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HABITAT CONDITIONS, POPULATION GENETICS AND NICHE PARTITIONING OF THE NAMIBIAN RESURRECTION PLANT *CHAMAEGIGAS INTREPIDUS* DINTER

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Abstract: *Chamaegigas intrepidus* is a tiny poikilohydrous member of the Linderniaceae which grows endemically in ephemeral rock pools on granite outcrops in Central Namibia. Habitat conditions are characterised by (1) frequent and fast desiccation and rehydration during the rainy summer season, (2) complete dehydration during the dry winter season of up to 11 months, (3) high solar irradiation (especially in the ultraviolet range) and high temperatures during the dry season, (4) extreme nutrient deficiencies, especially nitrogen, and (5) diurnal oscillations of pH in the pool water up to 6 units. The plants are adapted to this complex of multiple interacting stress factors via a range of anatomical, biochemical and physiological mechanisms. Furthermore, *Chamaegigas* populations on single inselbergs are genetically isolated, whereas gene flow between sub-populations from different pools on one inselberg is rather high. This pattern of gene flow is in accordance with the predominantly outcrossing breeding behaviour and seed dispersal mode of *Ch. intrepidus.* Within the pools, there is a clear niche partitioning between *Ch. intrepidus* and the less desiccation-tolerant species *Limosella grandiflora* (Scrophulariaceae) with respect to depth (i.e. maximum water level) of the pools. In conclusion, the patchy spatial distribution of suitable habitats within a rather impermeable landscape matrix causes a highly structured genetic diversity. *Chamaegigas intrepidus* survives at its most stressful habitats with dramatic fluctuations of environmental conditions only by immediate responses to de- and rehydration and availability of resources via constitutive mechanisms, which, however, comes at the cost of very slow growth rates. This restricts the habitat of *Ch. intrepidus* to the most extreme of all resurrection plants.

Keywords: poikilohydric cormophytes, limnology, desiccation, habitat isolation, gene flow, breeding system, niche partitioning, Chamaegigas, Namibia.

Introduction

Resurrection plants (poikilohydric vascular plants) are exceptional among higher plants since they can survive intensive dehydration, equilibrating their leaf tissues with air humidity down to 0%, and, during subsequent rehydration, be revived from this air-dried state [11;16]. They occur mostly as epi- or lithophytes in (sub-)tropical South and Southwest Africa (predominantly monocotyledons, but also members of Linderniaceae and Myrothamnaceae; [9]), South America (especially members of Velloziaceae and ferns and fern-related species, e.g. *Selaginella* spp.; [10]), India (e.g. grasses such as *Tripogon* spp.) and Western Australia (e.g. the genus *Borya*) [31]. A small number of resurrection plants can be found in Northern and Central America (grasses, ferns and fern allies such as *Selaginella* spp.), and in Europe (ferns, e.g. *Asplenium, Polypodium*; Gesneriaceae, e.g. *Ramonda* spp.; [32]).

Resurrection plants usually grow as pioneer species on sites with very harsh environmental conditions, especially limited seasonal water availability. A most typical habitat are rock outcrops (see Photo 1), where extensive stands of mat-forming monocotyledons can be found, e.g. in the Western Ghats [31].

Photo 1: Granite outcrops in the savanna transition zone of Central Namibia on the Farm Otjua (Omaruru District)

Poikilohydric species are not known within gymnosperms. However, within angiosperms desiccation tolerance has evolved independently several times. Among monocotyledons, resurrection plants are found e. g. within Asparagales (Boryaceae), Pandanales (Velloziaceae) and Poales (Cyperaceae, Poaceae). Resurrection plants within the dicotyledons evolved within Gunnerales (Myrothamnaceae) and Lamiales (Gesneriaceae, Linderniaceae, Plantaginaceae). Some poikilohydrous members of the genera *Craterostigma* and *Lindernia* and *Chamaegigas intrepidus* (all Linderniaceae) colonize seasonally water-filled rock pools [31].

