

Diversity of plant life histories in the Arctic

Bohatost životních forem rostlin v Arktidě

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Dedicated to the memory of Leoš Klimeš

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It is argued in this paper that the diversity of plant life histories in the Arctic is much greater than indicated by general descriptions in the literature. Three basic types of life cycle are suggested as a fundamental trait-based framework for exploring the diversity of plant life histories in the Arctic: (i) annual, (ii) non-clonal perennial and (iii) clonal perennial. An overview of current understanding of traits of arctic plant life histories is provided within this framework. Based on the overview it is concluded that (i) there is a substantial diversity of plant life histories in the Arctic, and (ii) there is no single life-history trait that is specific for arctic plants. Furthermore, it is proposed that because arctic environments differ in many respects from other environments, unique combinations of life-history traits are selected among arctic plants. Consequently, arctic plants should express a unique spectrum of life histories. It is also recognized that there are large gaps in the knowledge on arctic plant life-history traits and that fine-tuned trait–habitat relationships may be offset by historical, biogeographical or ecological factors, which may hamper analyses of life history–habitat relationships. On the other hand, it may be rewarding in terms of an improved understanding of functional and evolutionary responses of arctic plants to climate and other environmental changes to identify potential life history syndromes (strategies) among them.

Key words: arctic environment, clonal growth, dormant phase, life cycles, life-history traits, mature phase, premature phase, reproduction, survival

Introduction

Plant life-history adaptations to the severe environments of the Arctic are generally much less explored than physiological and morphological adaptations. Life-history traits, the quantification of the major features of a life cycle, are the key to understanding the action of natural selection, genetic variation and population dynamics (Stearns 1992) and they also influence processes at community and ecosystem levels (e.g. Violle et al. 2007). The combination of coevolved life-history traits of an organism make up its life history. Many different combinations have evolved, resulting in a large diversity of life histories both among and within different groups of organisms. In addition, substantial variation in life histories occurs within many species in response to the environment.

Despite the quantitative nature of life-history traits and often continuous variation, several attempts have been made to identify a few major life-history strategies, usually in relation to habitat stability or other environmental characteristics, of which the r- and K-selection is best known (MacArthur & Wilson 1967). Similar habitat-based approach to studying plant strategies are proposed for vascular plants (e.g. Grime 1977), arctic and alpine vascular plants (Molau 1993) and bryophytes (During 1979; later adopted for vascular

plants by Frey & Hensen 1995). However, the habitat approach may not always be consistent with the evolution of individual life-history traits (Stearns 1992). Furthermore, the proposed strategies are limited to only a certain range of habitats, which may restrict their application (Callaghan et al. 1996).

Life-history traits of arctic plants are consistently described in the literature as rather similar, giving an impression of low life-history diversity: arctic plants are long-lived perennials with relatively low resource allocation to sexual reproduction, low seed production and low seedling survival, relying to a high degree on asexual reproduction for population maintenance (e.g. Billings & Mooney 1968, Bliss 1971, Savile 1972, Callaghan & Collins 1976, McGraw & Fetcher 1992, Jonasson et al. 2000). This generalized life history is believed to be adaptive to short and cold growing seasons and low nutrient availability, where completion of a life cycle needs to be extended over several years and where sexual reproduction and genet recruitment may not be successful every year. Accordingly, the strong gradient in species diversity from tropical regions towards the poles in most groups of organisms (Gaston 2000) is likely to be reflected in similar gradients in life-history diversity.

However, in the context of plant life history it is not always fully recognized how variable the arctic environment is in space and time and that it may therefore select for diverse life-history traits and trait combinations. The generalization above should thus be viewed only as a general frame within which large diversity may be found. For example, maximum age among 'long-lived' species may vary from a couple of decades to several thousand years (e.g. Callaghan & Emanuelsson 1985, Jónsdóttir et al. 2000). Similarly, arctic plants adopt different breeding systems with implications for reproductive life-history trait diversity (Molau 1993, Brochmann & Steen 1999). Such trait diversity may significantly affect plant fitness in various arctic habitats and result in a greater diversity of life histories than usually indicated in the literature.

The aim of this paper is to explore arctic plant life-history diversity. I will suggest a simple trait-based framework as a first step in analysing life-history diversity and provide an overview of knowledge within that framework. There are many gaps in our understanding of arctic plant life-history traits, which hampers a thorough diversity analysis. The largest gap concerns life histories of arctic bryophytes, an important component of arctic vegetation (Longton 1988, 1997), although some insights may be provided from studies in other environments (see During 1979, 1992 for review). To set the scene I will begin by giving a brief account of the environmental variability that arctic plants are faced with.

Variability in the environmental conditions faced by plants in the Arctic

The treeless circumpolar arctic tundra covers about 7.5 million km² (ACIA 2005) and represents environmental variability in space and time at different scales. There are two main macro-scale climatic gradients within the Arctic that are usually not in parallel. The first is a south-north gradient with mean July temperatures ranging from 1 to 12 °C and fourfold difference in the length of growing season, ranging from a few weeks to more than three months (Walker et al. 2005). On this scale, there is a correlation between temperature and species diversity for most groups of organisms (Chapin & Körner 1994, Walker 1995, Matveyeva & Chernov 2000). The diversity of plant growth forms also decreases along this climatic gradient, trees being absent by definition and tall shrubs only present in the

southernmost parts. Although the average length of the growing season is positively related to July mean temperatures, it is also strongly affected by the second large-scale gradient, the oceanic-continental one. This gradient is largely controlled by the distribution of landmasses and ocean currents, which greatly modify the southern limits of the Arctic as well as the steepness of the latitudinal climate gradient. The Arctic reaches much further south in continental areas than in oceanic areas. Relatively warm ocean currents intensify the oceanicity and in the North Atlantic region the arctic limit is pushed as far north as 73°N. Consequently, day length and light conditions at the southern arctic limit differ widely between regions. On the basis of these major climatic gradients, the Arctic is subdivided into bioclimatic subzones (Walker et al. 2005).

