

Comparative analysis of *Deschampsia antarctica* Desv. population adaptability in the natural environment of the Admiralty Bay region (King George Island, maritime Antarctic)

Ivan Parnikoza¹ · Natalia Miryuta¹ · Iryna Ozheredova² · Iryna Kozeretska² · Jerzy Smykla^{3,5} · Victor Kunakh¹ · Peter Convey⁴

Received: 7 November 2014/Revised: 6 April 2015/Accepted: 10 April 2015
© Springer-Verlag Berlin Heidelberg 2015

Abstract Plants inhabiting extreme environments may possess features allowing them to tolerate sudden abrupt changes in their environment, a phenomenon often known as ‘adaptability.’ However, ability or success in developing adaptability varies among plant populations. Adaptability can be quantified by measuring variation in the response to the same environmental challenges between plant populations. In this study, we evaluate the adaptability of the iconic Antarctic plant, *Deschampsia antarctica*, based on traits reflecting three levels of organization: the population level (S, *D. antarctica* land cover), individual level (Ph, biometrics), and cell level (relative DNA content, rcDNA, in cells of the leaf parenchyma). We sampled a total of six *D. antarctica* populations in the Admiralty Bay region, King George Island (South Shetland Islands, maritime Antarctic), during the austral summer of 2005–2006, and analyzed pairwise interrelations between various indices reflecting plant population adaptability. The results of these pairwise comparisons were then used to estimate a pooled

measure of each population’s adaptability, designated as united latent quality indicator (ULQI). Our results demonstrated that the responses of individual adaptability indices were seldom synchronized, although one population from the central part of the Point Thomas oasis did show some degree of synchronicity. This population also demonstrated the highest ULQI, consistent with the relatively favorable microenvironmental conditions at this location. Two other populations located closer to the shoreline also demonstrated detectable synchronicity and moderate levels of ULQI, while the remaining populations revealed no synchronized responses and negative ULQI values. As the ULQI value obtained will be strongly influenced by the conditions experienced by any given population during a particular season, evaluation of population dynamics requires annual monitoring over multiple seasons.

Keywords Antarctic hairgrass · Land cover · Biometrics · Relative DNA content · United latent quality indicator

✉ Ivan Parnikoza
Parnikoza@gmail.com

¹ Institute of Molecular Biology and Genetics, National Academy of Sciences of Ukraine, 150 Academician Zabolotny Str., Kiev 03680, Ukraine

² Taras Shevchenko National University of Kyiv, 64 Volodymyrska Str., Kiev 01601, Ukraine

³ Department of Biodiversity, Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120 Kraków, Poland

⁴ British Antarctic Survey, NERC, High Cross, Madingley Road, Cambridge CB3 0ET, UK

⁵ Present Address: Department of Biology and Marine Biology, University of North Carolina, Wilmington, 601 S. College Rd., Wilmington, NC, USA

Introduction

The concept of ‘adaptability’ in ecology is often defined as an ability to cope with abrupt environmental changes (Conrad 1983). It is an appropriate concept to apply to plants growing in extreme environmental conditions, such as those of Antarctic terrestrial habitats. Such plants are ‘obliged’ to adapt both to the local microclimate mosaic and to general climatic fluctuations (Convey 1996a). For example, morphology and density of the widespread maritime Antarctic vascular plant, *Deschampsia antarctica* Desv., depend on distance from the coast and on local topography, both of which underlie the formation of

distinct habitats and microclimates in the same ice-free area (Bölter et al. 1989; Zwolska and Rakusa-Suszczewski 2002; Kozeretska et al. 2010). Even parts of the same population can experience different microclimates (Bölter et al. 1989). Additional challenges are also presented by recent climatic changes in parts of the Antarctic region (Turner et al. 2005, 2014; Convey 2011; Royles et al. 2013). Ameliorating conditions on the Argentine Islands are interpreted to have permitted rapid growth and spread of the local populations of *D. antarctica* between the 1960s and 1990s (Fowbert and Smith 1994; Smith 1994), although recent investigations have shown no further increase, possibly associated with a flattening in the local warming curve over the last 10–15 years (Parnikoza et al. 2009).

Many studies of *D. antarctica* have focused on anatomical, life cycle and ecology, physiological or biochemical features (e.g., Edwards 1972; Smith 2003; Mosyakin et al. 2007; Parnikoza et al. 2007a, 2011a; Krywult et al. 2013). However, little attention has been given to comparative analyses of different populations or their adaptability in the face of climatic and microclimatic variability. For instance, changes in plant reproductive strategy, with increased allocation of resources toward sexual reproduction (i.e., higher production of viable seeds) under less stressful conditions, may have contributed to the increase in populations and their local expansion that has already been observed (Convey 1996b).

Direct measurements of fitness indices in situ are generally recognized to be challenging, meaning that indirect approaches have to be used. The spatial area occupied by a population is often used as an indicator or proxy for fitness and may, for instance, be assessed in terms of land cover, overall area occupied by the species, plant crown cover, or area covered by leaves (Myers and Shelton 1980; Maarel 2005; Finnigan 2007). These important structural properties are known to be strongly related to ecosystem processes (Tømmervik et al. 2005).

The next scale of evaluation of adaptive parameters is the individual level. The use of this level is common in population ecology, including measurements of various biological parameters of mature individuals in the population (Causton and Venus 1981; Weiner and Thomas 1986; Jong and Klinkhamer 1994). Biomass and individual dimensions can be of great importance in the competition for limited resources (Uchamanski 2003).

Cytogenetic parameters provide further indices that can contribute to the evaluation of population adaptability. One such parameter is polyploidy, often a feature of plants growing under extreme environmental conditions (Wolf 1937; Strogonov 1973; Kunakh 2011). The associated increase in DNA content is thought to be indicative of metabolic activity and hence also an indicator of

adaptability under particular environmental conditions (Levin 2002; Parnikoza et al. 2008; Miryuta and Kunakh 2011). We have previously examined cytogenetic indices such as nucleus area and nuclear DNA content in leaf parenchyma cells of *D. antarctica* plants growing under different ecological conditions in the maritime Antarctic (Parnikoza et al. 2007b, 2011b).

In ecological investigations, different indices of population adaptability are generally used independently (Convey 1996b; Day et al. 2008). However, fitness interpretations based on the use of a single index alone may not be supported by other indices. Here, we propose a ‘united latent quality indicator’ (ULQI), enabling more reliable evaluation of the complexities of population fitness. In the process of developing this index, we consider correlations between indices of land cover, biometric parameters, and relative cellular DNA content in leaf parenchyma for different populations of *D. antarctica* in ice-free areas of Admiralty Bay region, King George Island, South Shetland Islands.

Materials and methods

Study area

The study was conducted on King George Island (South Shetland Islands, maritime Antarctic) in the ice-free areas of Admiralty Bay region during the 30th Polish and the 10th Ukrainian expeditions between December 2005 and February 2006. The cold climate, with mean annual temperature of -1.7 °C (2.4 °C in January and -6.8 °C in July), high relative humidity (84 %), strong oceanic influence, and high precipitation (530 mm per annum), is typical for the northern part of the maritime Antarctic. A major climatic feature of this area is strong katabatic winds, which often reach hurricane force (Kejna 1999).

