



Clonal growth forms in Arctic plants and their habitat preferences: a study from Petuniabukta, Spitsbergen

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Abstract: The ability to grow clonally is generally considered important for plants in Arctic regions but analyses of clonal characteristics are lacking for entire plant communities. To fill this gap, we assessed the clonal growth of 78 plant species in the Petuniabukta region, central Spitsbergen (Svalbard), and analyzed the clonal and other life-history traits in the regional flora and plant communities with respect to environmental gradients. We distinguished five categories of clonal growth organs: perennial main roots produced by non-clonal plants, epigeogenous rhizomes, hypogeogenous rhizomes, bulbils, and stolons. Clonal growth differed among communities of the Petuniabukta region: non-clonal plants prevailed in open, early-successional communities, but clonal plants prevailed in wetlands. While the occurrence of plants with epigeogenous rhizomes was unrelated to stoniness or slope, the occurrence of plants with hypogeogenous rhizomes diminished with increasing stoniness of the substratum. Although the overall proportion of clonal plants in the flora of the Petuniabukta region was comparable to that of central Europe, the flora of the Petuniabukta region had fewer types of clonal growth organs, a slower rate of lateral spread, and a different proportion of the two types of rhizomes.

Key words: Arctic, Svalbard, vascular plants, clonal growth, substrate.

Introduction

For plants in cold regions, like the Arctic and alpine zones, clonal growth (*i.e.*, vegetative growth resulting in the production of genetically identical and potentially physically independent offspring) is traditionally considered to be important because it helps to ensure the reproductive success in a stressful environment, and it enables the foraging for nutrients over a large area by means of an interconnected network of rooting units (Callaghan and Emanuelson 1985; Jónsdóttir *et al.* 1996; Callaghan *et al.* 1997). However, the paradigm of a high proportion of clonally

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growing species in cold regions was recently questioned (Jónsdóttir 2011; Klimešová and Doležal 2012). In these two studies, comparisons of available data indicated that the proportion of clonal plants in regional floras of cold environments (above alpine and Arctic timberline) is not higher than in reference regions from lower latitudes or altitudes. Moreover, the authors postulated that some kinds of clonal growth organs, namely belowground rhizomes, might be damaged by soil cryoturbation (and therefore maladapted to cold environments) and that some habitats traditionally inhabited by clonal plants in temperate zones, *e.g.*, open water, might be less vegetated or devoid of vascular plants in cold environments (Klimešová and Doležal 2011).

The first step in understanding the function of clonal growth in the Arctic is the assessment of the distribution and habitat preferences of clonal and non-clonal Arctic plants. Despite a long tradition in growth-form characterization and analyses over the last 200 years (von Humboldt 1806; Grisebach 1872; Drude 1887; Raunkiaer 1907; Warming 1923; Du Rietz 1931; Gimingham 1951; Hejný 1960; Łukasiewicz 1962; Den Hartog and Segal 1964; Serebrjakov 1964; Parsons 1976; Hallé *et al.* 1978; Barkman 1988; Halloy 1990; Kästner and Karrer 1995; von Lampe 1999; Krumbiegel 1998, 1999), data concerning the local flora of Arctic ecosystems are rare (Polozova 1981; Komárková and McKendrick 1988) and are not focused on clonal growth. On the other hand, we do have information on the clonal growth of a few of Arctic species (Warming 1908, 1909; Bell and Bliss 1980; Bauert 1996; Kjølner *et al.* 2006), and some clonal species that occur in the Arctic also occur in alpine regions (Hartmann 1957). For these species and according to a survey of the literature, clonal growth organs do not differ between species growing in the Arctic and in central Europe, where a detailed classification is available (Klimešová and Klimeš 2006, 2008). The classification developed for central Europe could be therefore used for Arctic regions (Klimešová and de Bello 2009).

Classification of clonal growth organs, which is based on simple morphological characters and especially on belowground organs, has two steps. First, one determines whether adventitious roots or adventitious shoots are formed. Second, one determines which organs bear buds for shoot iteration (*sensu* Hallé *et al.* 1978), which organ provides connections between ramets, and where these organs are located (aboveground or belowground). These steps or principles have already been successfully used for the classification of clonal growth organs in Ladakh, West Himalaya (Klimešová *et al.* 2011a).

The current study was conducted in a high Arctic site in central Spitsbergen of the Svalbard archipelago. We searched the local flora around Petuniabukta, an area that contains about 80 species of vascular plants (about half of the flora of the Svalbard archipelago; *cf.* Rønning 1996) and six plant communities could be distinguished there (Prach *et al.* 2012 this volume). We had the following aims: (i) to assess the diversity of clonal growth organs and other clonal traits of the flora in

the studied area, and (ii) to evaluate the distribution of clonal growth organs and other clonal traits in the plant communities of the area and along environmental gradients, with particular emphasis on the slope and stoniness of the substrate. We also analyzed other plant traits (*e.g.*, growth forms, Raunkiaer's life-forms) to enable comparison with data from the literature. To correlate clonality and environmental conditions, we used two different approaches: cross-species analysis and relative species abundance in a community; this enabled us to distinguish between rare and common plants (Grime 2006).

Materials and methods

Plant characteristics. — The field data were collected during three expeditions in 2008, 2009, and 2010 around Petuniabukta. This area is the northernmost part of Billjefjorden, and it represents a branch of the main Svalbard fjord Isfjorden. The time of sampling corresponded with the peak of the vegetation season, which in this area lasts from mid-June to mid-September. Plants for morphological description (several individuals of each species, if possible) were excavated with their belowground organs. Plants were cleaned of soil, and their morphology was examined and drawn. The plants were then dried between paper sheets for future comparison and determinations. The plant material is stored in the PRA herbarium (Institute of Botany, Academy of Sciences of the Czech Republic). In total 78 vascular plant species were collected and evaluated for vegetative morphology.

For the studied species, we recorded information on several life-history traits including growth form (dwarf shrubs, forbs, grasses, *etc.*), Raunkiaer's life form (hemicryptophytes, therophytes, *etc.* based on the position of renewing meristems, Raunkiaer 1907), leaf arrangement along the stem (erosulate, semirosette, rosette), type of root system (perennial main root or adventitious roots), and clonality. The clonal traits included type of clonal growth organ, lateral spread, and shoot cyclicity (life-span of a shoot) (Klimešová and Klimeš 2006, 2008). The traits recorded and their definition and functions are listed in Table 1.