As elsewhere, bedrock type and topography introduce large- and intermediate spatial scale variability within a bioclimatic subzone in both nutrient conditions and local climate. Relatively low nutrient availability limits plant growth in all zones of the Arctic, although there are some biological 'hotspots' or arctic oases, where conditions for plant growth become more favourable than average, resulting in higher productivity or species diversity, or both (Walker 1995). Some of these 'hotspots' are linked to marine ecosystems through nesting seabirds that manure the vegetation below bird cliffs and greatly enhance productivity.

Within a landscape, microtopography and periglacial processes strongly affect distribution of snow, drainage, active layer depths (top soil layer that thaws in summer in permafrost areas) and other soil processes and often create steep gradients in ecological conditions over short distances of metres or even decimetres (e.g. Webber 1978, Aleksandrova 1988, Bliss 1997, Chernov & Matveyeva 1997). Such sharp small-scale spatial contrasts are typical of the Arctic. In depressions, soil moisture, biological soil activity and nutrient availability are generally much higher than on exposed ridges a few metres away. However, where there are deep snow beds, productivity may be much reduced due to late snowmelt and shorter growing seasons. Similarly, in basins where permafrost prevents drainage of melt water, water logging and anoxic conditions are extended and may reduce biological activity, hence productivity. The spatial scale for detecting contrasting ecological conditions becomes narrower in high-arctic zones where annual precipitation and vegetation cover is extremely low. In this respect microscale surface structures become crucial for plant life, such as shallow frost or drought cracks, small stones and even neighbouring plants (Sohlberg & Bliss 1984, Aleksandrova 1988, Chernov & Matveyeva 1997, Elberling 2000). Such microtopographic features function as traps for seed and other plant propagules and shape the physical environment by trapping drifting snow and dust, thereby enhancing sedimentation and soil development, creating a suitable habitat for seed or spore germination and seedling survival.

Biotic interactions within and between trophic levels also shape local plant conditions in the Arctic. According to the Stress Gradient Hypothesis, positive (facilitative) plant-plant interactions are expected to outweigh negative (competitive) plant-plant interactions in harsh arctic environments (Bertness & Callaway 1994, Brooker & Callaghan 1998). Several studies have indeed demonstrated the importance of facilitation in relatively exposed arctic as well as alpine habitats (e.g. Addison & Bliss 1984, Sohlberg & Bliss 1984, Callaghan & Emanuelsson 1985, Carlsson & Callaghan 1991, Choler et al. 2001). Negative plant-plant interactions may, however, be expected to intensify as productivity increases, e.g. along moisture and topographic gradients within bioclimatic subzones. In moist habitats of the low arctic zones, shading by shrubs or other relatively high-growing

vascular plants plays a major role in shaping plant communities (e.g. Walker et al. 2006), while direct and indirect interactions between mosses and vascular plants become more prominent in moist habitats of the high-arctic zones, where the balance between positive and negative moss–vascular plant interactions depends on moss depth in a species specific way (Gornall et al. 2007, 2011). Herbivory varies across tundra regions and within landscapes and the intensity of various kinds of herbivory as well as pathogenic attacks, both below- and above-ground, are also generally highest in the most productive habitats (e.g. Jefferies et al. 1994, Jónsdóttir 2005).

Arctic plants are also faced with great temporal variability in conditions. Annual variation is a common feature of the arctic climate and various types of natural disturbances operate at different spatial and temporal scales such as cryoturbation (including frost boils), solifluction, landslides and sedimentation by dust storms or flooding. All these disturbances result in a dynamic mosaic of different successional stages across the landscape (Svoboda & Henry 1987, Callaghan et al. 1996, Bliss 1997, Chernov & Matveyeva 1997, Crawford 1997, Jónsdóttir 2005).

The arctic environment exerts variable selection pressures on life and considerable diversity is therefore to be expected, not only in physiological and morphological traits, but also in life-history traits. However, fine-tuned trait–habitat relationships may be offset in arctic plant species by historical, biogeographical or ecological factors. The distribution patterns we see today were shaped by repeated Pleistocene glaciations in some regions of the Arctic, causing frequent population fragmentation and recolonization (Abbott & Brochmann 2003, Alsos et al. 2007), which is also believed to have resulted in exceptionally high levels of polyploidy and taxonomical complexity in many arctic plants (Savile 1972, Brochmann et al. 2004). The evolutionary consequences of these historical events may overshadow, at least to some extent, the life-history trait–habitat relationships. On an ecological time scale, the dynamic nature of the arctic environment may help to explain why the same species may survive in different successional stages in the landscape (Svoboda & Henry 1987) or why different life-history solutions may be observed at the same spot.