Despite the harsh environmental conditions, ice-free areas of Admiralty Bay region provide conditions favorable for supporting a relatively diverse terrestrial biota. The vegetation of this area, as in other parts of the maritime Antarctic, is predominantly cryptogamic, consisting mostly of mosses, liverworts, lichens, algae, and cyanobacteria. The vascular flora is represented by only two native species, the Antarctic hair grass *Deschampsia antarctica* Desv. (Poaceae) and the Antarctic pearlwort *Colobanthus quitensis* (Kunth) Bartl. (Caryophyllaceae). Vascular plant communities are represented only by the Antarctic herb tundra formation (Rakusa-Suszczewski 1993; Ochyra 1998; Parnikoza et al. 2009). The Admiralty Bay region, particularly its western shore, is one of the richest botanical areas known in the Antarctic (Ochyra 1998; Krzewicka and Smykla 2004) and possesses the largest continuous stands

of vascular plant communities (Barcikowski et al. 2001, 2003). Detailed descriptions of terrestrial ecosystems of the Admiralty Bay region, addressing topography, geology, climate, vegetation, marine influence, edaphic, and trophic conditions, are the subject of various publications (e.g., Rakusa-Suszczewski 1993; Ochyra 1998; Beyer and Bölter 2002).

Sites selected for sampling were located in the ice-free areas of Admiralty Bay region on Point Thomas (62°10'S, 58°28'W) in the vicinity of the Polish Station Arctowski and on Keller Peninsula (62°05'S, 58°24'W) in the vicinity of the Brazilian Station Ferraz (Fig. 1). Our primary study area was the Point Thomas oasis, where five *D. antarctica* populations were investigated, with the sixth population being near Ferraz:

1. S 62°09.765', W 58°27.871', 5 m above sea level (asl). On the flank of a hill with north-west exposure (30°–40°), below a penguin colony and near a rivulet, 100 m from the shore;
2. S 62°09.560', W 58°28.245', 1 m asl. The flat area close to the coast, east of the flagpole;
3. S 62°09.748', W 58°28.267', 21 m asl. On the flank of a hill with north-east exposure (5°–10°), with a glacial origin streamlet;
4. S 62°10.349', W 58°31.080', 1 m asl. Near the foot of the hill flank, with north exposure (5°);

5. S 62°09.807', W 58°28.151', 100 m asl. Located on the summit of a hill flank with east exposure (5°), near Puchalski grave;
6. S 62°04.985', W 58°23.490', 7 m asl. Flat area on the flank of a small hill with east exposure (5°–10°).

Data collection

The six sampling sites all included relatively homogenous vegetation stands, within which sampling plots (one each of 3 × 3 m at each site) were established. These stands encompassed a broad range of important environmental gradients (Kozeretska et al. 2010; Parnikoza et al. 2011a), particularly with respect to topography (i.e., elevation, slope steepness, and exposure), water content of the substratum, and vertebrate impact. At each of these sampling sites, the population level of organization (S) was measured as the cover of *D. antarctica* as vertical (upright) projection of green plant parts on the ground surface, using a standardized approach (Kennedy and Addison 1987; Floyd and Anderson 1987; Dietz and Steinlein 1996; Röttgermann et al. 2000) (Fig. 2).

From each sampling site, one to five visibly undamaged grass tufts with inflorescences were collected and placed in sealed paper bags. Within a few hours of collection, all samples were transported to the laboratories of the Polish

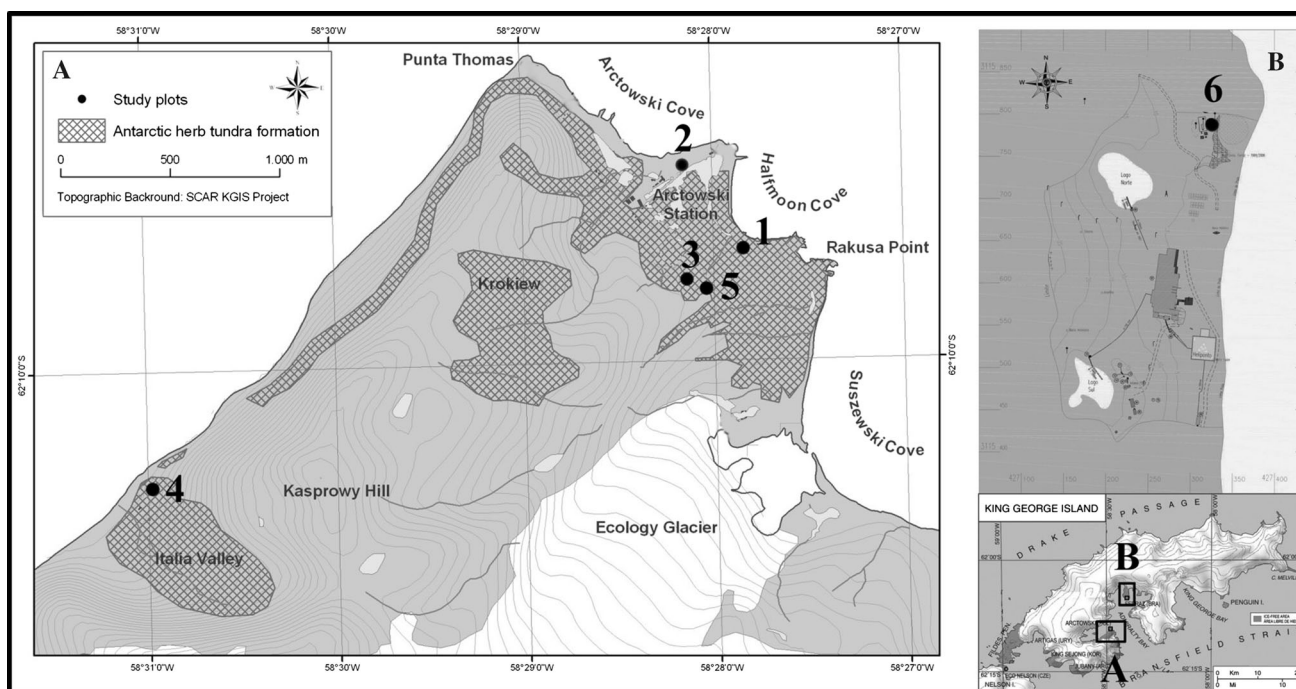


Fig. 1 Map of sampling *D. antarctica* populations in the Admiralty Bay region (King George Island, South Shetland Islands). Insets A—point Thomas Oasis, B—Ferraz station vicinity

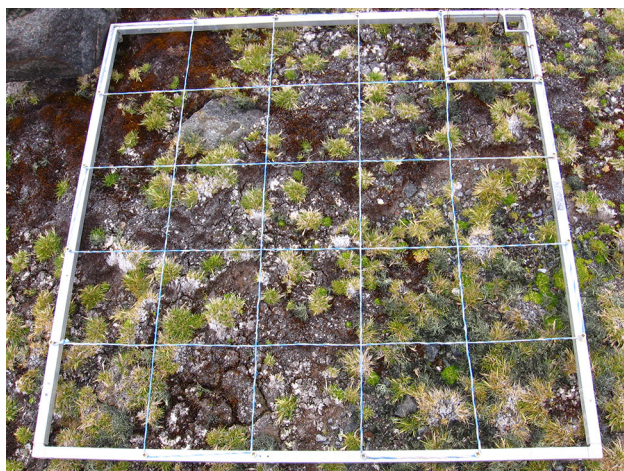


Fig. 2 Typical vegetated area with *D. antarctica*, including the 1 m grid used for cover estimation

Station Arctowski for processing. In the laboratory, green leaf subsamples were taken from each collected grass tuft for cytogenetic analyses and fixed in 96 % alcohol–acetic acid mixture (3:1, v/v; 30 min). After fixation, the material was stored in 70 % alcohol. The remaining parts of the samples were air-dried at low temperature. All the samples were then shipped to Ukraine for further analyses.

