea millefolium* c 3.3, *Holcus mollis* c 3.3, ***Anthoxanthum odoratum* c +**, *Dactylis glomerata* c +, *Gnaphalium sylvaticum* c +, *Potentilla anserina* c +, *Cerastium holosteoides* c r, *Plantago lanceolata* c r, *Rumex acetosa* c r, *Solidago virga-aurea* c r; *Musci* d 1.1.

Relevé 29. (Z.C., P.Sz. 25.05.2011 r.). Coverage of layer c 95%, layer d>1%; the relevé area 25 m^2; number of species – 17. *Avenula pubescens* c 3.2, ***Anthoxanthum odoratum* c 2.2**, *Ranunculus acris* c 2.2, *Rumex acetosa* c 2.2, *Cerastium holosteoides* c 1.1, *Festuca pratensis* c 1.1, *Galium mollugo* c 1.1, *Cardaminopsis arenosa* c +, *Carex hirta* c +, *Lychnis flos-cuculi* c +, *Poa pratensis* c +, *Potentilla anserina* c +, *Ranunculus repens* +, *Dactylorhiza majalis* c r, *Heracleum sibiricum* c r, *Holcus lanatus* c r, *Rumex crispus* c r; *Musci* d +.

Relevé 30. (Z.C., P.Sz. 01.06.2011 r.). Coverage of layer c 60%, layer d<5%; the relevé area 25 m^2; number of species – 15. *Filaga minima* c 2.2, *Scleranthus annuus* c 2.2, *Agrostis capillaris* c 1.1, ***Anthoxanthum odoratum* c 1.1**, *Conyza canadensis* c 1.1, *Equisetum arvense* c 1.1, *Hieracium pilosella* c 1.1, *Anthemis arvensis* c +, *Hypochoeris radicata* c +, *Myososotis micrantha* c +, *Senecio vernalis* c +, *Spergula morisonii* c +, *Helichrysum arenarium* c r; *Musci* d 1.1.

Relevé 31. (Z.C. 08.06.2011 r.). Coverage of layer c 80%; the relevé area 25 m^2; number of species – 16. ***Anthoxanthum aristatum* c 3.3**, *Conyza canadensis* c 2.2, *Elymus repens* c 2.2, *Artemisia campestris* c 1.1, *Berteroa incana* c 1.1, *Rumex acetosella* c 1.1, *Trifolium arvense* c 1.1, *Arabidopsis thaliana* c +, *Chondrilla juncea* c +, *Echium vulgare* c +, *Erodium cicutarium* c +, *Viola arvensis* c +, *Centaurea cyanus* c r, *Cirsium arvense* c r,*Papaver argemone* c r, *Veronica triphyllos* c r.

Relevé 32. (Z.C. 05.07.2011 r.). *Triticum vulgare* c 5.5, *Secale cereale* c 2.2. Coverage of layer c 50%; the relevé area 10 m^2; number of species – 14. *Bromus secalinus* c 3.3, *Anthemis arvensis* c 1.1, ***Anthoxanthum aristatum* c 1.1**, *Apera spica-venti* c 1.1, *Elymus repens* c +, *Centaurea cyanus* c +, *Gnaphalium uliginosum* c +, *Echinochloa crus-galli* c r, *Equisetum arvense* c r, *Papaver rhoeas* c r, *Plantago major* c r, *Raphanus raphanistrum* c r, *Sonchus asper* c r, *Viola arvensis* c r.

Relevé 33. (Z.C. 6.07.2011 r.). Density of layer a 40%, layer b 30%, coverage of layer c 60%, layer d 90%; the relevé area 25 m^2; number of species – 12. *Pinus sylvestris* a 4.4, *Quercus robur* a 1.1, *Betula pendula* a +; *Padus serotina* b 1.1, *Pinus sylvestris* b 1.1, *Betula pendula* b +, *Frangula alnus* b +, *Juniperus communis* b +, *Quercus robur* b +; *Deschampsia flexuosa* c 2.2, *Melampyrum pratense* c 2.2, *Vaccinium myrtillus* c 3.3, ***Anthoxanthum odoratum* c 1.1**, *Vaccinium vitis-idaea* c +, *Festuca ovina* c r, *Luzula pilosa* c r, *Trientalis europaea* c r; *Musci* d 5.5.