The tiny *Chamaegigas intrepidus* DINTER, formerly *Lindernia intrepidus* (DINTER) OBERM., is the most spectacular species among all poikilohydric angiosperms. It occurs endemically in Central Namibia [7], where it grows in shallow ephemeral rock pools on isolated granite outcrops (Photo 2). The German botanist Kurt Dinter described the extreme environmental conditions of the plant’s natural habitat nearly 100 years ago [4]. The bottom of the pool in which he discovered this resurrection plant in the year 1909 [3] remained, due to high temperature and a high evaporative demand of the atmosphere, permanently dry for at least half a year. This season of complete dryness is characterized by high solar irradiation, extreme temperatures and almost completely dry air. However, the plants survived in the form of tiny rhizomes (diameter about 1 mm) and shrivelled leaves, which densely covered the bottom of the pool within a 1 cm thick layer of sand grains, dehydrated algae, dead daphnia, animal faeces and leaf litter. As soon as the small pools were filled with water from the first summer rainfall events, a dense mat of small green *Chamaegigas* leaves covered the bottom of the pools within minutes. Already after two days Dinter could see pink-coloured flowers in the midst of small rosette leaves floating on the water on top of a thin stem. HEILMEIER & HARTUNG (2009) describe the history of discovery of *Ch. intrepidus* in detail [19]. In the following account we discuss the plant's habitus, habitat conditions and the plant's adaptations to the stressful site conditions, the implications of its isolated geographical distribution for generative reproduction and gene flow, and the niche partitioning between *Ch. intrepidus* and *Limosella grandiflora* Benth. (Scrophulariaceae), a second resurrection plant occurring also in ephemeral rock pools on these granite outcrops.

Photo 2: Water-filled rock pool on a granite outcrop nearly totally covered by *Chamaegigas intrepidus*

Habitus of *Chamaegigas intrepidus*

Chamaegigas intrepidus is a small aquatic rhizomatous plant. It is unique among resurrection plants since it possesses two types of leaves: (i) 8–15 mm-long lanceolate submerged leaves on a short main axis, (ii) two decussate pairs of sessile floating leaves which form a small rosette on top of the thin stem which is attached to the main axis (Photo 3). Dependent on the water level in the pools, the length of the stalk varies between 1.5 and 10 cm. The centre of the rosette of the floating leaves produces two flowers [1], whose appearance is fully described in [37] and [7]. The rhizome grows close to the bottom of the pools and bears a dense mat of fine roots.

Photo 3: Habit of *Chamaegigas intrepidus*, with lanceolate submerged leaves (length 8 to 15 mm), and floating leaves forming a small rosette on top of a thin stem

Distribution of *Chamaegigas intrepidus*

Within its range of distribution, the semi-desert and savanna transition zone [13;14], *Ch. intrepidus* grows exclusively in areas with granite outcrops (inselbergs). In this arid to semi-arid region annual precipitation amounts to 160 to 570 mm, and rainfalls occur on only 20 to 70 days during summer (November to April), with a high variability from year to year. For example, at the farm Otjua (Omaruru District, Namibia, 21°10'S, 16°E), where most of the studies described in this contribution were performed, precipitation in the season 1996/97 was much higher (453 mm) than in the two previous years (1995/96: 179 mm; 1994/95: 237 mm). During the wet season a large number (up to 60) of dry days may be interrupted by a few (5 to 12) rainy days [25]. The shallow rock pools (maximum water level ca. 15 cm) usually dry out completely during a sequence of several dry days. Over the whole wet season, these ephemeral pools may be filled with water for some 40 to 85 days in total. As a result, during a single rainy season the *Chamaegigas* plants can experience 15 to 20 rehydration-dehydration cycles [12]. Annual average temperature is 20 °C. However, during the dry season air temperatures may rise up to 42 °C, and sun-exposed rocks heat up to 50 °C at least [4]. Average air humidity is 40%, but only 22% at the end of the dry season (September) [25].