A framework for arctic plant life-history analysis

The approach used here in building a framework for exploring arctic plant life-history diversity is, as a first step, to identify those traits that result in fundamentally different life cycles. The focus will primarily be on the relatively simpler life cycles of vascular plants although bryophytes with the more complex diplohaplont life cycles will also be considered. To begin with, two traits are identified as the foundations for the framework, i.e. the frequency of (sexual) reproduction and the degree of clonal growth, and I will argue that these traits will result in three basic types of life cycle in arctic plants (Fig. 1). The life cycles are subdivided into three phases, the premature, mature and dormant. I deliberately use the term life cycle ‘phase’ to allow identification of different developmental ‘stages’ within a phase and further subdivision.

Frequency of reproduction

As for other organisms, semelpary (reproducing once in a lifetime) vs iteropary (reproducing repeatedly; in plants usually termed monocarpy and polycarpy, respectively), creates

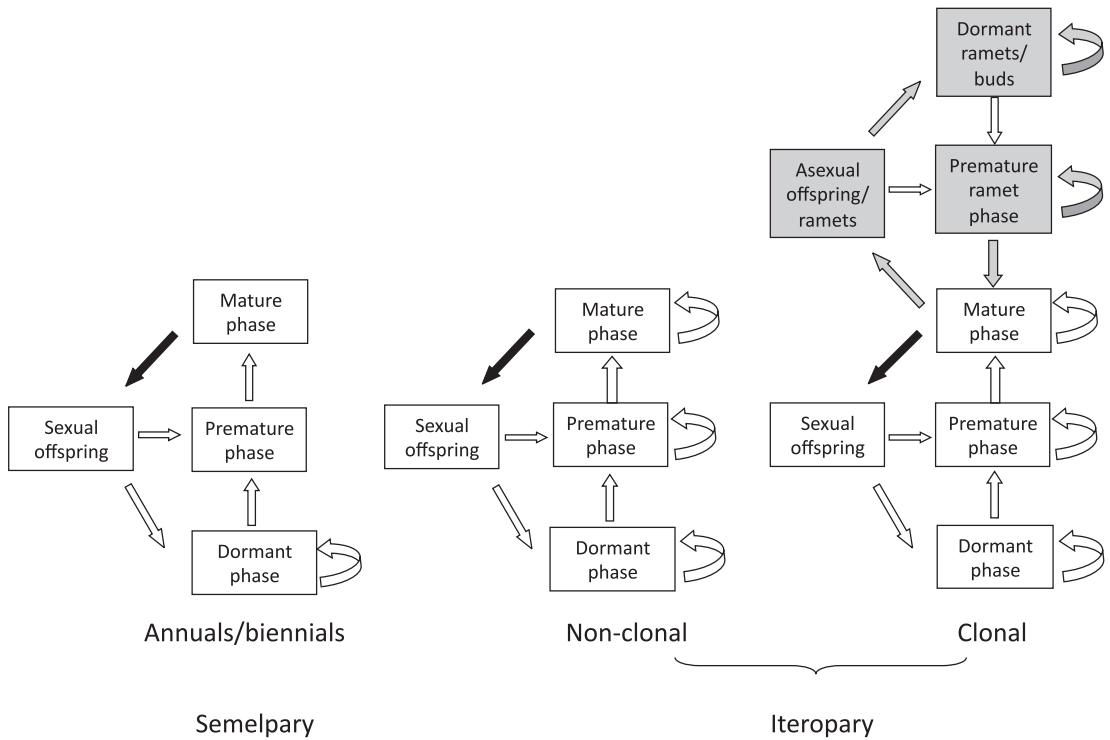


Fig. 1. – The three basic life-cycle types of arctic plants based on two life-history traits, frequency of reproduction (once in a lifetime or more) and degree of clonal growth. Each phase could be further broken up into different developmental stages to construct more detailed species-specific life cycle graphs (sensu Caswell 2001). Arrows indicate annual transitions. Black arrows represent (sexual) reproduction. Shaded boxes and arrows indicate the ramet life cycle embedded in the mature phase of the clonal life cycle.

a major life-cycle distinction in plants. Semelparous arctic plants are mainly annuals, although they may stretch their life span over two or more years due to slow flower-bud development (all termed annuals hereafter) and are a rather inconspicuous group of plants in the Arctic compared to bioclimatic zones further south (Billings & Mooney 1968). In the most extreme regions of the High Arctic annual vascular plants are completely absent while annual bryophytes most likely occur in natural disturbances such as frost boils (Steere 1978). It is argued that short growing seasons in combination with low temperatures and large inter-annual variation in climate select against annual life cycles in seed plants (Billings & Mooney 1968, Savile 1972) and bryophytes (Longton 1988). Indeed, the distribution of the annual seed-plant species reaching furthest north, *Koenigia islandica*¹, is thought to be due to special physiological adaptations that enable it to cope with a short and cold growing season (Dahl 1963, Heide & Gauslaa 1999). Consequently the frequency of reproduction, i.e. whether plants reproduce once or several times in a lifetime, results in two rather unequal-sized groups of arctic plants (Fig. 1).

¹Nomenclature follows cited papers. When no paper is cited it follows Lid & Lid (2005).