Vegetation and environmental characteristics. — Of the 78 species, 60 were recorded on 53 sampling plots (phytosociological relevés) of the surface 5 × 5 m. The plots where vegetation composition was recorded (species composition and visual estimation of cover by vascular plant species, mosses, and stones, and visual assessment of stoniness and slope) were non-randomly distributed because large areas were devoid of vascular plants (very unstable slopes, glaciers). The relevés were placed so as to include all vegetation types and habitats in all parts of the delimited areas. Taxonomy and nomenclature follows Elvebakk and Prestrud (1996).

Table 1

List of studied plant characteristics of vascular plants in Petuniabukta. Individual clonal growth organs are defined as follows: main root – perennial main root providing the only connection between aboveground and belowground plant parts and thus characterizing non-clonal perennials; hypogeogenous rhizome – belowground stem initiated belowground, bearing scale leaves and usually having long internodes; epigeogenous rhizome – belowground stem initiated aboveground and only later pulled into the soil or covered by soil, usually bearing green leaves and having short internodes; bulbils – bulbils and plantlets in axils of leaves and/or in inflorescence; stolons – aboveground creeping stems.

Plant characteristics	Categories	Definition / Reference	Function
Growth forms (%)	Shrub	Basic growth forms with delimitation based on taxonomy / Elvebakk and Prestrud 1996	Taxonomical groups share many traits and therefore they usually have similar functions in the ecosystem and similar strategies
	Forb		
	Grass		
	Sedge		
	Horsetail		
Leaf distribution (%)	Erosulate	Leaf distribution along shoot / Klimešová and Klimeš 2006	Competitive ability (erosulate) versus disturbance avoidance (rosette)
	Semirosette		
	Rosette		
Raunkiaer's life forms	Hemicryptophytes	Vertical distribution of overwintering parts from which spring regrowth occurs (renewal bud or seed) / Raunkiaer 1907	Response to climatic conditions: the more severe the conditions (winter frosts, summer draught), the lower the position of buds in relation to the soil surface; when permafrost is present, overwintering buds are concentrated on the soil surface
	Geophytes		
	Therophytes		
	Chamaephytes		
Clonal growth organ CGO (%)	Main root	Organ through which potential for clonal growth is realized / Klimešová and Klimeš 2006	Rhizomes anchor the plant and enable lateral spread and storage of carbohydrates whereas bulbils and stolons serve only for clonal multiplication. Perennial main roots increase plant anchorage and storage of carbohydrates but their potential for clonal growth by splitting is very limited
	Epigeogenous rhizome		
	Hypogeogenous rhizome		
	Bulbils		
	Stolone		
Lateral spread [cm/yr]	Nonclonal	Lateral spread due to clonal growth / Klimešová and Klimeš 2006	Lateral spread enables the plant to colonize a new substrate and avoid intraspecific competition. Limited lateral spread could be expected in situations where facilitation is important
	<1		
	1–5		
	5–10		
	Dispersable		
Shoot cyclicity	Monocyclic	Number of years (cycles) from resprouting of bud to flowering and fruiting of shoot / Klimešová and Klimeš 2006	In stressful environments, shoots tend to be polycyclic because they need more time for development
	Bicyclic		
	Polycyclic		
Root system	Main root	Main root develops from seminal root of embryo, roots formed on stem parts are adventitious roots / Klimešová and Klimeš 2006	Only plants capable of producing adventitious roots have the potential for clonal growth because the main root rarely splits; this restricts clonal multiplication
	Adventitious roots		

Table 2
The characteristics of plant communities in Petuniabukta (Prach *et al.* 2012 this volume).
Total area covered by vegetation was about 33 km².

Community type	Typical species	Habitat description	No. of vascular plants	No. of relevés	% of area with vegetation
<i>Dryas octopetala</i>	<i>Dryas octopetala</i> , <i>Carex misandra</i> , <i>C. nardina</i> , <i>C. rupestris</i> , <i>Saxifraga oppositifolia</i> , <i>Casiope tetragona</i> , <i>Salix polaris</i> , <i>Eutrema edwardsii</i> , <i>Salix reticulata</i>	Stabilized surfaces, dry and exposed sites, from low to high altitude	10	19	40
<i>Saxifraga oppositifolia</i>	<i>Saxifraga oppositifolia</i> , <i>Braya purpurascens</i> , <i>Draba</i> sp. div.	Sparse vegetation on young, unstabilized fluvial sediments, morains, screes, or maritime terraces	8	13	45
<i>Carex</i> -moss	<i>Carex subspathacea</i> , <i>C. paralella</i> , <i>Ranunculus pygmaeus</i> , <i>Equisetum</i> sp. div., <i>Puccinipissia vacillans</i> , <i>Eriophorum scheuchzeri</i>	In alluvial wet habitats, snow beds, or on seepages	13	12	6
<i>Deschampsia borealis</i>	<i>Deschampsia borealis</i> , <i>D. alpina</i> , <i>D. caespitosa</i>	Around streams and eutrophic spots near settlements	9	3	<1
<i>Papaver dahlianum</i>	<i>Papaver dahlianum</i> , <i>Silene uralensis</i> subsp. <i>arctica</i>	On fine screes at higher altitudes, with both low vegetation cover and species richness	5	3	<1
<i>Festuca baffinensis</i>	<i>Festuca baffinensis</i> , <i>Cochlearia groenlandica</i> , <i>Saxifraga hieracifolia</i> , <i>S. nivalis</i> , <i>S. cespitosa</i> , <i>S. cernua</i> , <i>Cerastium arcticum</i>	Species-rich vegetation developed on eutrophic soils under bird nesting sites	14	2	<1

For comparative purposes, phytosociological relevés were classified into six community types based on dominant species. Their description and extent in the studied area are indicated in Table 2 (for further details, see Prach *et al.* 2012 this volume).

Statistical analyses. — To assess whether the communities differed in studied plant traits, we calculated for each sampling plot (relevé) the proportion of species with given traits. In assessing these proportions, we used two approaches: (i) cross-species analysis based on presence or absence, *i.e.*, the analysis did not take into account species differences in abundance (abundance is equivalent to plant cover in this paper); and (ii) weighted analysis taking into account species abundance in a plot. Studies of trait composition may yield different results depending on whether or not species importance includes abundance. Differences in plant characteristics among the six community types were tested with ANOVA and *post hoc* unequal N HSD tests. Because of the non-normality of the data in some of the tested variables, significance levels of factors were determined using randomization procedures. The observed test statistic was compared with the null distribution

of the test statistic obtained via Monte-Carlo resampling with 9999 permutations. Analyses were run using R software (R Development Core Team 2010).