Habitat and stress adaptations of *Chamaegigas intrepidus*

The water of the rock pools, in which *Ch. intrepidus* grows, is very poor in nutrients. Possible reasons are the thin layer of debris at the bottom of the pools, the slow weathering of minerals from the granite, and low amounts of atmospheric deposition. Furthermore, after extensive rainfalls, when the shallow pools may overflow, mineral nutrients will be leached out from the sediment [12]. All these factors cause severe nutrient deficiencies. On the other hand, urine and dung are deposited on the rock surface by wild and domestic animals [17]. Especially during the early part of the wet season these excretions are washed into the pools by rainwater, and there may be high amounts of urea and perhaps other dissolved organic nitrogen (DON) compounds present in the pool water.

Chamaegigas is physiologically active during the warm rainy season, whereas it survives the long (up to 11 months) dry season in the dehydrated state [25]. Due to its unique habitat, *Ch. intrepidus* has to withstand a complex set of harsh and interacting environmental conditions: especially during the dry season extremely severe edaphic drought and high solar irradiation in combination with high air temperature and low air humidity pose an extreme, long-lasting set of stressors. In addition, the aquatic habitat exposes the plant to an additional constellation of stressful environmental factors, namely recurrent flooding and drying cycles, low nutrient contents and drastic diurnal fluctuations of pH of the water during the wet season [21]. Fluctuations in pH are caused by diurnally oscillations in carbon dioxide (CO_2) concentration due to (i) changing solubility of CO_2 caused by fluctuations of water temperature and (ii) an interplay of CO_2 consumption and production, with CO_2 depletion due to photosynthesis during the day and CO_2 accumulation due to respiration of plants, animals and microbes during the night [18].

We investigated the ecophysiological responses to this complex set of multiple stresses during several seasons in the natural habitat of *Ch. intrepidus* in Central Namibia, on the farm Otjua, Omaruru District (for site description refer to [18;20]). Due to the large elevation (ca. 1400 m above sea level) there is a high irradiation stress, especially in the ultraviolet range. When the rock pools dry out all parts of the plant become totally dry. Submerged leaves shrink by 80–90% in length, a process which is supported by the unique existence of contractive tracheids [36]. This shrinkage protects the leaves from high radiation stress. In contrast, roots shrink in the lateral direction by 30 to 35% due to shrinkage of the rhizodermis and the exodermis, whereas the large single-layered cortex cells do not shrink after complete desiccation. Pads on the exterior walls of short cells within the dimorphic exodermis may slow down water loss by roots, a trait which has not been found in other aquatic plants [23].

At the physiological, biochemical and molecular level there is a plethora of adaptation processes to the frequent fluctuations of wet and dry conditions through the plant’s ability for fast de- and rehydration – *Ch. intrepidus* shows the fastest stress responses among all poikilohydric cormophytes. Thus, plants dry within less than two hours without any damage to their tissues when water had evaporated from the pools [12]. In turn, the vegetative organs regain full metabolic activity within two hours after rewatering [25]. Protection of cellular integrity is considered to represent the major component of desiccation tolerance in *Ch. intrepidus* [18]. One biochemical component of these protective mechanisms is compatible solutes such as non-reducing sugars, which can maintain hydrophilic interactions in membranes and proteins and prevent crystallisation of the cytoplasm. In *Chamaegigas* leaves, especially stachyose and sucrose increase during dehydration (up to some 15% and 3% of total dry mass respectively) [18]. Macromolecular components of cellular protection are proteins such as dehydrins, which are thought to provide a ‘hydration shell’ around proteins and to sequester ions, whereby they prevent damage to proteins and other chemical cell constituents by excessive salt concentrations resulting from water loss. Such dehydrin-like proteins were found even in fully hydrated submerged leaves of *Ch. intrepidus,* indicating a constitutive mechanism of adaptation [33]. The synthesis of these proteins is triggered by abscisic acid (ABA), a signalling molecule (‘plant stress hormone’), which increased in concentration 20- to 30-fold during dehydration in submerged leaves and roots, correlated with the decrease in osmotic potential, without any threshold [33]. This dramatic increase, which is much higher than the 10-fold increase found usually in drought-stressed plants, indicates a rather fast and sensitive response of ABA biosynthesis to dehydration. Due to the shrinking of submerged leaves, which is associated with intense folding and curling, they will be protected from light induced damage of the photosynthetic apparatus, as has been shown via chlorophyll fluorescence, even after after repeated dehydration and rehydration [38].