Degree of clonality

The modular organization of plants introduces huge plasticity both in terms of growth and reproductive output (fecundity) and, in addition, facilitates clonal growth (here the term clonal growth will be used in a broad sense, i.e. including all forms of asexual reproduction, although agamospermy resembles sexual reproduction more closely in many ecological respects). Clonal growth has a major influence on plant life cycles. In clonal plants where a ramet is defined as a potentially independent unit, capable of completing a life cycle (Harper 1977), a ramet life cycle composed of a dormant phase (buds) and a premature ramet phase is embedded in the mature phase (Fig. 1). This corresponds with Fagerstöm's (1992) suggestion that fitness in clonal plants should be based on the meristem-meristem cycle rather than the zygote-zygote cycle where a meristem has three developmental options: (i) to propagate vegetatively; (ii) to propagate sexually; (iii) to remain dormant. Asexual reproduction is emphasized in the generalized life-history description of arctic plants referred to in the Introduction and assumed to be adaptive in arctic environments where short growing seasons and annual climatic variation prevent production of sexual offspring or their survival in some years. However, corresponding to the variability in arctic conditions for plants, not all arctic plants are clonal and for those that are, the degree of clonality ranges from almost non-clonal, with only occasional fragmentation of the original genet, to extremely clonal where population maintenance is dependent on ramet proliferation (Jónsdóttir et al. 1996).

Clonal growth has several life-history consequences which complicates the application of the traditional life-history theory (Harper 1977, Tuomi & Vuorisalo 1989, Eriksson & Jerling 1990, Vuorisalo et al. 1997, Fischer & van Kleunen 2002, Pan & Price 2002). At the genet level in clonal organisms senescence is delayed, or even prevented, by constant rejuvenation through production of new, potentially independent and genetically identical ramets (but see discussion on senescence through accumulated somatic mutation in clonal plants in Klekowski 1997, 2003 and de Witte & Stöcklin 2010) and through this process, mortality risk of the genet is spread among the independent units (Cook 1979, Eriksson & Jerling 1990). Genet longevity is a complex trait in clonal plants and is a function of demographic processes at the ramet level, which introduces fitness sensitivity to changes in mortality and fecundity of the component ramets of each genet (Eriksson & Jerling 1990, Fagerström 1992, Pan & Price 2002, de Witte & Stöcklin 2010). In addition, exhaustion after reproduction and senescence, the most likely post-mature mortality causes in non-clonal plants, can be largely bypassed in clonal plants (Cook 1979). As a consequence, reproductive values potentially continue to increase with genet age and number of ramets in contrast to those of non-clonal plants, whether semelparous or iteroparous (Fig. 2).

Clonality by itself is not a single trait. There is a large diversity in the mode of clonal growth and the different modes may prove adaptive to different conditions (see review for bryophytes in During 1990; for vascular plants in Klimeš et al. 1997, Klimešová & Klimeš 2006). Even though the full range in modes of clonal growth recorded in the temperate zone is not expressed among arctic clonal plants they show considerable diversity (e.g. Callaghan & Collins 1976, Webber 1978, Jónsdóttir et al. 1996). An important aspect of clonality in vascular plants, which is partly related to the mode of clonal growth, is when and how ramets split from the rest of the clone (Eriksson & Jerling 1990) and the extent of an 'integrated physiological unit' (IPUs, sensu Watson & Casper 1984). Clonal plants

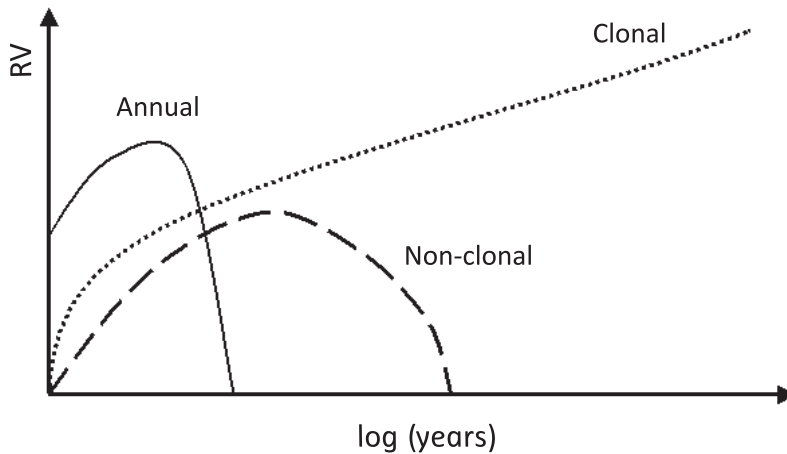


Fig. 2. – Hypothetical reproductive values for annual, non-clonal perennial and clonal perennial plants. RV = the expected future fecundity of an average organism in a particular age class.

range from ‘splitters’, where ramets split from the mother ramet shortly after their ‘birth’ to ‘extensive integrators’ where several interconnected ramets remain physiologically integrated throughout the ramet’s lifetime (Jónsdóttir & Watson 1997). Although this trait may have significant ecological consequences, it appears to be strongly constrained by phylogeny (Klimeš 2008). Examples of different modes of clonal growth and ramet splitting/integration categories among arctic plants are provided in Table 1.

In vascular plants, clonal growth adds yet another beneficial aspect in certain habitats as it enables a single genet to explore heterogeneous environments horizontally, facilitating foraging for limited resources (de Kroon & Hutchings 1995), sometimes even aided by division of labour between ramets (e.g. Jónsdóttir & Callaghan 1990, Alpert & Stuefer 1997). Efficient foraging requires relatively large integrated IPUs (intermediate to extensive integration), where the costs for maintaining ramet connections need to be balanced by the benefit. Such foraging behaviour may be of adaptive significance in certain resource-limited, unpredictable habitats in the Arctic, but less so in highly disturbed or extremely harsh habitats (Callaghan et al. 1996, Jónsdóttir et al. 1996, Jónsdóttir & Watson 1997).