Relevé 34. (Z.C. 6.07.2011 r.). Density of layer a 40%, layer b 5%, coverage of layer c 50%, layer d 95%; the relevé area 25 m^2; number of species – 16. *Pinus sylvestris* a 3.3, *Betula pendula* a +; *Juniperus communis* b +, *Padus serotina* b +, *Pinus sylvestris* b +, *Populus tremula* b +, *Quercus robur* b +, *Sorbus aucuparia* b r; *Melampyrum pratense* c 3.3, *Deschampsia flexuosa* c 2.2, ***Anthoxanthum odoratum* c 1.1**, *Vaccinium myrtillus* c 1.1, *Vaccinium vitis-idaea* c 1.1, *Calluna vulgaris* c +, *Festuca ovina* c +, *Luzula pilosa* c r, *Quercus robur* c r, *Rumex acetosella* c r; *Musci* d 5.5.

Explanations: ZC – Zbigniew Celka, PSz – Piotr Szkudlarz

Appendix 3. Mean values of 24 morphological characters measured in specimens from *Anthoxanthum odoratum* populations

Site	Habitat	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	PF	59.91	12.67	10.21	6.94	5.06	4.36	3.55	7.73	1.79	7.55	6.03	6.91	4.88	4.15	1.54	7.95	2.65	2.98
2	DM	54.41	13.59	8.88	5.50	4.06	3.38	2.91	7.91	1.41	8.09	5.91	7.41	9.91	4.53	1.83	8.39	3.10	3.01
3	pG	49.38	12.91	9.21	5.65	4.12	3.47	3.06	7.71	1.09	7.38	5.06	6.97	4.88	4.18	1.54	7.90	2.51	3.17
4	FR	53.24	12.71	9.82	6.82	5.29	4.35	3.82	7.53	1.35	7.59	6.18	6.94	9.06	3.92	1.92	7.75	2.60	3.02
5	FR	52.33	10.70	9.26	5.80	4.38	3.76	3.17	7.23	2.67	6.98	6.18	6.61	8.67	4.37	1.65	7.90	2.62	3.23
6	FR	50.74	10.77	8.37	5.94	4.42	3.73	3.32	7.27	2.03	7.15	6.31	6.76	7.51	4.42	1.76	7.57	2.61	3.26
7	MM	44.54	9.62	6.68	4.78	3.78	3.09	2.73	7.93	2.08	7.73	5.49	7.46	5.57	4.47	1.76	7.94	2.51	3.09
8	AR	45.80	8.80	7.47	6.03	4.62	3.68	3.24	7.02	3.30	7.07	6.50	6.69	10.1	4.24	1.79	6.96	2.59	2.83
9	FR	52.89	10.44	7.26	5.62	4.30	3.94	3.42	7.21	3.67	7.04	6.89	7.07	5.78	4.12	2.28	7.06	2.50	2.91
10	FR	45.00	9.50	7.78	5.20	4.20	3.35	3.05	6.98	3.00	6.75	9.75	6.25	4.50	3.95	2.19	7.03	2.52	2.54
11	DM	43.25	10.33	5.72	4.58	3.62	3.11	2.98	6.77	2.42	6.77	4.83	6.48	6.17	4.04	2.29	6.87	2.53	2.85
12	MM	46.32	10.03	7.68	5.02	3.82	3.12	3.07	7.42	3.06	7.38	6.52	7.23	8.20	4.29	1.81	7.61	3.22	3.31
13	PP	53.13	10.73	10.48	6.68	4.85	3.85	3.53	7.37	2.30	7.50	7.03	7.62	11.67	4.50	2.17	7.71	3.23	3.10
14	PF	50.17	11.13	9.48	6.25	4.52	3.80	3.32	7.04	2.67	7.18	5.53	7.28	12.63	4.17	1.93	7.26	2.76	2.88
15	MM	49.77	12.57	8.58	5.42	3.98	3.47	2.75	7.19	1.93	7.38	4.50	7.58	10.30	4.38	2.11	7.54	2.97	2.77