Apart from these adaptations to recurrent fast drought and rehydration, *Chamaegigas* plants have to adapt to specific stress factors of their limnic habitat, especially drastic diurnal fluctuations of the pH values of the pool water, and the low nutrient contents, especially nitrogen (N). H^+ concentrations of the pool water oscillate between pH 6.9 (median) in the morning and pH 9.3 in the evening. Maximum oscillations may be even larger (pH 5.8 to pH 12.0, [33]). In spite of these dramatic external pH fluctuations, *Ch. intrepidus* maintains a stable intracellular pH [34]. Although the concentration of nitrogenous compounds like nitrate and ammonium in the pool water is rather low [18], organic N compounds such as amino acids and especially urea are more abundant. *Chamaegigas* plants are able to take up amino acids like glycine and serine by a high-affinity uptake system [35]. This acquisition of amino acids may be especially important when, due to high pH values in the afternoon, ammonium (NH_4^+) is nearly absent from the pool water. The major source of NH_4^+ is urea, which can be utilised by *Ch. intrepidus* after enzymatic degradation via urease. This enzyme is very resistant against the harsh conditions, surviving temperatures up to 60 °C and high UV radiation during more than six months of dry season [22]. This may be an important mechanism for providing NH_4^+ to *Chamaegigas* plants when they resume growth at the beginning of the rainy season when urea deposited on the rock surface by animals is flushed into the pools by the first rainfalls [12].

Adaptations of *Chamaegigas* to habitat isolation: gene flow and breeding system

Endemic species with a limited range of distribution usually show a reduced genetic variability in comparison to widespread species [15]. In addition, rare species which are restricted to small isolated habitats may become genetically isolated and develop pronounced spatial genetic structures. The genetic structure of populations is a result of processes which lead to genetic differentiation (genetic drift and selection) on the one hand and processes that homogenise gene pools (gene flow) on the other. We expected a low gene flow among populations due to the high degree of spatial isolation of *Chamaegigas* habitats with an average distance between individual inselbergs of ca. 25 km. In order to test this hypothesis, we analysed genetic diversity within populations, and genetic differentiation and gene flow among populations by means of highly polymorphic AFLP (amplified fragment length polymorphism) markers [5]. Applying a hierarchical structuring of the populations (individuals nested within pools, pools nested within sites), 71 *Chamaegigas* plants from 17 pools at seven sites were analyzed with three primer combinations resulting in 82 AFLP markers.

Genetic diversity among individuals turned out to be high at the pool and site level, but there was no correlation between genetic diversity and population size [5]. Genetic differentiation between sites (17% of total variation) was higher than genetic variation among pools within sites (6%) as revealed by analysis of molecular variance. Surprisingly, most variability was found among individuals within pools (77% of total variation). Hence, *Chamaegigas* on the different inselbergs is genetically highly diverse. Genetic differentiation was not correlated with geographic distance. These findings agree with results from AFLP fingerprinting of two endemic monotypic Balkan Boraginaceae genera from serpentine outcrops, where the greatest proportion of genetic variation was found within, not between populations, and genetic distances were not related to geographic distances [2]. A high genetic diversity within clonal plants has also been reported for other long-lived vegetatively reproducing species [6]. In contrast, the clonal bromeliad *Pitcairnia encholirioides*, which grows on granitic inselbergs in the Brazilian Atlantic Forest, showed a highly structured genetic diversity with half of total genetic variance occurring between groups, due to limited dispersal of seeds [26].