Laboratory analyses

In the laboratory, after several weeks of storage and transportation, biometric and cytological parameters were measured on the collected samples. At the individual level of organization, biometric parameters of all samples were measured on air-dried specimens and included: height of generative stem (from base of stem to inflorescence top), leaf length, single flower length (lower glume length), inflorescence length (from first flower to the top of highest flower), and the number of flowers on an inflorescence. These parameters were selected as being representative of the *D. antarctica* life form, which consists of a leaf rosette and inflorescence shoots (Gielwanowska 2005; Parnikoza et al. 2011a). The land cover data and biometric parameters obtained during this study are given in Table 1.

At the cellular level of organization, cytological analyses focused on determination of the relative cellular DNA content (rcDNA) in leaf parenchyma cells. This parameter reflects the DNA content in nuclei of the investigated cells in comparison with those of anaphase cells. The rcDNA analyses followed the protocol described by Parnikoza et al. (2007b, 2011b). Briefly, from each leaf sample fixed in 96 % alcohol–acetic acid, four subsamples of leaf parenchyma cells were mounted on microscope slides and stained using the Feulgen technique (Kiernon 1990). Then, 25 nuclei were analyzed in each subsample.

Table 1 Geographical locations and brief ecological description of *D. antarctica* population success indices in the studied plots in Admiralty Bay region

Plot number	Individual projected cover	Population characteristics ^a			Leaf length (cm)	Generative stem height (cm)	Inflorescence length (cm)	Flower length (mm)	Number of flowers in the inflorescence
		reDNA, C							
1	5	100/1.4 ± 0.1/0.4/98–2	5/3.4 ± 0.1/0.1/5–0/0.3	126/2.4 ± 0.05/0.3/106–20/0.6	5/2.5 ± 0.1/0.1/5–0/0.2	33/4.8 ± 0.1/0.2/0–33/0.5	5/6.6 ± 1.7/1.4/4–1/3.4		
2	10	100/1.1 ± 0.1/0.3/99–1	10/2.2 ± 0.3/0.9/8–2/0.9	78/1.8 ± 0.1/0.7/67–11/0.8	10/1.3 ± 0.2/0.3/8–2/0.5	77/4.7 ± 0.1/0.4/0–77/0.4	10/7.2 ± 1.8/3.4/8–2/5.5		
3	90	100/0.9 ± 0.1/0.3/99–1	14/3.7 ± 0.3/0.6/9–5/0.7	119/2.0 ± 0.1/0.5/107–12/0.5	13/1.7 ± 0.2/0.3/5–8/0.5	138/4.9 ± 0.02/0.1/0–138/0.3	12/9.8 ± 1.2/1.2/6–6/3.5		
4	70	81/9.9 ± 0.8/55/1–80	3/2.8 ± 0.1/0.1/2–1/0.2	81/2.4 ± 0.1/0.6/62–19/0.8	3/2.2 ± 0.4/0.6/1–2/0.6	43/5.0 ± 0.1/0.4/0–43/0.5	3/1.4 ± 4.2/5.4/1–2/6		
5	25	100/2.2 ± 0.1/1.2/78–22	7/2.8 ± 0.2/0.3/3–4/0.5	128/1.61 ± 0.05/0.2/9/99–29/0.53	7/1.70 ± 0.02/0.08/5–2/0.04	64/4.5 ± 0.2/0.3/0–64/0.5	7/9.1 ± 1.2/1.0/3–4/3.0		
6	10	100/3.5 ± 0.2/3.5/43–57	3/2.9 ± 0.5/0.7/2–1/0.7	143/3.4 ± 0.2/2/72–7/1/1	3/1.9 ± 0.1/0.2/1–2/0.1	27/4.7 ± 0.1/0.3/0–27/0.5	3/9.0 ± 1.1/4/2–1/1.6		

^a Data in table cells are presented as: sample size/mean ± standard error/standard deviation/number of values in group below or equal to median group—number of values in group higher than median group/standard deviation

The slides were analyzed under an optical microscope (NU-2E, Carl Zeiss) equipped with a green light filter and a digital camera (Samsung CCD SAC-410 PA) with a video adapter (Konus Asus V 3000) and a red PAL-N filter. Digital photographs containing nuclei images were combined with anaphase images, with the comparative densitogram being obtained using the ScionImage program (<http://scion-image.software.informer.com/4.0/>). The rcDNA content was calculated as the ratio of the area under the densitogram peak of a stained nucleus to that of a stained anaphase nucleus from rootlet cells multiplied by four (cells of *D. antarctica* root meristem are usually taken for calibration, their DNA quantity being considered as 4C, where C reflects the relative DNA content in haploid karyotype; see Parnikoza et al. 2007b).

Statistical analyses

The distribution curves were plotted for each parameter over all sampling sites to investigate differences in population, biometric and cytological parameters of *D. antarctica* growing under different environmental conditions. Differences in the distribution curves between population pairs were tested using Mood's median test. This nonparametric test is a variation of the Chi-square test enabling the evaluation of intergroup differences for two populations without assumption of normal distributions of the population parameters (Pollard 1982). It was preferred over other tests as it is robust for heavy-tailed data and fairly robust against differences in the shapes of the distributions. Comparing values of the test statistics obtained to corresponding 5 % values of the Chi-square distribution (3.84 for pairwise comparisons) allows testing for significant differences between the medians of the given distributions (Pollard 1982). The test value was calculated using the equation $\chi^2 = (\text{observed value} - \text{expected value})^2 / (\text{expected value})$. Results of these pairwise comparisons are expressed in relative units (Pollard 1982).

Following an approach used in analogous studies (Aivazyan et al. 1989) for investigation of complex objects (such as groups of populations) described by many variables, the 'extreme grouping technique' (a form of heuristic method for reducing the parameter space) can be used to simplify the studied variables. However, interpretation is also complicated by the fact that the adaptability indices only indirectly reflect the properties of the studied populations. Therefore, the sets of population comparisons were grouped pairwise from the three adaptability parameters measured (cover, biometry, and cytometry). Correlations between pairs of indices determined by regression were grouped by the extremal grouping approach (Bauman and Moskalenko 2008) to generate a group of positive correlations ('positive' group) and group of

negative correlations ('negative' group), with the results being plotted to illustrate the positive or negative correlations.