16	EF	54.00	12.20	10.43	6.37	4.60	3.75	3.28	7.44	2.03	7.51	5.17	7.71	10.60	4.55	2.14	7.95	3.15	3.02
17	FR	47.38	10.50	9.31	6.06	4.75	3.44	3.38	7.3	1.50	7.42	4.75	7.63	11.38	4.42	1.89	8.14	3.18	3.20
18	pG	40.76	12.38	6.47	4.27	3.23	2.74	2.42	7.69	2.97	7.84	5.41	7.62	5.84	4.41	2.29	8.01	3.58	3.16
19	PP	41.99	12.11	6.50	4.59	3.22	2.86	2.45	7.44	2.47	7.57	5.92	7.41	7.44	4.46	2.31	7.95	3.57	3.18
20	pG	48.30	10.20	7.79	5.19	4.69	4.81	3.56	8.51	2.60	8.54	8.30	8.36	6.60	4.45	2.19	8.30	3.96	3.30
21	FR	45.92	10.23	7.92	5.31	4.36	3.49	3.71	7.45	2.23	7.22	7.23	7.12	7.23	4.29	2.10	7.31	3.55	3.11
22	PF	56.17	12.73	10.79	6.79	4.75	4.20	3.58	7.90	1.40	7.43	5.63	7.13	4.77	4.25	1.85	7.60	3.18	3.27
23	DM	47.84	11.33	6.30	4.62	3.70	3.08	3.17	7.62	2.79	7.49	6.24	7.31	7.18	4.31	1.83	7.62	3.32	3.25
24	W	46.87	9.42	7.77	5.74	4.54	3.66	3.39	7.38	3.03	7.47	6.61	7.09	8.82	4.38	2.44	7.92	3.73	3.19
25	DM	49.23	12.45	8.00	5.15	3.87	3.47	2.96	7.45	1.77	7.68	5.32	7.12	10.05	4.61	2.01	7.73	3.56	3.40
26	pG	47.36	12.33	7.40	5.16	3.84	3.52	3.44	7.93	3.06	8.19	5.89	7.99	5.94	4.49	2.28	8.16	3.75	3.18
27	DM	48.64	11.93	9.11	5.57	3.93	3.21	2.93	7.41	1.29	7.67	5.00	7.50	7.29	4.43	2.32	8.01	3.92	3.29
28	OF	51.00	11.62	9.12	5.96	4.38	3.96	3.56	7.27	2.08	7.08	5.95	7.16	7.38	4.35	2.24	8.21	4.10	3.28
29	DM	53.73	10.93	8.13	6.67	4.73	4.4	3.80	7.33	1.67	7.80	4.93	6.93	5.13	4.33	2.53	7.88	3.24	3.12
30	W	55.84	12.05	9.95	6.47	5.00	4.32	3.47	7.47	1.63	7.32	5.11	6.84	4.68	4.38	2.27	7.56	3.52	3.06
31	PF	57.75	13.44	9.88	6.44	4.56	4.06	3.38	7.88	1.25	7.63	5.44	6.69	5.00	4.41	2.60	8.16	4.13	3.31
32	PF	53.62	10.77	9.92	6.08	5.23	4.46	3.38	7.62	2.00	7.62	5.62	7.00	4.85	4.39	1.84	7.96	3.13	3.06
33	SR	52.23	12.88	9.90	6.28	5.03	3.95	3.58	7.83	1.18	7.65	5.95	7.13	10.08	4.29	1.58	8.41	2.86	3.23
34	DM	51.80	12.39	10.27	6.21	5.12	4.52	3.85	7.85	1.15	7.82	6.76	7.52	10.27	4.16	1.99	8.27	3.10	3.23
35	DM	46.20	12.37	8.90	5.77	4.53	3.97	3.37	7.80	1.03	7.53	4.93	7.03	8.07	4.07	1.76	7.97	2.91	3.14
36	LR	48.20	13.27	9.50	5.60	4.77	3.87	3.27	7.83	1.00	7.67	5.67	7.03	8.70	4.02	1.75	7.92	2.60	2.93
37	LM	62.10	15.60	10.70	6.90	5.10	4.40	4.00	7.50	1.00	7.10	7.20	6.90	11.6	3.59	1.75	7.26	2.79	2.85

Explanations: site numbers and habitat types – see Appendix 1 and Table 1, morphological characters – see Table 1