The high level of genetic diversity within pools and low differentiation between pools on a granite outcrop, are in accordance with the breeding system and dispersal mode. The pollen/ovule ratio (99) is rather low in *Ch. intrepidus* compared to xenogamous plant species [29]. However, pollination experiments indicated that *Chamaegigas* is a predominantly outcrossing species. In addition, a large amount of pollen could be found both on the wild bee and beetle species visiting the flowers [5]. At the natural site, two bee species *(Liotrigona bottegoi* and *Apis mellifera*) and mostly two beetle species of the genus *Condylops* (*C. erongoensis* and a newly identified species; family Malachidae) have been identified as main pollinators [39]. The zygomorphous flowers show a typical insect pollination syndrome: they are slightly protandric, distinctly coloured and intensively scenting and provide abundant pollen grains (5940 pollen grains per flower). Thus, despite low pollen/ovule ratios, outcrossing may be facilitated by synchronous flowering and efficient insect attraction. The flowers do not produce any nectar as a floral reward. Rather, dense layers of trichomes (400 to 1600 per mm^2) cover the lower lip, similar to well-known oil-flowers (e.g. in Plantaginaceae species: [28]). However, we could not find any hint that *Chamaegigas* lives in a symbiosis with oil-flower or oil-collecting bees [39].

The insects identified as potential pollinators will predominantly pollinate plants from the same inselbergs. Since they should not be restricted to single pools, visiting of *Chamaegigas* plants from several pools by pollinators will result in only slight differentiation among pools. However, due to the large distance pollinators only rarely will be able to migrate between different inselbergs. The numerous tiny seeds that are well dispersed by wind will also predominantly accomplish gene flow among pools within the same site but may be transported secondary [30].

In conclusion, this endemic species does not show any genetic impoverishment as shown by the high genetic diversity within pools, a result of large population sizes of the tiny plants and high gene flow via pollinating insects and wind dispersed seeds. In addition, the intense UV radiation at the high altitude of 1000 to 1500 m a.s.l. should result in many mutations and thus add to genetic variability. Both these processes may provide the genetic basis for a successful adaptation of *Chamaegigas* to its extreme habitat conditions.

Niche partitioning

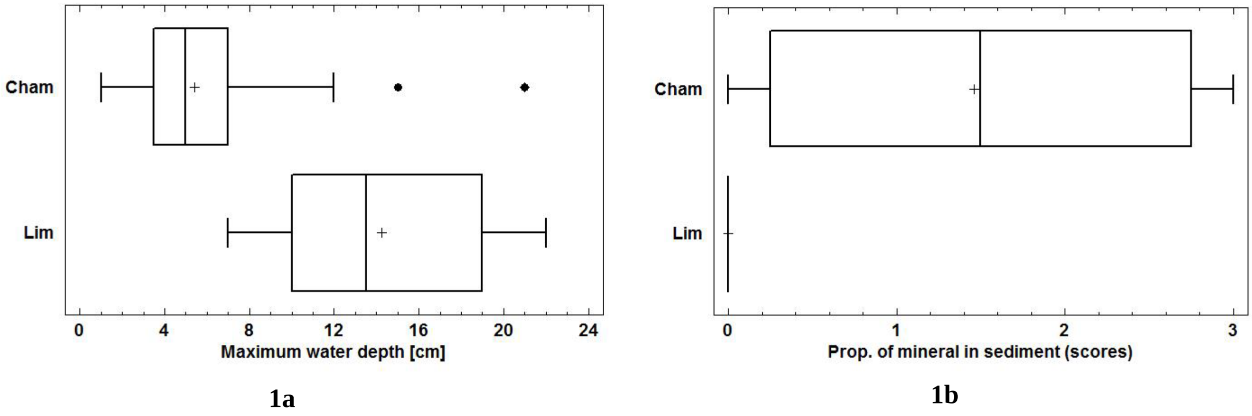
The complex stress factors described above act on a very short time scale, and most *Chamaegigas* plants are hydrated for three to five days only. Thus *Ch. intrepidus* can survive only due to the existence of constitutive mechanisms for desiccation tolerance [21]. The "productivity trade-off hypothesis" [1] states that this ability to tolerate desiccation involves costs that constrain growth and reproduction (see also [16]). As our measurements of photosynthetic activity have shown, the short period when the leaf tissues are sufficiently hydrated reduces carbon gain significantly [38]. As a result, competitive strength of *Ch.*