Overall differences in trait composition between the six communities were evaluated with constrained ordination and redundancy analysis (RDA, no standardization by samples was applied) using the program Canoco for Windows (Ter Braak and Šmilauer, 1998). The six community types were used as explanatory dummy variables, and their effects were tested using the Monte Carlo permutation test (999 unrestricted permutations). Additionally, plot level factors – slope inclination and proportion of ground covered by stones (stoniness) – were used as supplementary environmental variables. The results of multivariate analysis were visualized in the form of a bi-plot ordination diagram constructed by the CanoDraw program (<http://www.canodraw.com/>).

Results

Characteristics of the local flora. — In the local flora of Petuniabukta, we recorded one annual and 77 perennial species. Among the perennial species, we distinguished five categories of clonal growth organs: non-clonal plants with a perennial main root, clonal plants with epigeogenous rhizomes, hypogeogenous rhizomes, bulbils, and stolons (Figs 1–3).

The most abundant growth forms among vascular plants in Petuniabukta region were forbs, followed by grasses, sedges, dwarf-shrubs, and horsetails (Fig. 1). Most vascular plants were perennial hemicryptophytes, and most of the remainder were either chamaephytes or geophytes; only one species (*Koenigia islandica*) was classified as a therophyte. About 38% of the species were non-clonal perennial plants (forbs) with perennial main root (Fig. 1). Clonal plants generally prevailed over non-clonal plants, and included all grasses, sedges, and most of the forb species. The most abundant clonal plants were those with short epigeogenous rhizomes; clonal plants with hypogeogenous rhizomes were less abundant (Fig. 1). Only a few species were able to form longer rhizomes with lateral spread 5–10 cm per year (the horsetails *Equisetum arvense* and *E. variegatum*; the grasses *Dupontia psilosantha* and *Poa arctica*; the sedge *Carex subspathacea*; and cotton-grass *Eriophorum scheuchzeri*) (Fig. 2).

Plant characteristics in different plant communities. — When vegetation around Petuniabukta was divided into six community types (Table 2 and Fig. 4) and compared in terms of trait composition using multivariate redundancy analysis (RDA), the differences were highly significant and explained 40.4 and 42.8% of the total variation in abundance-weighted and cross-species (unweighted) data, respectively (both $P = 0.001$). The results of both weighted data and data unweighted by abundance showed similar patterns. Therefore, only results from the former approach are presented in the RDA ordination diagram (Fig. 5). The main trait

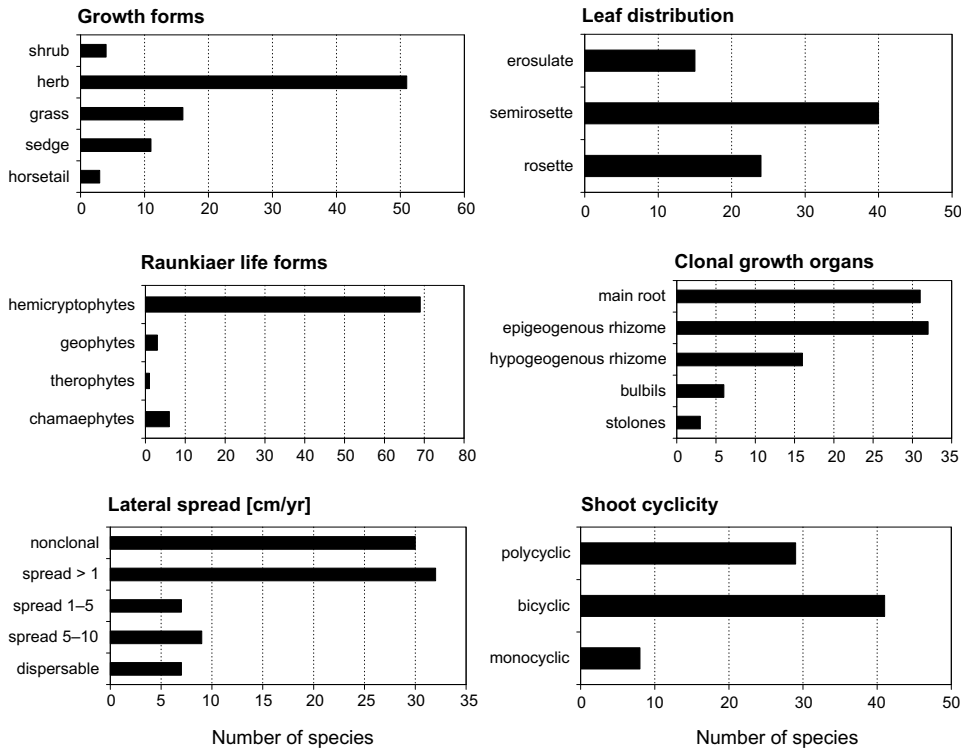


Fig. 1. Spectra of plant characteristics in the flora of Petuniabukta, central Spitsbergen, Svalbard.

compositional changes along the first ordination axis were associated with substrate age, *i.e.*, the first axis separated the *Dryas octopetala* community (drier, exposed places) and *Carex*-moss community (wet, alluvial habitats) on old, stabilized surfaces from the *Saxifraga oppositifolia* community (young, stony deposits from streams and glaciers) and *Papaver dahlianum* community (fine screes on steep slopes at higher altitudes) on young, unstabilized surfaces. The compositional changes along the second ordination axis seemed to be associated with the topographic moisture gradient, *i.e.*, the second axis separated drier habitats (*Dryas octopetala* community) from wetter habitats (*Carex*-moss and *Deschampsia* spp. alluvial communities).

The first RDA axis was associated with the occurrence of non-clonal forbs with perennial main roots, which prevailed in the *Papaver dahlianum* and *Saxifraga oppositifolia* communities on steep and stony slopes of young surfaces (Figs 4, 5). The smallest number of non-clonal forb species was found in the most widespread type of community (the *Dryas octopetala* community), where shrubby species (*D. octopetala*, *Cassiope tetragona*, *Salix polaris*, and *S. reticulata*) with erosulate polycyclic shoots predominated (Fig. 6) and were accompanied by clonal tussock sedges and grasses with short lateral spread and adventitious roots (*e.g.*, *Carex*