19	20	21	22	23	24
3.82	4.69	3.21	5.23	1.93	1.81
3.80	4.50	3.25	5.18	1.87	1.76
3.68	4.74	3.34	5.30	1.98	1.90
3.48	4.66	3.01	4.89	1.84	1.80
3.99	4.45	3.43	5.18	2.08	1.94
4.01	4.67	3.43	5.32	2.08	1.94
3.74	4.28	3.26	5.08	2.11	1.90
3.47	4.11	3.08	5.08	1.84	1.54
3.56	4.13	3.01	4.52	1.88	1.62
3.30	4.16	2.94	4.99	1.89	1.55
3.30	3.97	3.04	4.55	1.85	1.64
4.08	4.88	3.68	5.63	2.26	2.03
3.76	4.1	3.32	4.92	2.00	1.87
3.66	4.13	3.11	5.08	1.87	1.75
3.38	4.19	2.90	4.85	1.87	1.74
3.65	4.38	3.21	4.86	1.97	1.83
3.86	4.83	3.35	5.52	1.96	1.83
3.75	4.53	3.40	5.05	2.10	1.89
3.75	4.44	3.39	5.16	2.12	1.89
3.90	4.56	3.75	5.73	2.21	1.93
3.60	3.94	3.33	4.84	2.37	2.12
4.06	4.93	3.43	5.50	2.15	1.97
4.02	4.83	3.64	5.55	2.23	1.99
3.75	4.66	3.46	5.15	2.22	1.96
4.12	4.84	3.68	5.51	2.23	2.11
3.86	4.39	3.50	5.22	2.15	1.92
4.01	4.46	3.31	5.18	2.12	1.91
3.84	4.48	3.67	5.59	2.19	1.95
3.43	4.64	3.22	4.66	2.07	2.26
3.64	4.20	3.21	5.03	1.94	2.04
3.61	4.68	3.39	5.05	2.09	2.22
3.77	4.89	3.30	5.26	2.03	2.02
3.75	5.03	3.42	5.82	2.04	1.93
3.72	5.05	3.40	5.66	1.89	1.85
3.48	5.03	3.31	5.57	1.88	1.85
3.55	4.95	3.25	5.57	1.89	1.86
3.40	4.49	3.10	5.16	1.79	1.76

Appendix 4. Mean values of morphological, anatomical and soil characters for *Anthoxanthum alpinum*, *A. odoratum* and *A. aristatum* populations from investigated habitats

		Natural habitats					
Character no.	Species	AG	SG	SM	UG	PF	OF
Distribution pattern	A.a.	+	+	+	+	-	-
	A.o.	-	-	-	-	+	+
	A.ar.	-	-	-	-	-	-
1 – panicle length	A.a.	27	24.5	28.5	28	-	-
	A.o.	-	-	-	-	55.5	51
	A.ar.	-	-	-	-	-	-
2 – no. of nodes	A.a.	10.6	10.7	10.5	11.3	-	-
	A.o.	-	-	-	-	12.2	11.6
	A.ar.	-	-	-	-	-	-
3 – first internode length	A.a.	4.8	4.4	5.2	4.9	-	-
	A.o.	-	-	-	-	10.2	9.2
	A.ar.	-	-	-	-	-	-
4 – second internode length	A.a.	3.3	2.9	3.4	3.45	-	-
	A.o.	-	-	-	-	6.6	6.0
	A.ar.	-	-	-	-	-	-
5 – third internode length	A.a.	2.4	2.3	2.45	2.18	-	-
	A.o.	-	-	-	-	4.8	4.4
	A.ar.	-	-	-	-	-	-
6 – fourth internode length	A.a.	2.05	2.1	2.0	1.9	-	-
	A.o.	-	-	-	-	4.18	3.98
	A.ar.	-	-	-	-	-	-
7 – fifth internode length	A.a.	1.6	1.4	1.65	1.65	-	-
	A.o.	-	-	-	-	3.48	3.59
	A.ar.	-	-	-	-	-	-
8 – spikelet length on second uppermost panicle branch	A.a.	6.1	6.6	6.4	6.7	-	-
	A.o.	-	-	-	-	7.60	7.27
	A.ar.	-	-	-	-	-	-
9 – no. of spikelets on second uppermost panicle branch	A.a.	1.02	1.0	1.05	1.18	-	-
	A.o.	-	-	-	-	1.7	2.1
	A.ar.	-	-	-	-	-	-
10 – no. of spikelets on middle panicle branch	A.a.	6.38	6.5	6.77	6.8	-	-
	A.o.	-	-	-	-	7.45	7.05
	A.ar.	-	-	-	-	-	-
11 – no. of spikelets on middle panicle branch	A.a.	2.5	2.8	2.8	3.6	-	-
	A.o.	-	-	-	-	5.7	6.0
	A.ar.	-	-	-	-	-	-
12 – spikelet length on lowermost panicle branch	A.a.	6.1	6.3	6.7	6.62	-	-
	A.o.	-	-	-	-	7.05	7.19
	A.ar.	-	-	-	-	-	-
13 – no. of spikelets on lowermost panicle branch	A.a.	3.3	3.8	3.2	4.2	-	-
	A.o.	-	-	-	-	6.9	7.4
	A.ar.	-	-	-	-	-	-
14 – lower glume length	A.a.	3.85	3.55	3.84	3.9	-	-
	A.o.	-	-	-	-	4.25	4.35
	A.ar.	-	-	-	-	-	-
15 – lower glume width	A.a.	1.5	1.75	1.64	1.61	-	-
	A.o.	-	-	-	-	1.9	2.24
	A.ar.	-	-	-	-	-	-
16 – upper glume length	A.a.	6.7	6.7	6.9	7.1	-	-
	A.o.	-	-	-	-	7.72	8.21
	A.ar.	-	-	-	-	-	-
17 – upper glume width	A.a.	2.65	3.0	2.9	2.7	-	-
	A.o.	-	-	-	-	3.07	4.12
	A.ar.	-	-	-	-	-	-