For evaluation of significance in the regression technique, an *F* test or *t* test was used: test value $F_{1,N-2} = t_{n-2}^2 = (N-2)R^2 / (1-R^2)$ compared with 5 % α value of *F*-distribution for $n-2$, where *R* is correlation coefficient, *N* is point number. If the calculated value is above the upper 5 % of the *F*-distribution, the regression is considered significant (Pollard 1982). Ninety-five percent confidence intervals for σ^2 (variance) were calculated following the procedure described in Pollard (1982).

This scheme provides a mosaic description of interconnections between population characteristics. Further analysis was then carried out using the indicator scaling approach (Aivazyan et al. 1989). In this analysis, a value of +1 was assigned to each link in the 'positive' group and a value of -1 to each link in the 'negative' group. The point quantity was then calculated for each population, and after normalization, the data were plotted. Normalization in this case involved the division of the resulting value for each population by 15—the maximum possible intersection value for each population (Fig. 7). This created index corresponds to the 'united latent quality indicator' (ULQI) as described by Aivazyan et al. (1989). In this study, the approach is used to unite expert evaluations of land cover, biometric and cytometric parameters, and the outcomes of the pairwise comparisons obtained using the method of extreme grouping by regression. This enables better characterization of a particular population's state in relation to its microclimatic environment. The biological interpretation of the ULQI is that it relates to the complex population adaptability in response to macro- and microenvironmental influences.

Results

Deschampsia antarctica cover varied from 90 % in site 3 (valley with a glacial melt stream) to 5 % in site 1. This difference reflected the basic ecological gradient from coast to glacier slope (see Kozeretska et al. 2010) as well as local microclimatic features.

An example of the pattern of morphometric characteristics across populations of *D. antarctica* is presented in Fig. 3. Derived information relating to adaptability indices, such as cover differences by determination of absolute difference values and cytometric and biometric differences calculated using Mood's median test, is presented in Table 2.

The pairwise comparison of population pair differences (Fig. 4a) identified no correlation between individual (ΔPh) and population ($|\Delta S|$) level sets of pair differences. Population differences were divided into two groups, with

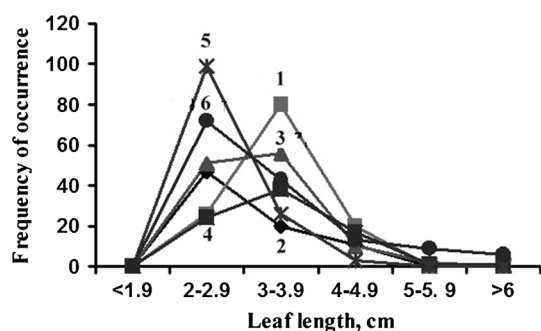


Fig. 3 Example comparison of distributions of a morphometric parameter (leaf length frequency) in populations of *D. antarctica* from the Admiralty Bay region

significant positive (Fig. 4b) and negative (Fig. 4c) correlations, using the extremal grouping method based on regression as described above. The purpose of this approach is to identify sets of population pairs that have stronger interactions in the new groups, as described by Aivazyan et al. (1989). R (correlation coefficient) and s (point variance) data are presented in Figs. 4, 5, and 6. Multiple pairwise comparisons were made by regression, indicating the absence of a linear relationship in the overall dataset and the presence of significant linear relationships in the separate positively or negatively correlated groups.

Similarly, the results of extreme grouping by regression analysis for the other two sets of differences between all studied population pairs are presented in Figs. 5 and 6. Figure 5 shows the results of analyses relating to cytometric (Δ rcDNA) and cover differences ($|\Delta S|$), and Fig. 6 illustrates the relationships between biometric (Δ Ph) and cytometric (Δ rcDNA) differences.

Next, the structures of the ‘positive’ and ‘negative’ groups were analyzed to determine the proportion of each population in these pairwise groups for three characteristic pairs presented in Fig. 7. This figure illustrates the pattern of interactions between pairs of populations in each of the three combinations of pairwise differences at population ($|\Delta S|$), individual (Δ Ph), and cell (Δ rcDNA) levels for each of the ‘positive’ and ‘negative’ correlation groups identified above. For example, population 2 appeared three times in the ‘positive’ and twice in the ‘negative’ groups across the pairwise comparisons Δ Ph– $|\Delta S|$, Δ rcDNA– $|\Delta S|$, and Δ Ph– Δ rcDNA. As described in Methods, a value of +1 was assigned to each link in the ‘positive’ group and a value of –1 to each link in the ‘negative’ group, meaning that population 2 generated +9 and –6 points (totalling +3). After normalization, this gives a ULQI of 0.2. The ULQI was similarly calculated for each population (Fig. 8).

Table 2 Pairwise differences between the medians of the biometric parameters, relative DNA content (Δ rcDNA) distribution, and projected cover ($|\Delta S|$) of *D. antarctica* in the studied plots in Admiralty Bay region

Pairs of studied plots	$ \Delta S $	Pairwise differences between the medians of the distributions of the relevant parameter obtained in each pair of studied plots					
		Δ rcDNA	Height of generative stem	Leaf length	Inflorescence length	Flower length	Number of flowers in the inflorescence
2–6	0	76.14	0	0	0	0	0
1–2	5	0	0	0	0	0	0
1–6	5	5.68	0	0	4.44	0	0
2–5	15	21.68	0	6.86	0	0	0
5–6	15	25.62	0	21.13	0	0	0
1–5	20	18.94	4.31	14.11	0	0	0
3–4	20	173.96	0	6.57	0	0	0
4–5	45	115.42	0	46.64	0	0	0
2–4	60	172.98	0	0	0	0	0
4–6	60	71.89	0	0	0	0	0
1–4	65	170.08	0	0	0	0	0
3–5	65	21.68	0	30.76	0	0	0
2–3	80	10.1	0	0	3.98	0	0
3–6	80	76.14	0	4.55	0	0	0
1–3	85	0	0	0	5.52	0	0

The data are ranked according to increasing difference in the projected cover value

