Parnikoza Ivan[1], Miryuta Natalia[1], Ozheredova Iryna[2], Kozeretska Iryna[2], Smykla Jerzy[3], Kunakh Victor[1,] Convey Peter[4]

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

I. Parnikoza (✉), N. Miryuta, V. Kunakh
Institute of Molecular Biology and Genetics,
National Academy of Sciences of Ukraine,
150 Academician Zabolotny Str., Kyiv, 03680, Ukraine
e-mail: Parnikoza@gmail.com

I. Ozheredova, I. Kozeretska
Taras Shevchenko National University of Kyiv,
64 Volodymyrska Str., Kyiv, 01601, Ukraine

J. Smykla
Department of Biodiversity,
Institute of Nature Conservation, Polish Academy of Sciences,
33 Adam Mickiewicz Str., 31-120 Kraków, Poland
Present address:
Department of Biology and Marine Biology,
University of North Carolina, Wilmington,
601 S. College Rd., Wilmington, NC, USA
e-mail: jerzysmykla@yahoo.com

P. Convey
British Antarctic Survey, NERC, High Cross, Madingley Road,
Cambridge CB3 0ET, UK

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. antartica* 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 Admiralty Bay, King George Island (South Shetland Islands, maritime Antarctic) during the austral summer of 2005-06, and analyzed pair-wise inter-relations between various indices reflecting plant population adaptability. The results of these pair-wise 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 micro-environmental 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.

Key words: Antarctic hairgrass, land cover, biometrics, relative DNA content, united latent quality indicator

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 underly 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 (Convey 2011; Turner et al. 2005, 2013; 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 y (Parnikoza et al. 2009).

Many studies of *D. antarctica* have focused on anatomical, life cycle and ecology, physiological or biochemical features (eg. Edwards 1972; Smith 2003; Mosyakin et al. 2007; Parnikoza et al. 2007a, 2011a). 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 towards sexual reproduction (i.e. higher production of viable seeds) under less stressful conditions, may have contributed to the increase of 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 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 Klinhamer 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 Argentine Islands (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* on ice-free areas of Admiralty Bay, 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 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 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 communites are represented only by the Antarctic herb tundra formation (Rakusa-Suszczewski 1993; Ochyra 1998; Parnikoza et al. 2009). The Admiralty Bay area, 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 area, 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 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;
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°).

Plce Fig. 1 near here

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 organisation (S) was measured as the cover of *D. antarctica* as vertical (upright) projection of green plant parts on the ground surface, using a standardised approach (Kennedy and Addison 1987; Floyd and Anderson 1987; Dietz and Steinlein 1996; Röttgermann et al. 2000) (Fig. 2)

Place Fig. 2 near here

From each sampling site one to five visibly undamaged grass tufts with generative organs were collected and placed in sealed paper bags. Within a few hours of collection, all samples were transported to the laboratories of the Polish Station "Arctowski" for processing. In the laboratory, green leaf sub-samples 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 organisation, biometric parameters of all samples were measured on air-dried specimens and included: height of generative stem (from base of steem to inflorescense 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.

Place Table 1 near here

At the cellular level of organisation, 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 sub-samples of leaf parenchyma cells were mounted on microscope slides and stained using the Feulgen technique (Kiernon 1990). Then, 25 nuclei were analyzed in each sub-sample. 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 non-parametric 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 χ^2 = (observed value – expected value)^2/(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 corelations ('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 $F_{1,N-2}=t^2_{n-2}=(N-2)R^2/(1-R^2)$ 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 confidential intervals for σ^2 (error dispersion) 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 divison of the resulting value for each population by 15 – the maximum possible interection 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 micro-environmental 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, are presented in Table 2.

Place Figure 3 and Table 2 near here

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 significant positive (Fig. 4b) and negative (Fig. 4c) correlations, using the external 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 dispersion) data are presented in Figs. 4-6. 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.