Fig. 3. Field view on representative species with selected clonal growth organs. **1.** *Dryas octopetala*, perennial main root and epigeogenous rhizomes. **2.** *Festuca baffinensis* epigeogenous rhizome. **3.** *Koenigia islandica* annual plant. **4.** *Salix polaris*, hypogeogenous and epigeogenous rhizomes. **5.** *Cassiope tetragona*, epigeogenous rhizome. **6.** *Papaver dahlianum*, non-clonal perennial, perennial main root. **7.** *Braya purpurascens*, non-clonal perennial, perennial main root. **8.** *Silene uralensis* subsp. *arctica*, nonclonal perennial, perennial main root. **9.** *Carex misandra*, epigeogenous rhizome. **10.** *Eryophorum scheuchzeri*, hypogeogenous rhizome. **11.** *Ranunculus pygmaeus*, epigeogenous rhizome. **12.** *Saxifraga cernua*, epigeogenous rhizome and bulbills in leaf axils. (Photo K. Prach)

nardina, *C. misandra*, *Puccinhippsia vacillans*). Clonal plants were in general more abundant on older, stabilized surfaces with better developed soils (*Dryas octopetala*, *Carex*-moss, and *Deschampsia borealis* community types) than on young, unstabilized surfaces. Clonal plants with short epigeogenous rhizomes were common in all community types (representing >40% of the species, Fig. 7); they were most common in the *Deschampsia borealis* alluvial vegetation (repre-

- ← Fig. 2. Herbarium specimens of representative species with selected clonal growth organs. **1.** *Carex parallela*, short hypogeogenous rhizome. **2.** *Festuca vivipara*, epigeogenous rhizome and plantlets in inflorescence. **3.** *Carex misandra*, epigeogenous rhizome. **4.** *Cochlearia groenlandica*, biennial or monocarpic perennial. **5.** *Carex subspathacea*, long hypogeogenous rhizome. **6.** *Braya purpurascens*, non-clonal perennial, perennial main root. **7.** *Equisetum scirpoides*, long hypogeogenous rhizome. **8.** *Draba oxycarpa*, non-clonal perennial, perennial main root. **9.** *Carex saxatilis*, hypogeogenous rhizome. **10.** *Ranunculus sulphureus*, epigeogenous rhizome. **11.** *Silene uralensis* subsp. *arctica*, nonclonal perennial, perennial main root. **12.** *Eutrema edwardsii*, nonclonal perennial, perennial main root. **13.** *Saxifraga flagellaris* subsp. *platysepala*, stolons with offspring plantlets. **14.** *Saxifraga hieracifolia*, epigeogenous rhizome. **15.** *Poa alpina*, epigeogenous rhizome and plantlets in the inflorescence. **16.** *Saxifraga nivalis*, epigeogenous rhizome. **17.** *Taraxacum arcticum*, nonclonal perennial, perennial main root. **18.** *Koenigia islandica*, annual plant. **19.** *Saxifraga oppositifolia*, epigeogenous rhizome. **20.** *Salix reticulata* epigeogenous rhizome. (Photo M. Dvorský)



Fig. 4. The most common vegetation types in Petuniabukta, central Spitsbergen, Svalbard. **1–4.** *Dryas octopetala* community: **1.** wetter habitats with *Carex misandra* and *Salix polaris*; **2.** soil polygons; **3.** fell fields; **4.** dry habitats with *Carex rupestris*. **5.** Early successional stages with *Saxifraga oppositifolia* community, sparse vegetation on young, unstabilized fluvial and morainic sediments. **6.** *Carex*-moss community of alluvial wet habitats, snow beds, and seepages. **7.** *Deschampsia borealis* community around streams and eutrophicated spots near settlements. **8.** *Papaver dahlianum* community on scree at higher altitudes. **9.** *Festuca baffinensis* community, species-rich vegetation of eutrophic soils under bird nesting sites. (Photo K. Prach)

senting >70% of the species) but were also very common in the *Saxifraga oppositifolia* vegetation on fresh fluvial and moraine deposits and in the *Festuca baffinensis* vegetation developed under bird nesting sites (Figs 4, 5, 7). The species with epigeogenous rhizomes that most contributed to vegetation cover in individual communities were *Deschampsia borealis* and *Bistorta vivipara* in the *Deschampsia borealis* community type; *Trisetum spicatum*, *Festuca baffinensis*, and *Saxifraga cernua* in the *Festuca baffinensis* community type; and *Dryas octopetala* and *Cassiope tetragona* in the *Dryas octopetala* community type.

Relative to plants with epigeogenous rhizomes, those with hypogeogenous rhizomes were less abundant (Fig. 7) and more spatially restricted; they were abundant in alluvial habitats and snow beds, *i.e.*, in the *Carex*-moss community type (Figs. 4, 5). Plants with longer hypogeogenous rhizomes (lateral spread >1 cm per year) that most contributed to vegetation cover were *Carex subspathacea*

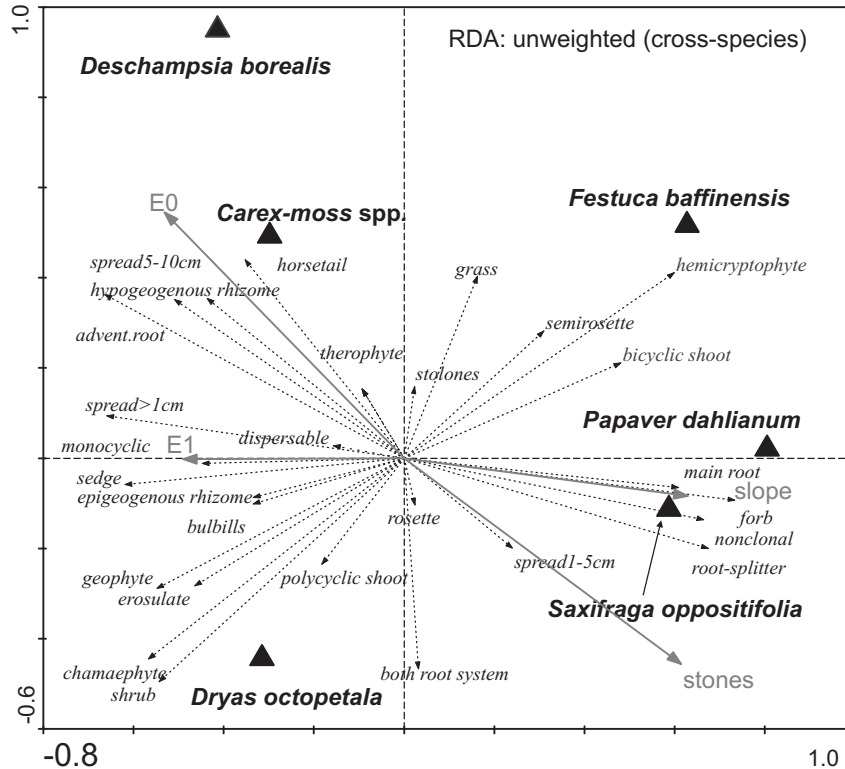


Fig. 5. Redundancy analysis biplot of plant life-history traits (response variables) in relation to six vegetation types. Response variables are represented by dotted arrows, while supplementary environmental variables are represented by solid gray arrows. Plant communities are represented by centroids (triangles). The angles between arrows indicate correlations between variables.