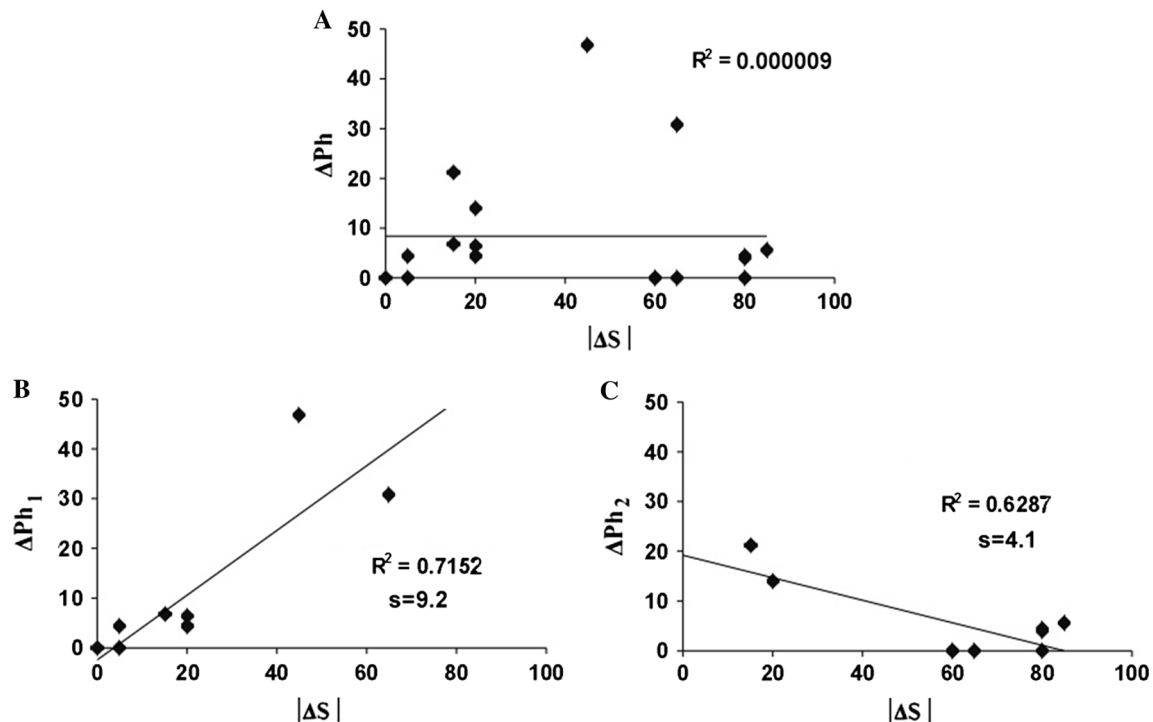


Fig. 4 Pairwise comparison of population pair differences (a) was used to divide populations into two groups with either positive (b) or negative (c) correlation based on regression between individual (ΔPh) and population level pair difference ($|\Delta S|$) sets for *D. antarctica* from the Admiralty Bay region. The graphs show the squares of the respective correlation coefficients and the point variance. The test statistics for R^2 values in the graphs {a $F_{1,16} = 0.00001$ [below the upper 5 % threshold of the F -distribution for $N = 18$ ($F_{1,16} = 4.49$)],

b $F_{1,7} = 17.58$ and c $F_{1,7} = 11.85$ [above the upper 5 % of the F -distribution for $N = 9$ ($F_{1,7} = 5.59$)] indicate the absence of a linear relationship in the overall dataset and the presence of significant linear relationships in the separate positively or negatively correlated groups. Groups showing significant positive correlations ('positive' groups) are indicated by subscript 1, and those with significant negative correlations by subscript 2. 95 % confidential limits for σ^2 (variance) were 36.97 and 350.6 for b and 7.34 and 69.6 for c

Discussion

The ULQI allows inferences to be made about the studied populations. Populations 1, 2, and 5 generated positive values of ULQI (Fig. 8), meaning that for these populations all the indices determining the value of the ULQI tended to increase together. Synchronous changes in all adaptability indices were rare in our dataset and were clearest in population 5 which had an ULQI of 0.294. Our data and analyses suggest that this population, situated in the central part of the Point Thomas oasis, is in the optimal position for the development of the Antarctic herb tundra formation in terms of cover development and the simultaneous increase in other indices measured in this study. A similar tendency is also indicated for the populations with lower positive ULQIs—1 and 2.

Populations 3, 4, and 6 generated negative values of the ULQI (Fig. 8), meaning that for these populations an increase in any one index was associated with a decrease in all other indices. In such cases, the ULQI did not depend on geographical factors (see also Fig. 1), and the patterns were

consistent with the concept of a mosaic of microenvironmental conditions even at small physical scale in the maritime Antarctic. Populations with negative ULQIs provide an illustration of the complex interactions that can occur between different adaptability indices at microenvironmental scale. A practical illustration of this complexity is seen in locations where areas for development are limited because of rocky substrata. In such locations, plants in the population can increase adaptability at the expense of increasing biomass (biometric index) and of tissue functional activity (index of relative nuclear DNA content). In an analogous fashion, in locations that are open and exposed to wind abrasion, it is important to develop considerable vegetative mass, which may be compensated by larger cover difference or lower functional activity of leaf cells (cf. Kozeretka et al. 2010; Parnikoza et al. 2011b). In this context, plant responses to environmental changes can be understood as the integration of responses through epigenetic self-regulated networks (Tchuraev 2006a, b) at cellular (due to cell physiological activities), individual (change in plant size), and population levels (cover being

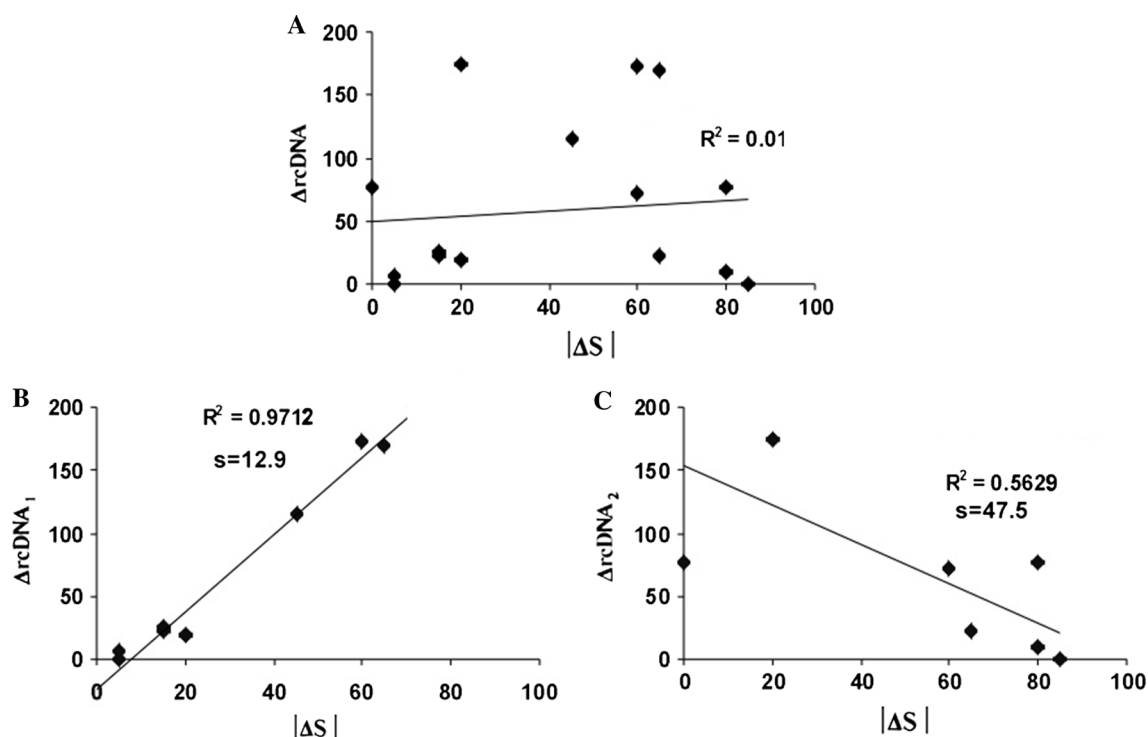


Fig. 5 Pairwise comparison of population pair differences (a) was used to divide populations into two groups with either positive (b) or negative (c) correlation based on regression between cell (Δ rcDNA) and population ($|\Delta S|$) level pair difference sets for *D. antarctica* from the Admiralty Bay region. The graphs show the squares of the respective correlation coefficients and the point variance. The test statistics for R^2 values in the graphs {a $F_{1,15} = 0.16$ [below the 5 %

threshold of the F -distribution for $N = 18$ ($F_{1,16} = 4.49$), b $F_{1,7} = 236.05$ and c $F_{1,7} = 9.02$ [above the 5 % threshold of the F -distribution for $N = 9$ ($F_{1,7} = 5.59$)] indicate the absence of any significant relationship in the overall dataset and the presence of significant linear relationships in the separate positively or negatively correlated groups. 95 % confidential limits for σ^2 (variance) were 72.7 and 689.2 for b and 985.9 and 1061.4 for c

influenced by ground relief and soil conditions) to current microenvironmental conditions, while each of these parameters if considered alone shows their own specific pattern.