Seminatural habitats								Synanthropic habitats						
LM	MM	DM	fG	pG	aG	EF	PP	SR	LR	FR	AR	W	F	A
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
+	+	+	-	+	-	+	+	+	+	+	+	+	-	-
-	-	-	+	+	+	-	-	-	-	-	+	-	+	+
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
57	46.5	49.5	-	46	-	54	47	52.3	48.3	51.0	45.9	50	-	-
-	-	-	27.5	30	27	-	-	-	-	-	36.5	-	33	29
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12.8	10.5	12.3	-	12.4	-	12.3	11.5	12.9	13.4	10.9	8.8	10.3	-	-
-	-	-	10.0	9.9	9.2	-	-	-	-	-	12.2	-	12.4	9.4
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9.2	7.6	8.4	-	7.8	-	10.5	8.4	9.9	9.5	8.7	7.5	8.5	-	-
-	-	-	4.6	4.7	3.9	-	-	-	-	-	6.5	-	5.7	4.5
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6.75	5.05	5.4	-	5.05	-	6.38	5.55	6.25	5.6	4.55	4.61	4.7	-	-
-	-	-	3.0	3.5	3.3	-	-	-	-	-	4.5	-	3.8	3.2
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4.9	3.82	4.2	-	3.82	-	4.6	3.95	5.0	4.68	4.55	4.6	4.7	-	-
-	-	-	2.5	2.8	2.7	-	-	-	-	-	3.9	-	3.29	2.7
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4.4	3.2	3.6	-	3.83	-	3.75	3.3	3.98	3.9	3.78	3.68	3.7	-	-
-	-	-	2.18	2.4	2.25	-	-	-	-	-	3.17	-	2.81	2.3
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3.9	2.9	3.22	-	2.98	-	3.3	2.95	3.59	3.25	3.39	3.25	3.41	-	-
-	-	-	1.95	2.28	2.05	-	-	-	-	-	2.81	-	2.45	2.0
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7.40	7.50	7.65	-	7.81	-	7.42	7.41	7.81	7.81	7.32	7.01	7.41	-	-
-	-	-	6.6	6.5	6.38	-	-	-	-	-	6.9	-	7.1	6.7
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1.4	2.51	1.65	-	2.3	-	2.05	2.4	1.2	1.1	2.3	3.3	2.6	-	-
-	-	-	2.2	1.79	1.35	-	-	-	-	-	1.1	-	1.1	1.78
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7.5	7.5	7.65	-	7.81	-	7.5	7.55	7.65	7.65	7.18	7.1	7.41	-	-
-	-	-	6.5	6.28	6.39	-	-	-	-	-	6.61	-	7.05	6.62
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5.9	5.7	5.8	-	5.7	-	5.2	6.5	6.0	5.6	6.4	6.5	6.1	-	-
-	-	-	5.3	4.79	5.1	-	-	-	-	-	5.05	-	5.21	4.41
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6.95	7.35	7.25	-	7.55	-	7.7	7.5	7.15	7.05	6.85	6.7	7.0	-	-
-	-	-	6.19	6.29	6.3	-	-	-	-	-	6.5	-	6.65	6.55
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7.8	7.9	8.7	-	5.5	-	10.5	9.4	10.1	8.8	8.1	10.1	7.5	-	-
-	-	-	7.2	5.49	6.4	-	-	-	-	-	6.2	-	7.9	6.4
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4.05	4.35	4.32	-	4.35	-	4.55	4.48	4.29	4.02	4.29	4.24	4.38	-	-
-	-	-	3.61	3.73	3.64	-	-	-	-	-	3.65	-	3.8	3.99
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2.22	1.87	1.92	-	2.01	-	2.15	2.24	1.57	1.73	1.85	1.79	2.39	-	-
-	-	-	1.11	1.14	1.12	-	-	-	-	-	1.21	-	1.37	1.27
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7.63	7.7	7.92	-	8.1	-	7.95	7.85	8.41	7.91	7.65	6.95	7.80	-	-
-	-	-	6.31	6.45	6.39	-	-	-	-	-	6.45	-	6.86	6.79
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3.08	2.95	3.20	-	3.3	-	3.15	3.42	2.85	2.60	2.75	2.60	3.65	-	-
-	-	-	1.88	2.02	1.95	-	-	-	-	-	2.31	-	2.45	2.15