and *Equisetum variegatum* (dominant in permanently wet depressions), *Carex parallela* (dominant in alluvial habitats with fluctuating water table), and *Salix polaris* and *Equisetum arvense* (dominant in old, sufficiently wet surfaces that did not dry in summer). The only species with short hypogeogenous rhizomes (lateral spread <1 cm per year) that attained relatively high cover (>20%) was *Carex rupestris*, a co-dominant of *Dryas octopetala* on old and dry surfaces. Plants with hypogeogenous rhizomes were rare in the *Festuca baffinensis* community type (the only representative was *Salix polaris*), which was the most species-rich community in Petuniabukta and which occurred on eutrophic spots under bird nesting sites. Plants attaining higher cover in the *Festuca baffinensis* community type were forbs (*Saxifraga cespitosa*, *Saxifraga cernua* and *Cerastium arcticum*) and grasses (*Trisetum spicatum*) with semirosette leaf distribution, epigeogenous rhizomes and short lateral spread; these forbs and grasses were accompanied by rosette forbs (*Draba corymbosa*, *D. oxycarpa*, *D. subcapitata*, *Papaver dahlianum*, and *Cochearia groenlandica*) with dicyclic shoots and perennial main root (Figs 2, 4, 5, 7).

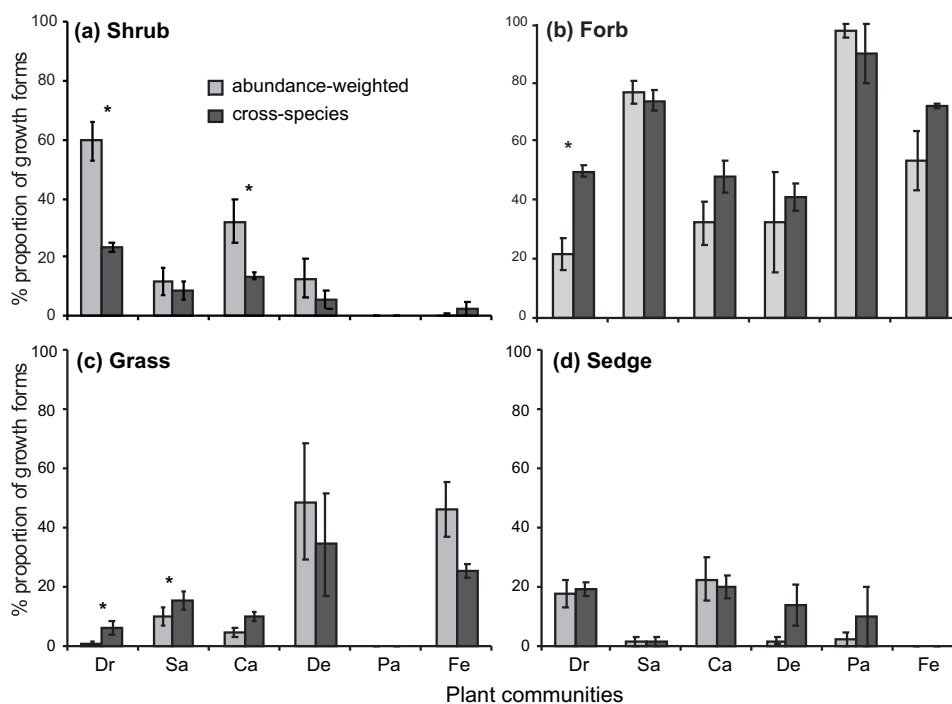


Fig. 6. Pair-wise comparisons of abundance-weighted proportions vs. cross-species proportions of four abundant growth form categories among six community types in Petuniabukta. Dr: *Dryas octopetala* shrubby vegetation on old, stabilized surfaces; Sa: *Saxifraga oppositifolia* community, sparse vegetation on young, unstabilized fluvial and morainic sediments; Ca: *Carex*-moss community on alluvial wet habitats, snow beds, and seepages; Da: *Deschampsia borealis* community around streams and eutrophicated spots near settlements; Pa: *Papaver dahlianum* community on scree at higher altitudes; Fa: *Festuca baffinensis* community, species-rich vegetation of eutrophicated soils under bird nesting sites. * significant differences between the two means (*post-hoc* test – unequal N HSD test).

Individual clonal traits, growth forms, and life forms showed similar patterns with respect to their occurrence in communities when unweighted data and data weighted by abundance were considered (Table 3, Figs 6, 7). Exceptions were shrubs with erosulate shoots and forbs with semirosette shoots; the former were overrepresented when analysis was based on abundance (indicating their ability to occupy space and dominate vegetation), and the latter were underrepresented when analysis was based on abundance, especially in the *Dryas octopetala*, *Saxifraga oppositifolia*, and *Carex*-moss community types (Figs 4, 6).

Plant characteristics along environmental gradients. — Differences in habitat preferences for plants with different growth and life form categories were also evident from correlations with the plot-level environmental factors of slope inclination and stoniness (Fig. 8). Species number and cover of non-clonal forbs with perennial main root increased with increasing stoniness and steepness of the