intrepidus will be low, which should restrict the species to habitats with an extreme constellation of environmental factors. It was already noted by GAFF & GIESS in 1986 that *Ch. intrepidus* occurs in the shallowest ephemeral pools, whereas *Limosella grandiflora*, a species which is also considered as a resurrection plant, grows in deeper pools [12]. However, leaves of *L. grandiflora* are not desiccation tolerant in contrast to *Ch. intrepidus*, only the rhizomes can survive desiccation. Thus we tested the hypothesis that there is a clear differentiation between the pools in which *Ch. intrepidus* occurs and those with *L. grandiflora* with respect to maximum water level: Deep pools should not be colonized by *Ch. intrepidus*, first because of its low competitive ability, second because of the maximum length of its flowering stalk of about 10 cm (see above). On the other hand, shallow pools should not be colonized by *L. grandiflora*, since the leaves of this species would not tolerate the frequent drying cycles, which, due to costs in leaf regeneration upon rewetting of the pools, would reduce competitive strength in pools with a low maximum water depth. When the pools investigated were tested with respect to occurrence of these two species, a clear pattern emerged (Table 1): Maximum water levels of pools in which *Ch. intrepidus* was occurring ranged from 3 to 7 cm (first and third quartile), whereas *L. grandiflora* occurred in pools with a minimum water depth of 7 cm only (Fig. 1a). A second pool parameter which discriminated occurrence of both species was the proportion of mineral particles in the sediment. Whereas *L. grandiflora* was found in pools where the sediment was purely organic, the bottom of pools in which *Ch. intrepidus* was growing can be covered with completely mineral sediment (Fig. 1b). The parameters depth of sediment (as an indicator for nutrient pools and long-term persistence of plants by anchoring roots and rhizomes) and electric conductivity (as an indicator for the nutrient concentration) of the pool water did not differentiate between pools with *Ch. intrepidus* versus *L. grandiflora* (Table 1).

Table 1: Levels of significance for presence of *Chamaegigas intrepidus* versus *Limosella grandiflora* as dependent on properties of ephemeral rock pools

Parameter	*Ch. intrepidus*		*L. grandiflora*		Mann-Whitney U-test	
	Range	Median	Range	Median	U	P
Maximum water level (cm)	1–21	5	7–22	13.5	44.5	< 0.004
Depth of sediment (cm)	0.1–3	0.1	0.1–1	0.3	267.5	0.544
Mineral proportion in sediment (scores: 0: no; 3: 100%)	0–3	1.5	0	0	748.0	< 0.001
Electrical conductivity (μS cm^{-1})	3.8–40	10.5	6.0–20	16.4	45.0	0.531

A habitat model also revealed maximum water level as a significant predictor for the presence of both species. In addition, for *Ch. intrepidus* both type and depth of sediment were significant predictors, but not conductivity. Thus the probability of occurrence of *Ch. intrepidus* declined with increasing water level (i.e. more stable conditions with respect to hydration), and with increasing proportion of minerals in the sediment [24].



1a

1b

Fig 1: Presence of the two aquatic resurrection plants *Chamaegigas intrepidus* (Cham) and *Limosella grandiflora* (Lim) in rock pools on granite outcrops in Central Namibia with respect to (a) maximum water depth (maximum water level) and (b) proportion of mineral particles in the sediment. The box shows lower and upper quartiles, the central vertical line the median, the cross indicates the arithmetic mean. Whiskers indicate the lowest and largest value in the data set, except in the case of outside points according to Tukey which are shown as dots.