Based on the analyses performed, we conclude that the simple measure of land cover is among the best parameters for estimating population fitness. However, this interpretation should still be treated with caution. The successful colonization of, and subsequent population development in, any area will involve both generative and vegetative reproduction. Populations occupying areas of rocky relief, for instance, will only be capable of reaching limited cover values. Such populations may still possess higher biometric indices, due to the creation of small-scale protected microhabitat components.

Biomass-dependent biometric indices are also one of the key parameters of population fitness. Plants with higher biomass have greater opportunity for both sexual and vegetative reproduction (Uchamanski 2003). Increasing biomass of generative and vegetative plant parts may also suggest a positive consequence of regional climate changes (Convey 1996b; Day et al. 2008). Local biomass increase in some populations, in spite of limited cover value, may be

accompanied by the formation of larger numbers of mature seeds and, hence, provide positive feedback for future colonization opportunity.

Environmental variability on intra- or inter-annual timescales may influence the various indices measured here, hence affecting the ULQI calculated in any given year. Comparative analyses of Antarctic plant population adaptability therefore also should be supported by monitoring over a period of years. Furthermore, while the current study demonstrates the potential utility of the ULQI approach, the spatial coverage of sampling areas should be extended beyond the Admiralty Bay region alone, which is known to be experiencing rapidly changing climatic conditions (Rakusa-Suszczewski 1993). For instance, as a result of successive favorable seasons, the cover parameter may increase quite rapidly, only for this trend to be reversed following an unfavorable season (for instance due to extended periods of winter snow cover, or summer drought). Such dynamics are consistent with the results of population studies of *D. antarctica* (Fowbert and Smith 1994; Parnikoza et al. 2009; Vera 2011). Also consistent with this, we have shown variations in biometric parameters and relative DNA content during a month-long

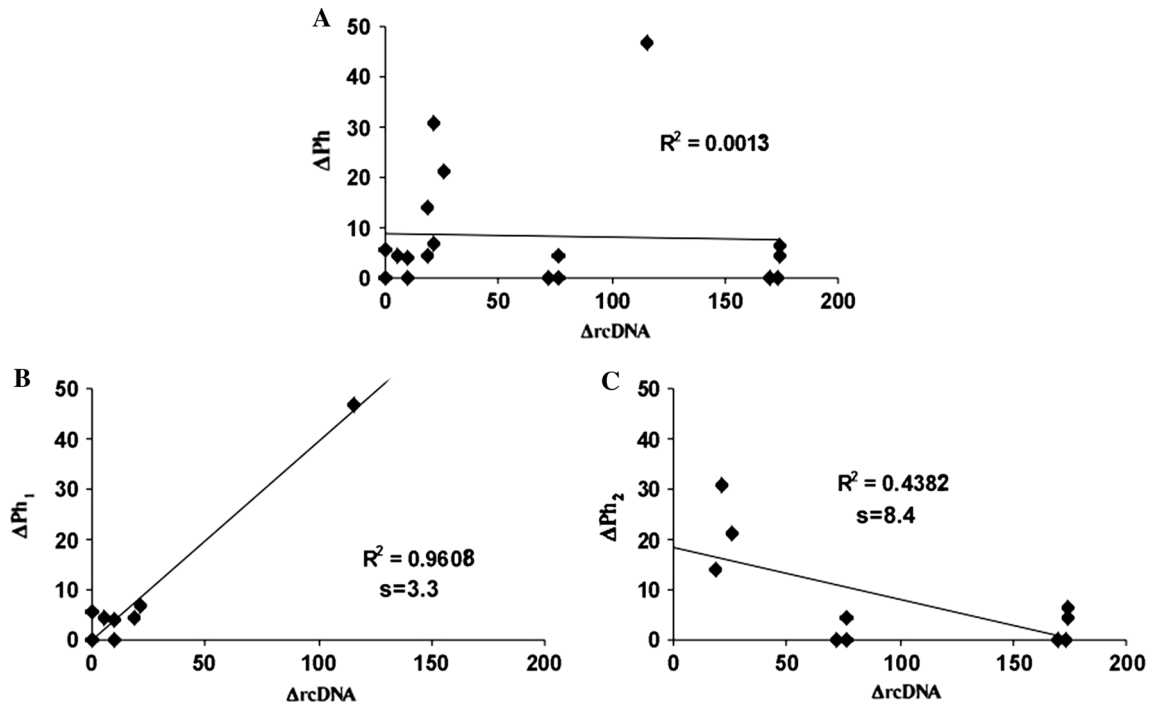
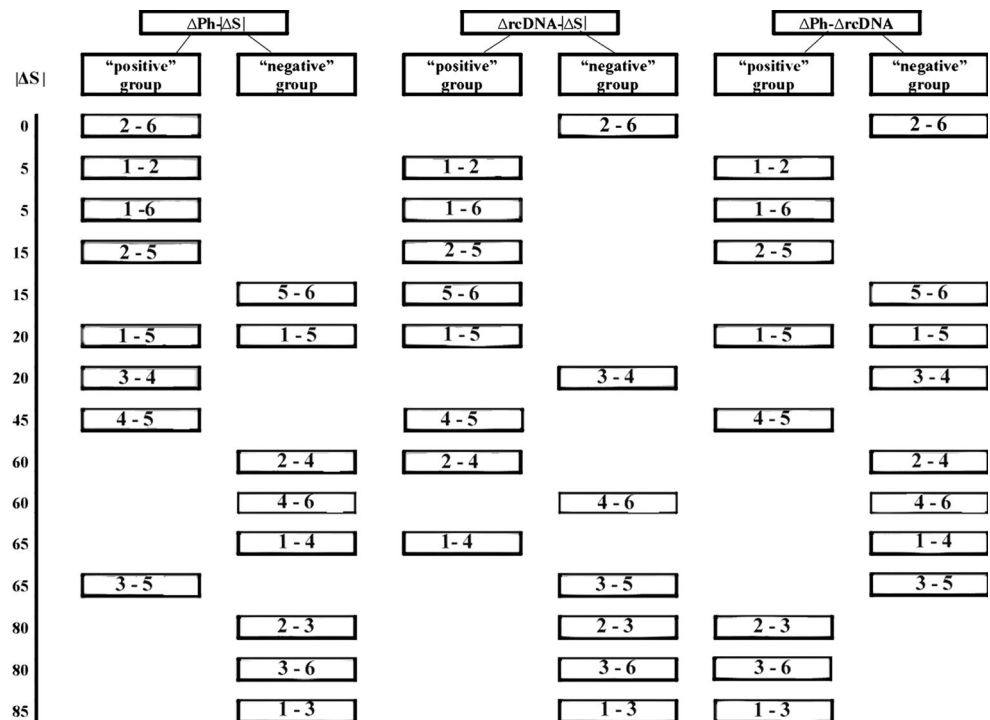