Three basic types of life cycle

Although clonal growth may occur in annual plants with significant implication for their fitness, it is probably not common in the short growing season of the Arctic. Therefore, on the basis of the two traits, frequency of reproduction (semelparity vs iteropary) and degree of clonality, arctic plant life cycles may be separated into three basic types, annual/biennial, perennial non-clonal and perennial clonal (Fig. 1). This framework will be used here to explore the diversity of life history traits linked to the different developmental phases of the life cycles.

Table 1. – Examples of different modes of clonal growth in arctic plants of different growth forms and of different categories of integrated physiological units (IPUs) and genet ‘splitting’. Clonal growth modes are arranged within each splitting category according to decreasing specialisation of organs involved. Observe that some species have two or more alternative modes of clonal growth.

Mode of clonal growth	Growth form			
	Graminoid	Dicot herb	Dwarf shrub	Bryophyte
Splitters				
Asexual seed (agamospermy)	<i>Poa arctica</i>	<i>Potentilla nivea</i> , <i>Antennaria</i> spp., <i>Taraxacum</i> spp.	<i>Potentilla</i> spp.	–
Bulbils /plantlets	<i>Poa arctica</i> , <i>Deschampsia alpina</i>	<i>Bistorta vivipara</i> , <i>Saxifraga cernua</i> ,	–	<i>Marchantia</i> spp., <i>Grimmia torquata</i>
Branches	–	<i>Cerastium regelii</i>	–	<i>Campylopus</i> spp.
Intermediate integrators				
Stolons	<i>Puccinellia phryganoides</i>	<i>Ranunculus hyperboreus</i> , <i>Saxifraga flagellaris</i>	<i>Vaccinium oxycoccus</i>	–
Rhizomes	<i>Eriophorum vaginatum</i> <i>Eriophorum angustifolium</i>			
Root shoots	–	<i>Cardamine bellidifolia</i>	–	–
Branches	–	–	–	<i>Sphagnum</i> spp., <i>Hylocomium splendens</i>
Thallus growth	–	–	–	Some liverworts
Extreme integrators				
Rhizomes	<i>Poa arctica</i> , <i>Puccinellia phryganoides</i> , <i>Carex</i> spp.	<i>Oxyria digyna</i> , <i>Saxifraga hirculus</i> , <i>Rubus chamaemorus</i>	<i>Vaccinium myrtillus</i> , <i>V. vitis-idaea</i>	–
Layering and adventitious rooting	–	–	<i>Salix</i> spp., <i>Cassiope</i> spp.	–

The premature and dormant phases

The premature phase covers all life-cycle stages before maturity, i.e. before the onset of sexual reproduction. Population growth rate and the potential rate of evolutionary change are largely affected by the average length of the premature phase, i.e. the generation time, and the frequency of successful establishment of genets. Development of both vegetative and flower buds in many arctic plants is characterized by preformation over one or more years, which facilitates rapid emergence at the onset of the growing season (Sørensen 1941, Billings & Mooney 1968). The majority of arctic plants apparently have delayed maturity, even some ‘annuals’, and a long bud-development period may contribute to that. According to life-history theory, the demographic costs of delayed maturity in the form of decreased probability of surviving to maturity need to be balanced out by some type of benefit, such as higher initial fecundity (discussed below as part of the mature phase) or higher offspring quality (Stearns 1992). In addition, environments that are variable in time, should select for various ‘bet-hedging strategies’ linked to the premature phase, and dormancy (spore, seed) can be viewed as such a strategy.

Offspring quality

Seed size, seed germinability and viability are all aspects of offspring quality in seed plants. In general there is a trade-off between the number and size of seed (Lloyd 1987).

Such a trade-off has not been explicitly investigated in arctic plants, but both traits may be under strong selection in the Arctic: small seed are more likely to be dispersed over long distances (Alsos et al. 2007) and seed size may be critical for germination and successful seedling establishment. Seed germination in arctic plants has been widely studied. The studies reveal that within all bioclimatic subzones seed germinability ranges between 0 and 100% and that it depends strongly on species (phylogeny) and seed size, which is in turn also affected by local climatic conditions during seed ripening (e.g. Söyrinki 1938, Sørensen 1941, Bliss 1958, Euroala 1972, Bell & Bliss 1980, Grulke & Bliss 1985, Khodachek 1993, Jónsdóttir 1995, Laine et al. 1995, Wookey et al. 1995, Molau & Shaver 1997, Bliss & Gold 1999, Klady et al. 2011). Therefore, without accounting for phylogeny and phenotypic plasticity, any possible trends in germinability or seed viability among life-cycle types, or correlations with age at maturity, will be masked.

Seeds that do not immediately germinate either die or enter the dormant seed bank for a variable length of time. Seed dormancy is considered to be an adaptive trait in environments where conditions for establishment are variable in time (Harper 1977). An increasing number of studies show that viable seed banks may occur in all bioclimatic subzones of the Arctic although seed-bank sizes differ considerably among habitats within zones. The general picture emerging is that seed-bank size is largest in habitats of high productivity (e.g. McGraw & Vavrek 1989 and references therein, Khodachek 1993, Lévesque & Svoboda 1995, Bliss & Gold 1999, Larsson 2002, Cooper et al. 2004), although herbivory frequently reduces the number of seeds in the seed bank (Cooper 2006, Kuijper et al. 2006, González et al. 2010). McGraw & Vavrek (1989) estimated that approximately 50% of the species of tundra plants in arctic Alaska and Canada have viable seed banks and Cooper et al. (2004) found that almost 70% of the species at various study sites on high-arctic Svalbard had a seed bank. However, only a few studies are available on arctic seed-bank dynamics (see e.g. McGraw & Vavrek 1989) and it is therefore difficult to evaluate the extent to which arctic plants adopt seed dormancy as a 'bet-hedging strategy' or whether the three life cycle types differ in this respect.