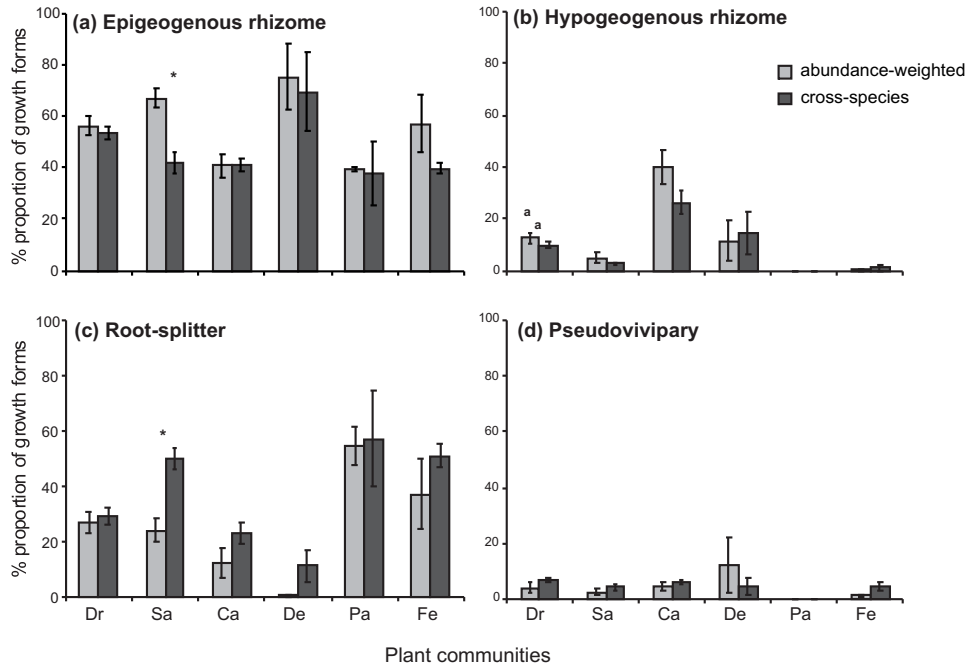


Fig. 7. Pair-wise comparisons of abundance-weighted vs. cross-species proportions of four clonal growth organs among six community types in Petuniabukta. Abbreviations for community types on the horizontal axis as in Fig. 6. * significant differences between the two means (post-hoc test – unequal N HSD test)

slope, while clonal species, both sedges and horsetails with hypogeogenous rhizomes and long lateral spread, decreased with increasing stoniness and slope steepness (Table 3 and Fig. 8).

Discussion

All but one plant species from Petuniabukta (central Spitsbergen) were perennial, and two-thirds of the plant species were clonal. Clonality was represented by four types of clonal growth organs. The six principal plant communities in the studied area differed with respect to composition of growth forms, Raunkiaer life forms (except for rare therophytes), leaf distribution along the shoot (except for rosette shoots), clonal growth organs, lateral spread, and root system. Most plant characteristics were also correlated with the two examined gradients: slope and stoniness. These general findings are discussed in greater detail in the following sections.

Characteristics of the local flora. — The current study documented annual plants, non-clonal plants with perennial main roots, and clonal plants with other types of clonal growth organs (epigeogenous rhizome, hypogeogenous rhizome,

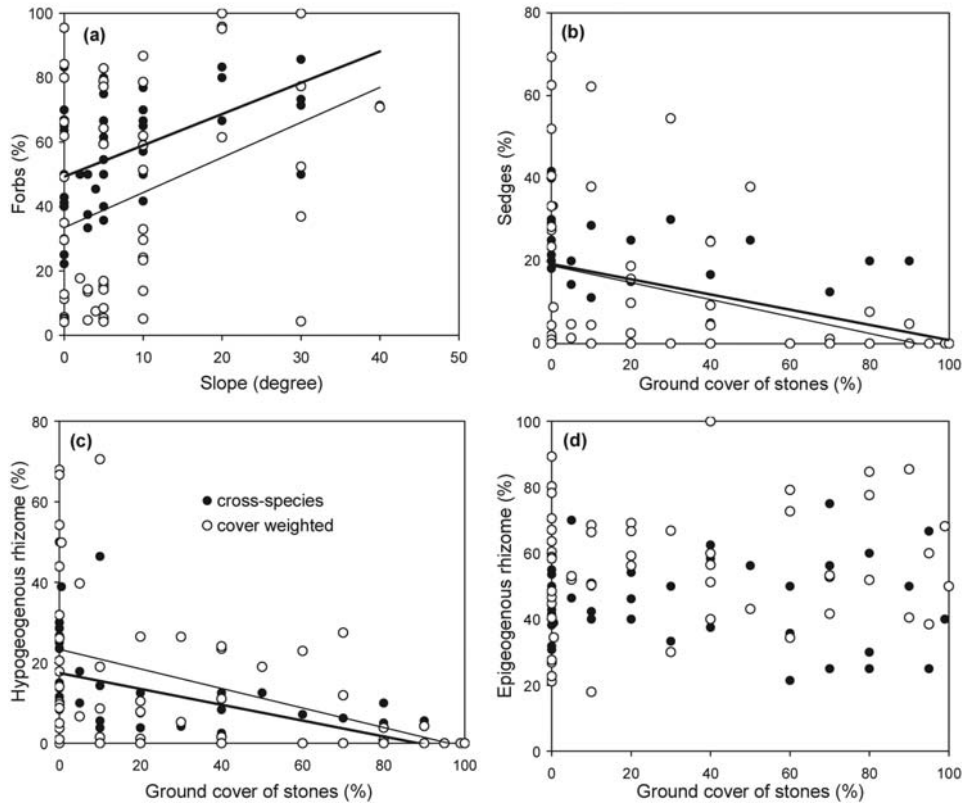


Fig. 8. Relationships between selected growth forms, clonal growth organs, and environmental variables (stoniness and slope inclination). Abundance unweighted data are represented by filled circles, and abundance weighted data are represented by open circles. The significant relationships are fitted by regression lines (see Table 1).

bulbils and stolons) in Petuniabukta. These general categories of plant traits also occur in central Europe, where the clonal classification was elaborated (Klimešová and Klimeš 2008). Another 12 categories of clonal growth organs that were identified in central Europe were not found in Petuniabukta (*e.g.*, turions, plant fragments, budding plants, bulbs, and tubers). While the most common types of clonal growth organs in Petuniabukta is perennial main root of non-clonal plants and epigeogenous rhizomes, the most common in central Europe are epigeogenous and hypogeogenous rhizomes (Klimešová and Klimeš 2008). The lack of certain clonal growth organs in Petuniabukta is largely due to the lack of aquatic plants, which possess specialized clonal growth organs that are not found in nonaquatic communities (Sosnová *et al.* 2010, 2011).

The clonal growth spectrum in Petuniabukta is characterized by a high proportion of plants multiplying by bulbils produced either in inflorescences or in leaf axils. The most abundant species dispersing only by bulbils is *Bistorta vivipara*.

Table 3
List of studied life-history traits of vascular plants in plant communities of Petuniabukta, number of species in individual categories, differences between abundance weighted and cross-species proportions (% difference), *P* values (for Type I error estimate) from ANOVA analyses comparing six community types for each trait category (weighted or not by species cover), and correlation coefficients with environmental variables.