Place Figures 4-6 near here

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. Fig. 5 shows the results of analyses relating to cytometric (ΔrcDNA) and cover differences ($|\Delta S|$), and Fig. 6 illustrates the relationships between biometric (ΔPh) and cytometric (ΔrcDNA) differences.

Next, the structures of the 'positive' and 'negative' groups were analysed to determine the proportion of each population in these pairwise groups for three characteristic paires presented in Fig. 7. Fig. 7 illustrates the pattern of interactions between pairs of populations in each of the three combinations of pairwise differences at population ($|\Delta S|$), individual (ΔPh), and cell (ΔrcDNA) levels for each of the 'positive' and 'negative' groups correlation groups identified above. For example, population 2 appeared three times in the 'positive' and twice in the 'negative' groups across the pairwise comparisons ΔPh - $|\Delta S|$, ΔrcDNA - $|\Delta S|$ and ΔPh - ΔrcDNA. 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).

Place Figures 7 and 8 near here

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 of 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

304 of the complex interactions that can occur between different adaptability indices at micro-
305 environmental scale. A practical illustration of this complexity is seen in locations where areas for
306 development are limited because of rocky substrata. In such locations, plants in the population can
307 increase adaptability at the expense of increasing biomass (biometric index) and of tissue
308 functional activity (index of relative nuclear DNA content). In an analogous fashion, in locations
309 that are open and exposed to wind abrasion it is important to develop considerable vegetative
310 mass, which may be compensated by larger cover difference or lower functional activity of leaf
311 cells (cf. Kozeretska et al. 2010; Parnikoza et al. 2011b). In this context, plant responses to
312 environmental changes can be understood as the integration of responses through epigenetic self-
313 regulated networks (Tchuraev 2006a,b) at cellular (due to cell physiological activities), individual
314 (change in plant size) and population levels (cover being influenced by ground relief and soil
315 conditions) to current micro-environmental conditions, while each of these parameters if
316 considered alone shows their own specific pattern.
317
318 Based on the analyses performed, we conclude that the simple measure of land cover is amongst
319 the best parameters for estimating population fitness. However, this interpretation should still be
320 treated with caution. The successful colonization of, and subsequent population development in,
321 any area will involve both generative and vegetative reproduction. Populations occupying areas of
322 rocky relief, for instance, will only be capable of reaching limited cover values. Such populations
323 may still possess higher biometric indices, due to the creation of small-scale protected micro-
324 habitat components.
325 Biomass-dependent biometric indices are also one of the key parameters of population fitness.
326 Plants with higher biomass have greater opportunity for both sexual and vegetative reproduction
327 (Uchamanski 2003). Increasing biomass of generative and vegetative plant parts may also suggest
328 a positive consequence of regional climate changes (Convey 1996b; Day et al. 2008). Local
329 biomass increase in some populations, in spite of limited cover value, may be accompanied by the
330 formation of larger numbers of mature seeds and, hence, provide positive feedback for future
331 colonization opportunity.
332 Environmental variability on intra- or inter-annual timescales may influence the various indices
333 measured here, hence affecting the ULQI calculated in any given year. Comparative analyses of
334 Antarctic plant population adaptability therefore also should be supported by monitoring over a
335 period of years. Furthermore, while the current study demonstrates the potential utility of the
336 ULQI approach, the spatial coverage of sampling areas should be extended beyond the Admiralty
337 Bay area alone, which is known to be experiencing rapidly changing climatic conditions (Rakusa-
338 Suszczewski et al. 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 study of the effects of natural environmental variation in the Antarctic environment at Point Thomas (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.

AcknowledgementsWe express our gratitude to the National Antarctic Scientific Center of the State Agency for Science, Innovation, and Informatization of Ukraine for assistance in this project. 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' (2011-12). 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' (2012-14), 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 A. Rozhok for help 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 Programme. This paper also contributes to the SCAR AnT-ERA programme.

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