Establishment

Successful seedling establishment can be viewed as a function of life-history traits (fecundity, offspring quality) in interactions with ecological factors, including safe sites. It is frequently claimed that seedling establishment is a rare event in populations of arctic plants. The main evidence for both non-clonal and clonal plants is indirect, i.e. based on uneven population age or size-class distributions, where there are high frequencies of a few age classes whereas others are present at a low frequency or completely absent (Wager 1938, Callaghan & Emanuelsson 1985, Philipp et al. 1990, Havström 1995, Philipp 1997). Although such patterns are far from unique for arctic populations, it is possible that the 'windows of opportunity' for establishment (sensu Jelinski & Cheliak 1992, Eriksson 1997) open at considerably longer time intervals in some places in the Arctic than elsewhere (Callaghan 1974, Philipp et al. 1990, Havström 1995). However, an accumulating number of studies demonstrate that in spite of infrequent successful establishments of new genets, it is frequent enough in many arctic populations of both clonal and non-clonal species to preserve genetic variation and genet diversity in the same range as in temperate plant populations (e.g. Jefferies & Gottlieb 1983, Bauert 1996, Jonsson et al. 1996, Philipp

1997, Gabrielsen & Brochmann 1998, Stenström et al. 2001, Kjølnner et al. 2004, Douhovnikoff et al. 2010).

For iteroparous plants, the risk of mortality is generally greatly reduced as plants approach maturity. This is indicated by the shape of age-class distributions of iteroparous non-clonal arctic and alpine plants, i.e. *Silene acaulis* (Philipp et al. 1990), *Papaver radicum* (Nordal et al. 1997) and *Pedicularis* spp. (Philipp et al. 1996). Similar age-class distributions are difficult to obtain for clonal plants, but an even greater reduction in mortality towards maturity can be expected among those that start clonal growth before they become sexually mature.

The mortality rates at different stages of the premature phase of arctic bryophytes (protonema establishment, growth of the gametophyte and formation of the sporophyte) are not well studied and remain unknown for the majority of species. In general, the viability of sexual offspring of bryophytes is highly variable (spore germination, spore bank) as is the length of the premature phase (During 1979, 1992, Longton 1988).

Age at maturity

Information on the length of the premature phase in the Arctic is rather limited for perennial plants, especially clonal plants. Slow growth of seedlings and juveniles of most arctic plants (Wager 1938, Billings & Mooney 1968, McGraw & Shaver 1982, Bliss & Gold 1999, Hagen 2002) provides indirect evidence for a relatively greater age at maturity compared to temperate plants. Grulke & Bliss (1988) estimated that in the High Arctic, the small tufted, moderately clonal grass species *Phippisia algida* (in mesic disturbed habitats) and *Puccinellia vaginata* (in xeric undisturbed habitats) start flowering at the age of 8–10 years. Molau (1997) estimated that 18 years was the average age at first flowering in a sub-arctic-alpine population of the non-clonal, evergreen cushion plant *Diapensia lapponica*. Depending on substrate, average generation time in alpine populations of the non-clonal *Papaver radicum* (also common in the Arctic) ranged between 8 and 20 years (Nordal et al. 1997). Records of age at maturity for clonal plants are scarce and there are no indications for differences in the length of the premature phase between non-clonal and clonal plants. The bud formation time and the length of the premature phase are, however, most likely negatively related to the length of the growing season. This was demonstrated in cultivation under constant optimal conditions for the clonal plant *Carex bigelowii*: plants started to produce ramets within a few months after germination and flowered after one year, while observations under natural conditions showed that the premature phase stretched over several years (I. S. Jónsdóttir, unpublished). The longer it takes to reach maturity, the longer the period the juvenile plants are exposed to the risk of mortality, which should exert strong selection on offspring quality.

The mature phase

The mature phase in semelparous annual or biennial plants is short per definition. For iteroparous plants, the length of the mature phase is expected to be significantly extended by clonal growth, which should also be reflected by differences in reproductive traits between non-clonal and clonal plants.

Reproductive life span and longevity

Life-history theory predicts that variation in offspring survival rates from one reproduction event to the next produces a selective pressure for longer reproductive life span (Stearns 1992), which can be regarded as another ‘bet-hedging’ option for plants (i.e. in addition to seed bank) in environments that are variable in time. A long life span increases the probability of viable offspring production that coincides with ‘windows of opportunity’ for establishment.

Many non-clonal arctic-alpine plants have fairly long reproductive life spans and can thus be assumed to have adopted this strategy; maximum age records of between 20 and 100 years are not unusual (see review in Callaghan & Emanuelsson 1985). The largest individuals in a subarctic-alpine population of the non-clonal species *Diapensia lapponica* were estimated to be over 400 years old (Molau 1997). Long life span is, however, not a specific arctic plant trait, neither in non-clonal (cf. Inghe & Tamm 1985) nor clonal plants (de Witte & Stöcklin 2010).