Plant characteristics	Category	Number of species	% difference	Differences between six communities		Correlation with stoniness		Correlation with slope	
				<i>P</i> _{weighted}	<i>P</i> _{unweighted}	<i>r</i> _{weighted}	<i>r</i> _{unweighted}	<i>r</i> _{weighted}	<i>r</i> _{unweighted}
Growth forms (%)	Shrub	4	18.9	0.000	0.000	-0.31	-0.28	-0.25	-0.22
	Forb	35	-14.8	0.001	0.000	0.55	0.56	0.33	0.51
	Grass	11	-2.7	0.032	0.008	0.03	0.11	0.29	-0.03
	Sedge	8	-1.1	0.000	0.120	-0.43	-0.50	-0.35	-0.36
	Horsetail	2	-0.4	0.000	0.010	-0.29	-0.45	-0.21	-0.32
Leaf distribution (%)	Erosulate	10	24.6	0.008	0.001	-0.35	-0.07	-0.25	0.11
	Semirosette	30	-18.4	0.024	0.001	0.19	0.05	0.22	-0.04
	Rosette	20	-6.2	0.706	0.368	0.07	0.00	0.05	-0.09
Raunkiaer life forms	Hemicryptophytes	52	-15.4	0.000	0.000	0.34	0.26	0.31	0.33
	Geophytes	2	-1.6	0.000	0.208	-0.23	-0.25	-0.17	-0.30
	Therophytes	1	-0.1	0.389	0.372	-0.12	-0.05	-0.12	-0.05
	Chamaephytes	5	17.1	0.000	0.000	-0.36	-0.23	-0.25	-0.21
Clonal growth organ CGO (%)	Epigeogenous rhizome	25	8.4	0.061	0.003	-0.25	0.00	-0.01	0.15
	Hypogeogenous rhizome	10	4.4	0.000	0.000	-0.41	-0.53	-0.39	-0.44
	Main root	27	-11.3	0.000	0.073	0.45	0.42	0.36	0.41
	Bulbils	5	-1.4	0.137	0.172	-0.17	-0.26	0.21	0.09
	Stolones	1	-0.2	0.387	0.308	0.05	-0.06	0.15	-0.12
Lateral spread [cm/yr]	Nonclonal	26	-12.9	0.000	0.216	0.44	0.39	0.39	0.46
	<1	26	2.3	0.000	0.000	-0.38	-0.51	-0.25	-0.52
	1–5	5	9.0	0.183	0.000	0.00	0.53	0.09	0.45
	5–10	6	2.0	0.000	0.000	-0.33	-0.50	-0.31	-0.37
	Dispersable	5	2.9	0.532	0.348	0.21	-0.17	0.09	-0.26
Shoot cyclicity	Monocyclic	6	6.9	0.050	0.008	-0.16	-0.40	-0.21	-0.39
	Dicyclic	31	-15.7	0.006	0.019	0.12	0.04	0.32	0.29
	Polycyclic	23	8.9	0.098	0.003	-0.01	0.27	-0.03	0.15
Root system	Main	27	-9.0	0.003	0.010	0.42	0.27	0.15	0.12
	Adventitious	33	9	0.005	0.002	-0.42	-0.27	-0.15	-0.12

Bulbils are a very efficient alternative to regeneration by seed; they are larger than seeds but smaller than offspring produced by other clonal growth organs, and for some plants bulbils are the predominant or only way of multiplication (*e.g.*, *Saxifraga cernua*, Kjølner *et al.* 2006; *Bistorta vivipara*, Bauert 1996). The number of plant species that depend on bulbils and plantlets in the studied area is

Table 4
Average cover (%) of the most abundant growth forms in the plant communities. Data (except of Petuniabukta) from Komárková and McKendrick (1988).

Growth form	Petuniabukta Svalbard 78°38'	Edgeøya Svalbard 78°05'	Devon Canada 75°33'	Barrow Alaska 71°18'	Atkasook Alaska 70°29'
Shrubs	18	0	12	8	38
Graminoids	30	30	60	54	38
Forbs	52	70	28	38	24

phylogenetically constrained in that the taxonomic diversity of bulbil- or plantlet-producing plants is not high (they are produced only by *Bistorta vivipara* and several species in the *Saxifraga* genus and Poaceae family), and it is therefore difficult to decide whether it is the production of bulbils or the other shared characteristics that is responsible for the success of the species in the high Arctic.

There is little comparative information on clonal growth in cold climates, and the principles of clonal-trait description used in the CLO-PLA 3 database for central Europe could serve as a basis for comparison (Klimešová and de Bello 2009). Before the current study, however, the approach was only applied to the flora of central Europe and East Ladakh (Klimešová *et al.* 2011a). Relative to the flora of the Czech Republic, the Ladakh flora has a lower proportion of clonal species, a higher diversity of non-clonal growth forms, and fewer plants with hypogeogenous rhizomes, especially outside of wetlands (see below). East Ladakh and Svalbard are similar in that they both have a cold climate, but they differ in other environmental factors: Ladakh is arid, and the plant communities occur along a large altitudinal gradient, and Svalbard is mesic, with plants occurring preferentially at a very low altitude.

Although we lack comparative data on clonal growth traits from the Arctic, the current study provides useful information on the proportions of growth forms (shrubs, graminoids, forbs and horsetails) (Table 4). The data indicate that the composition of vegetation in Svalbard, and presumably in other Arctic regions is quite variable, especially in the proportion of shrubs. While shrubs play an important role in Petuniabukta, no species was recorded from Edgeøya, Svalbard. Graminoids attain their highest cover in Devon, Canada, whereas graminoids were the least abundant growth forms on two of the Petuniabukta sites. Forbs, on the other hand, represented the highest proportion of growth forms at Petuniabukta (Table 4). Because graminoids are often rhizomatous, it seems likely that the spectra of clonal growth forms will differ among different parts of the Arctic.

A preponderance of hemicryptophytes among Raunkiaer's life forms is typical of high Arctic and alpine subnival communities (Nakhutsrishvili and Gamtsemidze 1984; Pokarzhevskaya 1995; Klimeš 2004). In those habitats where low snow cover hinders the occurrence of shrubs and the stoniness of the substratum and/or permafrost prohibit deep placement of bud-bearing organs, the hemicrypto-

phytes, which produce their renewal buds close to the soil surface, are the most successful life form. However, dominance by chamaephytes has been reported from Arctic locations, as well (*e.g.*, Matveyeva 1994).