Fig. 6 Pairwise comparison of population pair differences (a) was used to divide populations into two groups with either positive (b) or negative (c) correlation based on regression between individual (ΔPh) and cell ($\Delta cDNA$) level pair difference sets for *D. antarctica* from the Admiralty Bay region. The graphs show the squares of the respective correlation coefficients and the point variance. The test statistics for R^2 values in the graphs {a $F_{1,16} = 0.016$ [below the 5 % threshold of the F -distribution for $N = 18$ ($F_{1,16} = 4.49$)],

b $F_{1,6} = 147.06$ and c $F_{1,8} = 6.24$ [above the 5 % threshold of the F -distribution for $N = 8$ ($F_{1,6} = 5.99$) in b and for $N = 10$ ($F_{1,8} = 5.32$) in c]} indicate the absence of any significant relationship in the overall dataset and the presence of significant linear relationships in the separate positively or negatively correlated groups. 95 % confidential limits for σ^2 (variance) were 4.41 and 52.37 for b and 32.26 and 260.17 for c

Fig. 7 Individual *D. antarctica* population pair differences at cell, individual, and population levels for the ‘positive’ and ‘negative’ correlation groups identified (see Figs. 4, 5, 6). Each pair is positioned along the vertical ($|\Delta S|$, cover pair difference) axis in order of increasing difference



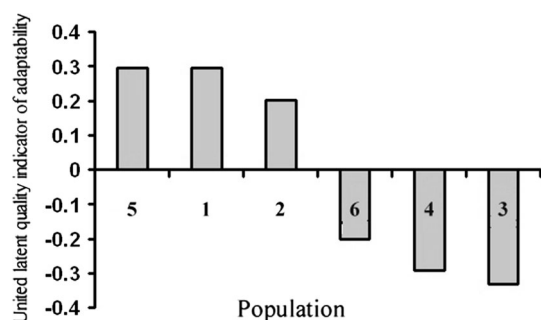


Fig. 8 Calculated values of the united latent quality indicator of adaptability (ULQI) for each of the studied populations of *D. antarctica*. See Fig. 1 and Table 1 for population numbers

study of the effects of natural environmental variation in the Antarctic environment at Point Thomas Oasis (Parnikoza et al. 2011b). The ULQI value obtained will be strongly influenced by the conditions experienced by any given population and season. The ULQI therefore provides a useful indicator of adaptability for annual monitoring over multiple seasons, for use in evaluation of population dynamics.

Acknowledgments We express our gratitude to the National Antarctic Scientific Center of Ministry of the Education of Ukraine and Department of Antarctic Biology of Institute of Biochemistry and Biophysics Polish Academy of Science for assistance in this research. This study was carried out under a contract between the National Antarctic Scientific Center of the Ministry of Science and the Institute of Molecular Biology and Genetics (NAS of Ukraine), # H/3-2011 ‘Development of a Bioindicator System of Climate Change in Coastal Antarctica Based on the Dynamics of Terrestrial Plant Cenoses’ (2011–2012). This work was also supported by the agreement on scientific cooperation between the Polish Academy of Sciences and the National Academy of Sciences of Ukraine within the project ‘Adaptive strategy of mutual survival of organisms in extreme environmental conditions’ (2015–2017), and by the Polish Ministry of Science and Higher Education within the program ‘Supporting International Mobility of Scientists’ and Grant No. NN305376438. We also thank Dr. S. Rakusa-Suszczewski for organizing this expedition, Dr. A. Rozhok for helping with manuscript preparation, and anonymous referees for their constructive input. P. Convey is supported by NERC core funding to the British Antarctic Survey’s Ecosystems Program. This paper also contributes to the SCAR AnT-ERA program.

References

- Aivazyan SA, Buchstaber VM, Yenyukov IS, Meshalkin LD (1989) Applied statistics. Classification and reduction of dimensionality. Finances and statistics, Moscow (**in Russian**)
- Barcikowski A, Czaplowska J, Gielwanowska I, Loro P, Smykla J, Zarzycki K (2001) *Deschampsia antarctica* (Poaceae)—the only native grass from Antarctica. In: Frey L (ed) Studies on grasses in Poland. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, pp 367–377
- Barcikowski A, Czaplowska J, Loro P, Łyszkiwicz A, Smykla J, Wojciechowska A (2003) Ecological variability of *Deschampsia antarctica* in the area of Admiralty Bay (King George Island, maritime Antarctic). In: Frey L (ed) Problems of grass biology. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, pp 393–407
- Bauman EV, Moskalenko NE (2008) Methods of extremal grouping of the fractional parameters. Autom Remote Control 69:1955–1972
- Beyer L, Bölter M (2002) Geoecology of Antarctic Icefree Coastal landscapes. Ecological studies 156. Springer, Berlin
- Bölter M, Kappen L, Meyer M (1989) The influence of microclimatic conditions on potential photosynthesis of *Usnea sphacelata*: a model. Ecol Res 4:297–307
- Causton DR, Venus JC (1981) The biometry of plant growth. Edward Arnold, London
- Conrad M (1983) Adaptability, the significance of variability from molecule to ecosystem. Plenum Press, New York
- Convey P (1996a) The influence of environmental characteristics on life history attributes of Antarctic terrestrial biota. Biol Rev 71:191–225
- Convey P (1996b) Reproduction of Antarctic vascular plants. Antarct Sci 8:127–134
- Convey P (2011) Antarctic terrestrial biodiversity in a changing world. Polar Biol 34:1629–1641
- Day AT, Ruhland CT, Xiong FS (2008) Warming increases above-ground plant biomass and C stock in vascular-plant-dominated Antarctic tundra. Glob Change Biol 14:1827–1843
- Dietz H, Steinlein T (1996) Determination of plant species cover by means of image analysis. J Veg Sci 7:131–136
- Edwards JA (1972) Studies in *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv.: V. Distribution, ecology and vegetative performance on Signy Island. Br Antarct Surv Bull 28:11–28
- Finnigan JJ (2007) The turbulent wind in plant and forest canopies. In: Johnson EA, Miyanishi K (eds) Plant disturbance ecology, the process and the response. Academic Press, London, pp 15–58
- Floyd DA, Anderson JE (1987) A comparison of three methods for estimating plant source. J Ecol 75:221–228
- Fowbert JA, Smith RL (1994) Rapid population increases in native vascular plants in the Argentine Islands, Antarctic Peninsula. Arct Alp Res 26:290–296
- Gielwanowska I (2005) Specific developmental characters of Antarctic vascular plants *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv. Dissertation, University of Warmia and Mazury, Olsztyn (**in Polish**)
- Jong TJD, Klinkhamer PGL (1994) Plant size and reproductive success through female and male function. J Ecol 82:399–402
- Kejna M (1999) Air temperature on King George Island, South Shetland Islands, Antarctica. Pol Polar Res 20:183–201
- Kennedy KA, Addison PA (1987) Some considerations for the use of visual estimates of plant cover in biomonitoring. J Ecol 75:151–157
- Kiernon JA (1990) Histological & histochemical methods. Theory and practice. Pergamon Press, New York
- Kozeretska IA, Parnikoza IYu, Mustafa O, Tyschenko OV, Korsun SG, Convey P (2010) Development of Antarctic herb tundra vegetation near Arctowski station, King George Island. Polar Sci 3:254–261
- Krywult M, Smykla J, Wincenciak A (2013) The presence of nitrates and the impact of ultraviolet radiation as factors that determine nitrate reductase activity and nitrogen concentrations in *Deschampsia antarctica* Desv. around penguin rookeries on King George Island, Maritime Antarctica. Water Air Soil Poll 224:1563
- Krzewicka B, Smykla J (2004) The lichen genus *Umbilicaria* from the neighbourhood of Admiralty Bay (King George Island, maritime Antarctic), with a proposed new key to all Antarctic taxa. Polar Biol 28:15–25