Because longevity is a complex trait in clonal plants, it is usually more complicated to age individual genets than non-clonal plants, apart from whether they are vascular plants or bryophytes, especially in those with extensive lateral spread. Consequently there are few data available. Existing estimates of genet age for vascular clonal plants in general indicate that clonal-plant life span is one order of magnitude longer than in non-clonal plants (de Witte & Stöcklin 2010). Available age estimates for arctic plants show that genet age of horizontally spreading ‘extensive integrators’ may reach over thousand years (rhizomatous *Carex* species; Jónsdóttir et al. 2000), while the age of mature clones of the caespitose ‘intermediate integrator’ *Eriophorum vaginatum* (Table 1) ranged between 120–180 years (Mark et al. 1985), which is comparable to long-lived non-clonal plants. No reliable age records are available for extreme clonal ‘splitters’ in the Arctic such as the bulbil forming species *Bistorta vivipara* and *Saxifraga cernua* or the numerous viviparous species of arctic grass. Since ‘splitters’ may spread the risk of mortality more efficiently than laterally spreading ‘extensive integrators’ their life expectancy should be even greater.

The most extreme ‘splitters’ may perhaps be found among bryophytes because, lacking vascular tissue, they have limited possibilities to integrate the different parts of the plant. Even though the maximum age of intact shoot segments of perennial bryophytes typically ranges between 2–20 years (Callaghan et al. 1978, 1997, During 1979) the genet may be substantially older, potentially reaching thousands of years (e.g. Reichard 1860 in During 1979, Karlin et al. 2011).

In an ever-changing environment, extreme longevity may severely reduce possibilities for fine-tuning adaptations through natural selection unless new variation is introduced via somatic mutations. The selection pressure prevailing during the premature phase of a parent plant that was established hundreds or thousands of years ago is most likely not the same as its offspring will experience today, which may set a limit to the maximum life span of clonal plants in terms of fitness. Consequently, continued reproduction of such old genets may not add to their fitness anymore, unless offspring can be widely dispersed into new habitats, or if the plant has adopted high phenotypic plasticity (Stenström et al. 2002). In this context the question regarding somatic mutation is highly relevant, i.e. whether adaptive somatic mutations occur within the genet (Klekowski 1997, 2003). Furthermore, high levels of heterozygosity in high-level polyploids among arctic plants, may buffer

against such maladaptations of extreme longevity in both clonal and non-clonal plants (Brochmann et al. 2004). However, in clonal plants, clonal growth contributes to population growth without involving sexual reproduction and ramet population dynamics thus directly affects the longevity of the genet. Ramet population dynamics is in turn affected by ramet life history.

Ramet life history

Ramets may be either semelparous or iteroparous and demographic studies at the ramet level reveal a large diversity in ramet life history. As for the genet level, the ramet life cycle can be divided into a premature, dormant and mature phases and in the case of ramets it is more appropriate to define maturity at first daughter-ramet production (i.e. initiation of new potentially independent unit) than at first sexual reproduction (Fig. 1). With the exception of asexual seed (agamospermy), a single ramet is usually much more costly to produce than a single sexual offspring like a spore or a seed, at least in terms of the resources required. Already at birth, a ramet may be quite well developed in some species and the high resource investment can be balanced by benefit in form of lower premature mortality rates than in sexual offspring. In vascular ‘intermediate’ and ‘extensive integrators’ in the Arctic, daughter ramet survival may be further enhanced by prolonged resource subsidy through the vascular connections with the mother ramet, a process equivalent to extended parental care (e.g. Callaghan 1984, Jónsdóttir & Callaghan 1988, Jónsdóttir et al. 1996). In addition, ‘integrators’ may stabilize ramet population dynamics through various innate regulations of resource utilization among interconnected ramets (e.g. Callaghan et al. 1986, Jónsdóttir & Callaghan 1988, Lomnicki 1988, Svensson & Callaghan 1988, Eriksson & Jerling 1990, Jónsdóttir 1991), which may contribute to population maintenance and community resistance to fluctuating environmental conditions in the Arctic (Callaghan et al. 1996, Jónsdóttir et al. 1996). On the other hand, a prolonged period of bud formation may constrain ramet dynamics in response to the environment in arctic plants (Carlsson & Callaghan 1990).

In the Arctic, ramet demography and life history are most extensively studied in graminoids of various degrees of integration (e.g. Callaghan 1976, Fetcher 1983, Kotanen & Jefferies 1987, Carlsson & Callaghan 1990, Jónsdóttir 1991, Tolvanen et al. 2001a, Stenström & Jónsdóttir 2006). For some clonal plants, such as bryophytes and dwarf shrubs, ramet demography studies may be complicated simply because the ramet is not easily defined. For those plants, demography has been successfully analysed in terms of branches or meristems (e.g. Collins 1976, Callaghan et al. 1978, 1997, McGraw & Antonovics 1983, Tolvanen et al. 2001b). Viable bud (meristem) bank, yet another bet-hedging strategy, would be of adaptive significance in temporally variable habitats in the Arctic, but only a few studies have addressed the size of the bud bank (Jónsdóttir 1991, Jónsdóttir et al. 2000, Tolvanen et al. 2001b) and its viability (Jónsdóttir & Callaghan 1988). A thorough analysis of ramet life-history diversity among clonal plants would need to consider both the degree of integration and bud dormancy (Klimešová & Klimeš 2007).