Conclusions

Apart from temporal unpredictability, the spatial arrangement of suitable habitats for *Chamaegigas* within the (semi-)arid landscape matrix is rather irregular. The distribution patterns of inselbergs in the savannah landscape which is nearly impermeable for *Ch. intrepidus* are highly random. The high genetic variability found within the local population in single pools agrees with the predominantly outcrossing breeding behaviour and seed dispersal mode. In view of the short distances between pools inhabited by *Chamaegigas* on one granite outcrop, the high abundance of pollinating beetles and wild bees and seed dispersal by wind enable a high gene flow both within and among pools on a single inselberg, which decreases genetic subdivision within populations [27]. On the other hand, the minimum distance between inselbergs (ca. 10 km) is much larger than the flight distance of the insects which pollinate *Ch. intrepidus*. Furthermore, seed dispersal by birds or animals which visit the pools for drinking water and could act as vectors for seeds should be rare over these large distances. This assumption is supported by two lines of evidence from the AFLP analyses: (i) the high level of genetic differentiation between sites, (ii) the non-significant correlation between genetic differentiation and geographic distance which suggests that isolation by distance does not occur. Rather, the patchy spatial distribution of suitable habitats within a landscape matrix with low connectivity drastically reduces gene flow between inselbergs and enhances differentiation between *Chamaegigas* populations.

The contrasting desiccation tolerance of the two resurrection plants *L. grandiflora* and *Ch. intrepidus* is clearly related to their occurrence in different types of pools, depending on the duration of pools being water filled, and the frequency and velocity of desiccation. Due to its strongly expressed mechanisms of stress tolerance described above, *Ch. intrepidus* is able to respond immediately to the frequent and fast desiccation events, which are characteristic for shallow pools, without any damage to molecular, sub-cellular and cellular structures. On the other hand, the rapid resumption of photosynthesis after rehydration and the utilisation of urine, which is especially abundant in the pool water at the beginning of the growing season, and of amino acids allow an effective acquisition of resources. Nevertheless, the short period of resource availability and the slow growth rate, which results from the high metabolic costs associated with constitutive tolerance mechanisms, restrict the habitat of *Ch. intrepidus*, the "fearless dwarf giant", to the most extreme of all resurrection plants.

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CONDIŢIILE ECOLOGICE, GENETICA POPULAŢIEI ŞI PARTIŢIONAREA NIŞEI PLANTEI NAMIBIENE *CHAMAEGIGAS INTREPIDUS* DINTER

(Rezumat)

Chamaegigas intrepidus este o plantă poikilohidră din familia Linderniaceae care este endemică şi creşte, cu caracter efemer, în bazine stâncoase, pe aflorimente de granit, în centrul Namibiei. Condiţiile de habitat se caracterizează prin (1) desicări şi rehidratări frecvente şi rapide în timpul sezonului ploios de vară, (2) deshidratarea completă în timpul

sezonului uscat de iarnă – până la 11 luni, (3) radiaţie solară ridicată (mai ales în gama ultravioletelor) şi temperaturi înalte în timpul sezonului secetos, (4) deficienţe nutritive extreme, mai ales azot şi (5) oscilaţii diurne ale pH-ului din apă cu până la 6 unităţi. Plantele sunt adaptate acestui complex de factori de stres printr-o serie de mecanisme anatomice, biochimice şi fiziologice. În plus, populaţiile de *Chamaegigas* de pe un singur afloriment sunt izolate genetic, iar fluxul genetic între subpopulaţiile din diferite bazine de pe acelaşi afloriment este destul de ridicat. Aceste model de flux genetic este în concordanţă cu comportamentul de înmulţire şi modul de dispersie a seminţelor pentru *Ch. intrepidus.* În interiorul aceluiaşi bazin există o partiţionare clară a nişelor între *Ch. intrepidus* şi *Limosella grandiflora* (Scrophulariaceae), o specie mai puţin rezistentă la uscăciune, în ceea ce priveşte adâncimea (nivelul maxim al apei) bazinului. În concluzie, distribuţia spaţială neuniformă a habitatelor favorabile într-o matrice peisagistică destul de impermeabilă cauzează o diversitate genetică foarte structurată. *Chamaegigas intrepidus* reuşeşte să supravieţuiască în habitate cu mulţi factori de stres şi cu fluctuaţii dramatice ale condiţiilor de mediu prin răspunsuri imediate la deshidratare şi rehidratare şi disponibilitatea resurselor prin mecanisme constitutive, care însă determină rate de creştere foarte reduse. Toate acestea restricţionează habitatul pentru *Ch. intrepidus* la condiţii extreme.

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