		Natural habitats					
Character no.	Species	AG	SG	SM	UG	PF	OF
18 – palea length in sterile floret	A.a.	3.27	3.19	3.09	3.33	-	-
	A.o.	-	-	-	-	3.7	3.28
	A.ar.	-	-	-	-	-	-
19 – palea awn length to knee in sterile floret	A.a.	3.25	3.34	3.28	3.7	-	-
	A.o.	-	-	-	-	3.80	3.84
	A.ar.	-	-	-	-	-	-
20 – palea awn length from knee in sterile floret	A.a.	4.51	4.35	4.25	4.43	-	-
	A.o.	-	-	-	-	4.65	4.50
	A.ar.	-	-	-	-	-	-
21 – lemma length in sterile floret	A.a.	3.35	3.46	3.15	3.49	-	-
	A.o.	-	-	-	-	3.27	3.68
	A.ar.	-	-	-	-	-	-
22 – lemma awn length in sterile floret	A.a.	4.88	4.61	4.41	4.7	-	-
	A.o.	-	-	-	-	5.25	5.59
	A.ar.	-	-	-	-	-	-
23 – lemma length in fertile floret	A.a.	1.95	1.94	1.90	2.11	-	-
	A.o.	-	-	-	-	2.00	2.19
	A.ar.	-	-	-	-	-	-
24 – palea length in fertile floret	A.a.	1.94	2.03	1.80	2.02	-	-
	A.o.	-	-	-	-	1.91	1.95
	A.ar.	-	-	-	-	-	-
No. of vascular bundles in stem	A.a.	11 to 14	-	14	14	-	-
	A.o.	-	-	-	-	12 to 14	-
	A.ar.	-	-	-	-	-	-
No. of layers of sclerenchyma cells in stem	A.a.	4 to 5	-	4 to 5	4	-	-
	A.o.	-	-	-	-	4 do 6	-
	A.ar.	-	-	-	-	-	-
No. of vascular bundles in leaf	A.a.	12 to 23	-	14 to 16	16	-	-
	A.o.	-	-	-	-	14 to 16	-
	A.ar.	-	-	-	-	-	-
No. of stomatal rows in abaxial part of leaf	A.a.	3	-	43 to 4	3 to 4	-	-
	A.o.	-	-	-	-	2 to 4	-
	A.ar.	-	-	-	-	-	-
Presence of short cells in abaxial part of leaf	A.a.	0/1	-	1	1	-	-
	A.o.	-	-	-	-	0/1	-
	A.ar.	-	-	-	-	-	-
Presence of long hairs in abaxial part of leaf	A.a.	0/1	-	0/1	1	-	-
	A.o.	-	-	-	-	0/1	-
	A.ar.	-	-	-	-	-	-
No. of stomatal rows in adaxial part of leaf	A.a.	4 to 5	-	3 to 4	4 to 6	-	-
	A.o.	-	-	-	-	3	-
	A.ar.	-	-	-	-	-	-
Presence of short cells in adaxial part of leaf	A.a.	0/1	-	1	1	-	-
	A.o.	-	-	-	-	0/1	-
	A.ar.	-	-	-	-	-	-
Presence of long hairs in adaxial part of leaf	A.a.	0	-	0	0/1	-	-
	A.o.	-	-	-	-	0/1	-
	A.ar.	-	-	-	-	-	-
Stomatal length in abaxial part of leaf	A.a.	35 to 36.4	-	32.2 to 35	35	-	-
	A.o.	-	-	-	-	36.3 to 51	-
	A.ar.	-	-	-	-	-	-