The prevailing shoot architecture for *Petuniabukta* in the current study was semirosette, which was typical of half of the examined plants in the area, and which also was typical of plants in the subnival zone of the Caucasus (Nakhutsrishvili and Gamtsemlidze 1984). In the alpine zone of the Caucasus, however, Pokarzhevskaya (1995) reported that about 80% of the plants had semirosette shoots. We could speculate that shoot architecture is less important in harsh environments (high Arctic and subnival zone) than in less extreme environments because the plants in harsh environments are very small. On the other hand, the spatial distribution of shoots could be important in harsh environments, as is indicated by the increasing number of cushion plants at high altitudes in mountains (Nakhutsrishvili and Gamtsemlidze 1984; De Bello *et al.* 2011). Only one typical cushion plant (*Silene acaulis*) was, however, detected in the current study.

The plants in *Petuniabukta* have much less mobility (lateral spread) than the plants in central Europe (Klimešová and Klimeš 2008; Klimešová *et al.* 2011b). This result is in accord with other observations in cold climates (Nakhutsrishvili and Gamtsemlidze 1984; Pokarzhevskaya 1995; Klimeš 2003), although we still lack data for another Arctic locality.

A root system consisting exclusively of a main root that lacks the ability to form adventitious roots, and consequently that lacks the ability to grow clonally, was characteristic of one-third of the plants from the *Petuniabukta* area (and nearly half of plants recorded in plant communities). This value is similar in that reported for other cold areas (Polozova 1981; Nakhutsrishvili and Gamtsemlidze 1984; Pokarzhevskaya 1995; Rusch *et al.* 2011) with the exception of dry regions of the Western Himalayas (Klimeš 2003).

Plants from *Petuniabukta* have biennial (dicyclic) or perennial (polycyclic) shoots whereas those in the more temperate central European region have mainly annual (monocyclic) shoots (Klimešová and Klimeš 2008). These results suggest that plants require more time for inflorescence development in the stressful environment of the high Arctic than in temperate regions (Alexandrova 1983).

Plant characteristics in different plant communities. — The plant characteristics differed substantially among the plant communities in *Petuniabukta*. Characteristics were similar only for the *Papaver dahlianum* and the *Saxifraga oppositifolia* communities (both typically occur on slopes and host non-clonal forb species with perennial main roots) and for the *Carex*-moss and *Deschampsia borealis* communities (both occur in wet and flat habitats and host clonal plants with long, hypogeogenous rhizomes). Other communities had unique characteristics.

The largest differences in clonal growth organs among the plant communities in *Petuniabukta* were found in the proportion of hypogeogenous rhizomes. Plant species possessing this clonal growth organ represented 20% of the species or

plant cover in the wet plant community dominated by mosses along brooks, snow beds, and seepages while their representation on young substrates, stony slopes, and under bird cliffs was negligible. The opposite tendency was recorded for plants with perennial main roots, which were dominant on young substrates but less represented in wet habitats. This replacement of rhizomatous plants by non-clonal plants with perennial main roots in communities along a gradient of reduced water availability is in accord with observations from temperate areas that wetland habitats host higher number of rhizomatous species than mesic or dry sites (van Groenendael *et al.* 1996; Klimeš *et al.* 1997; Sosnová *et al.* 2011).

Plants that grow clonally using plantlets or bulbils (pseudovivipary) were the most represented in Petuniabukta communities growing on fine soil in alluvial deposits or in snow beds under bird cliffs, whereas they were missing in the *Papaver dahlianum* community that spread over stony substrates. In a glacier foreland in the Alps, in contrast, regeneration of *Poa alpina* by plantlets was found in areas with stony substrate in early successional stages with poor vegetation cover but not later, when plant cover was high (Winkler *et al.* 2010).

Several plant characteristics differed or did not differ between the studied communities depending on whether plant cover was or was not taken into account (*i.e.*, depending on whether abundance weighting was or was not used). These characteristics were the proportion of plants that were sedges, were non-clonal, had a lateral spread of 1–5 cm, had a main root, or had polycyclic shoots. In these cases, taking or not taking plant cover into account greatly affected the statistical analysis because of the dominance or the rarity of the species with these characters in the communities. The determination of whether characteristics differed among communities was unaffected by abundance weighting for only a few characteristics, which were the proportion of plants with rosette shoots and with dispersible vegetative diaspores; this further indicates the large differences among the communities in the area.

Plant characteristics along environmental gradients. — The sensitivity of hypogeogenous rhizomes to unstable and stony substrates was confirmed by a significant negative correlation with stoniness and slope and the occurrence of plants with hypogeogenous rhizomes. This relationship indicates that a negative correlation between spacer length (length of rhizomes between shoots) of hypogeogenous rhizomes and temperature (Klimešová *et al.* 2011b) is probably mediated by soil properties.

The idea that substrate instability negatively affects belowground rhizomes dates back to Hess (1909), who found that the most successful growth forms on screes in the Alps had perennial main roots, which enabled the plant to explore deeper, more stable, and wetter scree strata. Similar results were obtained in the current study, in that non-clonal plants with perennial main roots were concentrated in a similar kind of habitat. Furthermore, Jonasson (1986) found that rhizomatous species were more abundant on stable parts of soil polygons rather than in

their active centers. Klimeš (2003, 2008) considered that the small proportion of clonal plants in the flora of Ladakh was a consequence of substrate instability, which makes horizontal growth in stony soils difficult. This inference was confirmed (Klimešová *et al.* 2011a) when the occurrence of individual clonal growth organs in relation to environmental gradients was evaluated, and the ratio of hypogeogenous to epigeogenous rhizomes was also found to be smaller in Ladakh than in Central Europe. It is, however, questionable whether this is the general pattern for the Arctic because not all Arctic environments are characterized by stony substrates, and steep slopes are also not a general characteristic of the Arctic landscape. Perhaps flatter Arctic landscapes that are covered by a fine-grain substrate (*e.g.*, north slopes in Alaska, see Reynolds *et al.* 2008) will host more rhizomatous species than reported for Petuniabukta in the current study. In contrast to below-ground rhizomes, aboveground clonal growth organs are not subject to breakage (creeping branches of dwarf shrubs). It is also possible that plants with above-ground clonal growth organs are adapted to disturbance and easily re-root after disturbance (Hagen 2002). This is especially true for *Saxifraga oppositifolia*, which dominates highly disturbed habitats near periodic streams.

Conclusion

Our results indicate that the spectrum of clonal growth organs is narrower in the high Arctic than in central Europe. In particular, the high Arctic lacks plants with clonal growth organs typical of aquatic species. In agreement with our expectations, the proportion of hypogeogenous rhizomes was low, especially in habitats with steep slopes and substrate stoniness where non-clonals with perennial main roots prevailed. Broader generalizations on the function of clonal growth in the Arctic will require the collection of additional data by the same methodology.

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