- Kunakh VA (2011) Zhebrak Readings. III. Ontogenetic plasticity of the genome as a basis of plant adaptation. Institute of Genetics and Cytology, NAS of Belarus. Pravo i Ekonomika, Minsk
- Levin DA (2002) The role of chromosome changes in plant evolution. Oxford University Press, Oxford
- Maarel E (2005) Vegetation ecology—an overview. In: Maarel E (ed) Vegetation ecology. Wiley, Malden, pp 1–51
- Miryuta NYu, Kunakh VA (2011) Dynamic of cell population systems in vitro. 2. Temporal organization and robustness of *Rauwolfia serpentina* Benth. culture tissues system at passage level organization. Biotechnology (Ukraine) 4:16–29 (**in Ukrainian**)
- Mosyakin SL, Bezusko LG, Mosyakin AS (2007) Origins of native vascular plants of Antarctica: comments from historical phyto-geography viewpoint. Cytol Genet 41:54–63
- Myers WL, Shelton RL (1980) Survey methods for ecosystem management. Wiley, New York
- Ochyra R (1998) The moss flora of King George Island, Antarctica. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków
- Parnikoza I, Maidanuk DN, Kozeretska IA (2007a) Are *Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunth) Bartl. migratory relicts? Cytol Genet 41:36–40
- Parnikoza IYu, Miryuta NYu, Maidanyuk DN, Loparev SA, Korsun SG, Budzaniwska IG, Shevchenko TP, Polischuk VP, Kunakh VA, Kozeretska IA (2007b) Habitat and leaf cytogenetic characteristics of *Deschampsia antarctica* Desv. in maritime Antarctic. Polar Sci 1:121–127
- Parnikoza IYu, Miryuta NYu, Al-Ammouri Yu, Kunakh VA (2008) *Rauwolfia serpentina* Benth. Cell populations dynamic in the context of different cultivation conditions in vitro. Biopolym Cell 24:300–309
- Parnikoza I, Convey P, Dykyy I, Trokhymets V, Milinevsky G, Inozemtseva D, Kozeretska I (2009) Current status of the Antarctic herb tundra formation in the central Argentine Islands. Glob Change Biol 15:1685–1693
- Parnikoza I, Kozeretska I, Kunakh V (2011a) Vascular plants of the maritime Antarctic: origin and adaptation. AJPS 2:381–395
- Parnikoza IYu, Loro P, Miryuta NYu, Kunakh VA, Kozeretska IA (2011b) The influence of some environmental factors on cytological and biometric parameters and chlorophyll content of *Deschampsia antarctica* Desv in maritime Antarctic. Cytol Genet 45:170–176
- Pollard JHP (1982) A handbook of numerical and statistical techniques. Finances and statistics, Moscow (**in Russian**)
- Rakusa-Suszczewski S (1993) The maritime Antarctic Coastal ecosystem of Admiralty Bay. Department Antarctic Biological Polar Academical Sciences, Warsaw
- Röttgermann M, Steinlein T, Beyschlag W, Dietz H (2000) Linear relationships between aboveground biomass and plant cover in low open herbaceous vegetation. J Veg Sci 11:145–148
- Royles J, Amesbury MJ, Convey P, Griffiths H, Hodgson DA, Leng MJ, Charman DJ (2013) Plants and soil microbes respond to recent warming on the Antarctic Peninsula. Curr Biol 23:1702–1706
- Smith RIL (1994) Vascular plants as indicators of regional warming in Antarctica. Oecologia 99:322–328
- Smith RIL (2003) The enigma of *Colobanthus quitensis* and *Deschampsia antarctica* in Antarctica. In: Huiskes AHL, Gieskes WWC, Rozema J et al (eds) Antarctic biology in a global context. Backhuys, Leiden, pp 234–239
- Strogonov BR (1973) Plant metabolism under salinization: materials of the XXXIII Timiryazev readings. Nauka, Moscow (**in Russian**)
- Tchuraev RN (2006a) Genetal principles of organization and laws of functioning in governing gene networks. In: Kolchanov N, Hofesyaedt R (eds) Bioinformatics of genome regulation and structure. Springer, New York, pp 367–377
- Tchuraev RN (2006b) Epigenetics: gene and epigene networks in the onto—phylogenesis. Genetica 42:1276–1296 (**in Russian**)
- Tømmervik H, Wielgolaski FE, Neuvonen S, Solberg B, Høgda KA (2005) Biomass and production on a landscape level in the mountain birch forest. In: Wielgolaski FE (ed) Plant ecology, herbivory and human impact in Nordic Mountain Birch Forests. Series: Ecological studies, vol 180, Analysis and synthesis. Springer, Berlin, pp 53–70
- Turner J, Colwell SR, Marshall GJ, Lachlan-Cope TA, Carleton AM, Jones PD, Lagun V, Reid PA, Iagovkina S (2005) Antarctic climate change during the last 50 years. Int J Climatol 25:279–294
- Turner J, Barrand NE, Bracegirdle TJ, Convey P, Hodgson DA, Jarvis M, Jenkins M, Marshall G, Meredith MP, Roscoe H, Shanklin J, French J, Goosse H, Guglielmin M, Gutt J, Jacobs S, Kennicutt MC, Masson-Delmotte V, Mayewski P, Navarro F, Robinson S, Scambos T, Sparrow M, Summerhayes CP, Speer K, Klepikov A (2014) Antarctic climate change and the environment: an update. Polar Rec 50:237–259
- Uchamanski J (2003) Ecology of individuals. In: Ambasht RS, Ambasht NK (eds) Modern trends in applied terrestrial ecology. Springer, Berlin, pp 247–274
- Vera ML (2011) Colonization and demographic structure of *Deschampsia antarctica* and *Colobanthus quitensis* along an altitudinal gradient on Livingston Island, South Shetland Islands, Antarctica. Polar Res 30:7146
- Weiner J, Thomas SC (1986) Size variability and competition in plant monocultures. Oikos 47:211–222
- Wolf EB (1937) Polyploidy and geographic distribution of plants. Uspekhi Sovrem Biol 7:161–197 (**in Russian**)
- Zwolska I, Rakusa-Suszczewski S (2002) Temperature as an environmental factor in the Arctowski station area (King George Island, South Shetland Islands). Glob Change 9:51–65