Seminatural habitats								Synanthropic habitats						
LM	MM	DM	fG	pG	aG	EF	PP	SR	LR	FR	AR	W	F	A
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3.01	3.13	3.17	-	3.18	-	3.02	3.15	3.23	2.93	3.15	2.82	3.15	-	-
-	-	-	2.84	2.86	2.84	-	-	-	-	-	2.82	-	2.73	2.93
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3.43	3.83	3.79	-	3.75	-	3.65	3.75	3.75	3.55	3.83	3.47	3.72	-	-
-	-	-	3.41	3.41	3.49	-	-	-	-	-	3.45	-	3.45	3.81
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4.59	4.55	4.75	-	4.59	-	4.39	4.30	5.03	4.95	4.50	4.12	4.50	-	-
-	-	-	4.68	4.95	4.75	-	-	-	-	-	4.81	-	4.62	4.85
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3.17	3.39	3.41	-	3.45	-	3.21	3.35	3.42	3.25	3.31	3.08	3.38	-	-
-	-	-	2.99	2.99	2.96	-	-	-	-	-	2.83	-	2.85	3.07
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4.87	2.30	5.41	-	5.1	-	4.87	5.07	5.81	5.58	5.12	5.10	5.12	-	-
-	-	-	5.65	5.75	5.71	-	-	-	-	-	5.52	-	5.30	6.08
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1.95	2.13	2.00	-	2.08	-	1.96	2.06	2.05	1.88	2.05	1.85	2.14	-	-
-	-	-	1.57	1.57	1.59	-	-	-	-	-	1.49	-	1.53	1.67
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2.05	1.92	1.89	-	1.90	-	1.84	1.89	1.93	1.86	1.90	1.55	1.99	-	-
-	-	-	1.39	1.45	1.43	-	-	-	-	-	1.48	-	1.51	1.51
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8 to 14	14	-	-	-	-	8 to 10	12 to 14	-	-	-	12 to14	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	8 to 12	10 to 12
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5 to 6	6 to 7	-	-	-	-	4 to 5	5 do 6	-	-	-	4 to 5	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	4 to 5	3 to 4
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11 to 14	13 to 15	-	-	-	-	12 to 14	13 to 19	-	-	-	11 to 20	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	15 to 16	15 to 16
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3 to 4	4	-	-	-	-	4	4	-	-	-	4	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	2	2
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0/1	0/1	-	-	-	-	0/1	0/1	-	-	-	0/1	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	0/1	1
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0/1	1	-	-	-	-	0/1	1	-	-	-	0/1	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	1	0/1
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	4	-	-	-	-	4	4	-	-	-	4	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	4	4
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1	1	-	-	-	-	0	0/1	-	-	-	0/1	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1	0	-	-	-	-	0/1	1	-	-	-	0/1	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	0/1	0
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
39 to 42	42 to 46	-	-	-	-	37 to 43	42 to 43	-	-	-	36.5 to 40	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	33 to 37.3	32.7 to 33.5

		Natural habitats					
Character no.	Species	AG	SG	SM	UG	PF	OF
Stomatal length in adaxial part of leaf	A.a.	35 to 36.1	-	34.2 to 36	34.5 to 36	-	-
	A.o.	-	-	-	-	37 to 50	-
	A.ar.	-	-	-	-	-	-
pH	A.a.	3.6	-	3.2	3.1	-	-
	A.o.	-	-	-	-	3.45	3.25
	A.ar.	-	-	-	-	-	-
CEC	A.a.	29.8	-	3.2	3.1	-	-
	A.o.	-	-	-	-	36	18
	A.ar.	-	-	-	-	-	-
G	A.a.	0.03	-	0.03	0.13	-	-
	A.o.	-	-	-	-	0.039	0.03
	A.ar.	-	-	-	-	-	-
P	A.a.	0.7	-	2.7	0.7	-	-
	A.o.	-	-	-	-	3.6	2.9
	A.ar.	-	-	-	-	-	-
K	A.a.	7	-	10.5	6.1	-	-
	A.o.	-	-	-	-	4.3	6.8
	A.ar.	-	-	-	-	-	-
N	A.a.	47.5	-	42.5	57	-	-
	A.o.	-	-	-	-	17	12
	A.ar.	-	-	-	-	-	-
N:P	A.a.	75	-	18	88	-	-
	A.o.	-	-	-	-	9	45
	A.ar.	-	-	-	-	-	-
N:K	A.a.	6.9	-	4	9.2	-	-
	A.o.	-	-	-	-	3.9	2.95
	A.ar.	-	-	-	-	-	-
C:N	A.a.	15.8	-	17	12.5	-	-
	A.o.	-	-	-	-	30	15
	A.ar.	-	-	-	-	-	-
C	A.a.	7.5	-	7.25	7.1	-	-
	A.o.	-	-	-	-	4.4	1.9
	A.ar.	-	-	-	-	-	-
Humus	A.a.	13	-	12.5	12.1	-	-
	A.o.	-	-	-	-	7.8	3.5
	A.ar.	-	-	-	-	-	-

Seminatural habitats								Synanthropic habitats						
LM	MM	DM	fG	pG	aG	EF	PP	SR	LR	FR	AR	W	F	A
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
41 to 46	45 to 46.5	-	-	-	-	36.5 to 47	45 to 47	-	-	-	39 to 43	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	32.8 to 34	33.5 to 34
-	-	-	-	-	-	-	-	-	-	-	-	-	-	
3.75	4.45	4.58	-	3.9	-	4.25	3.15	-	3.78	3.9	-	4.25	-	
-	-	-	3.65	3.75	3.4	-	-	-	-	-	3.55	-	4.6	4
-	-	-	-	-	-	-	-	-	-	-	-	-	-	
48	15	31	-	19	-	25	51	-	3.78	14	-	12	-	
-	-	-	1.9	4.5	13	-	-	-	-	-	10	-	1	6
-	-	-	-	-	-	-	-	-	-	-	-	-	-	
0.015	0.041	0.045	-	0.059	-	0.052	0.05	-	0.099	0.016	-	0.04	-	
-	-	-	0.033	0.036	0.026	-	-	-	-	-	0.038	-	0.013	0.41
-	-	-	-	-	-	-	-	-	-	-	-	-	-	
0.5	1.9	1.4	-	2.9	-	1.3	1.8	-	2	2.7	-	1.3	-	
-	-	-	2.8	5	4.9	-	-	-	-	-	7.8	-	5	5.1
-	-	-	-	-	-	-	-	-	-	-	-	-	-	
7.3	2.9	6.1	-	5.7	-	3.2	6.9	-	11.1	3.5	-	4.4	-	
-	-	-	4.9	3.7	2.8	-	-	-	-	-	3.6	-	4	5.5
-	-	-	-	-	-	-	-	-	-	-	-	-	-	
27	25	35	-	10	-	42	29	-	26.5	6	-	19	-	
-	-	-	15	11.5	11.8	-	-	-	-	-	10	-	7.5	12
-	-	-	-	-	-	-	-	-	-	-	-	-	-	
32	19	25.5	-	4.5	-	34	17.5	-	14	3	-	27	-	
-	-	-	5.7	3	2.5	-	-	-	-	-	1.2	-	1.5	2.75
-	-	-	-	-	-	-	-	-	-	-	-	-	-	
2.2	8.8	5.5	-	1.8	-	12.5	4.5	-	0.8	1.9	-	4.2	-	
-	-	-	3.1	3.2	4.25	-	-	-	-	-	2.75	-	1.9	3.5
-	-	-	-	-	-	-	-	-	-	-	-	-	-	
12.5	11.5	12.5	-	8	-	14	15.5	-	14.2	17.5	-	10.5	-	
-	-	-	8.1	13.5	14	-	-	-	-	-	16.1	-	13	10.5
-	-	-	-	-	-	-	-	-	-	-	-	-	-	
3.15	2.8	3	-	0.4	-	5.8	3.9	-	3.75	0.9	-	1.9	-	
-	-	-	1.15	1.15	1.5	-	-	-	-	-	1.6	-	0.9	1.15
-	-	-	-	-	-	-	-	-	-	-	-	-	-	
5.8	4.5	5.5	-	0.7	-	10.1	6.5	-	-	1.8	-	3	-	
-	-	-	1.9	1.9	2.62	-	-	-	-	-	2.79	-	1.6	2

Explanations: AG – alpine grassland, SG – subalpine grassland near trail, SM – subalpine matgrass meadow, UG – upper montane forest glade, PF – pine forest, OF – reed-grass oak forest, LM – lower montane meadow, MM – moist meadow, DM – dry meadow, fG – sandy grassland near pine forest, pG – sandy grassland near pine forest plantation, aG – sandy grassland near arable field, EF – edge of pine forest, PP – pine forest plantation, SR – submontane ruderal roadside, LR – lower montane forest roadside, FR – roadside in pine forest, AR – field roadside, W – wasteland, F – fallow, A – arable field; A.a. – *Anthoxanthum alpinum*, A.ar. – *A. aristatum*, A.o. – *A. odoratum*