Reproduction

There are three general life-history aspects of reproduction to consider: (i) the reproductive effort, (ii) the reproductive output in terms of produced offspring (fecundity) and (iii)

the reproductive success in terms of offspring establishment, the last already addressed in the section on the premature phase. An early prevailing view among arctic ecologists was that sexual reproduction is considerably less important in arctic plants than asexual reproduction (clonal growth in the broad sense), which is supported by observations such as low seed production in many tundra plants, especially in severe habitats (Billings & Mooney 1968, Bliss 1971) and low seed set even in favourable years (Billings 1974). This view was later challenged (e.g. McGraw & Shaver 1982, Billings 1987, Philipp et al. 1990).

Life-history theory assumes a trade-off between reproduction, growth and/or survival. Studies on such trade-offs in plants are faced with a suite of methodological problems in measuring reproductive effort because of difficulties in separating the allocation of resources to growth and reproduction and which currency to use, and results are thus often conflicting (e.g. Reekie & Bazzaz 1987). Implicit in previous views on reproduction in arctic plants was the notion that reproductive investment would be generally lower than that recorded for plants at lower latitudes. However, acknowledging the great diversity of plant life histories, there is no evidence for generally lower reproductive investment in plants adapted to cold environments (e.g. Thorén et al. 1996).

A trade-off between survival (or longevity) and reproduction was indicated by a study of three non-clonal (or moderately clonal) plant species of contrasting longevity in low-arctic West Greenland (Philipp et al. 1990). In two relatively long-lived species, *Dryas integrifolia* and *Silene acaulis*, biomass (dry weight) allocation to reproduction was on average 0.8 and 3.2%, respectively, while the shorter-lived *Ranunculus nivalis* allocated up to 17% of its total dry weight to reproduction [published records on oldest genet-age estimates of the two former species or their close relatives: 108 years for *Dryas octopetala* in Russian Lapland (Kihlman 1890) and between 250 and more than 300 for *Silene acaulis* in alpine populations (McCarthy 1992, Morris & Doak 1998, respectively)]. Apparently, the two longer-lived species passed through a phase of relatively vigorous flowering after which flowering declined as can be expected in plants where rejuvenation through clonal growth is absent or at low levels (Fig. 2). Dry weight allocation to reproduction in *D. integrifolia* and *S. acaulis* was found to be even lower on the high-arctic Ellesmere Island than on Greenland, i.e. 0.2 and 1.6%, respectively (Maessen et al. 1983). In contrast, an Ellesmere Island population of the relatively short-lived non-clonal *Papaver radicum* (estimated maximum age of 30 years), typical of exposed habitats of polar semi-deserts, allocated 25–34% of its dry weight to reproduction (Lévesque et al. 1997). The few studies that have explicitly addressed the allocation to sexual reproduction in arctic clonal plants suggest that it is generally lower on a genet basis in clonal plants than in non-clonal plants (e.g. Chester & Shaver 1982, Jónsdóttir 1995, Stenström 1999, Stenström & Jónsdóttir 2006), indicating a trade-off between sexual and asexual reproduction (i.e. clonal growth) and even providing further support for a trade-off between reproduction and survival.

Modular organisms only have a limited number of growing points (meristems) and another way to evaluate reproductive effort is to assess the proportion of growing points allocated to reproduction (Watson 1984). Surprisingly few assessments of that kind have been made and most studies report the number of flowers per individual without relating it to the number of meristems. In annual plants, up to 100% of the meristems may be allocated to reproduction because no meristems are needed for overwintering. In plants of temporally variable environments meristems may be allocated both to overwintering and to extended bud dormancy (Klimešová & Klimeš 2007). Annual fluctuation in flowering

is typical of subarctic and arctic plant populations of perennial clonal plants and, although triggered by fluctuating climate, there are strong indications that it is a consequence of inter-annual variation in reproductive effort in terms of meristem allocation to flowering in combination with prolonged flower bud development (Sørensen 1941, Carlsson & Callaghan 1990).

Pollen limitation and mating systems (degree of cross- vs self-pollination) affect reproductive output (fecundity) in arctic plants (e.g. Molau 1993, Philipp et al. 1996, Brochmann & Steen 1999). In general, reproductive output tends to be higher in self-pollinating plants, while cross-pollinating plants have a higher reproductive effort. Self-pollination is apparently more common in the Arctic than elsewhere (Molau 1993, Brochmann & Steen 1999) and it seems to occur equally in all three life-cycle types. Molau (1993) demonstrate that the occurrence of different mating systems in arctic and alpine plants may be linked to flowering phenology, such that species that flower early tend to be cross-pollinated, while late flowering species are commonly self-pollinated.

The proportion of ovules that develop seed is one estimate of reproductive output per unit effort. Typical seed:ovule proportion in annuals is high, i.e. around 0.85 compared to 0.50 in perennial plants (Wiens 1984). However, in high-arctic populations of the annual *Koenigia islandica* on Svalbard seed:ovule proportion was similar to that in perennials, i.e. 0.5 on average (I. S. Jónsdóttir, unpublished data). In spite of this, seed production was apparently adequate to sustain dense populations: densities ranged between 860 and 2375 individuals per m² in patches within wet and mesic habitats (I. S. Jónsdóttir, unpublished data). In arctic perennial plants the reproductive output per unit effort is highly variable and may depend on breeding system and phenology (Molau 1993).

Both reproductive effort and output in annuals are affected by conditions within the same season. For perennials and some arctic ‘annuals’ where flower-bud development may be extended over more than one year, reproductive effort is also a function of conditions during the previous growing seasons, while reproductive output is largely determined by the current season. Consequently, reproductive output can be low or absent in spite of immense flowering effort if the current season is unfavourable (Philipp et al. 1990).

Conclusions

The main messages from this overview are that (i) arctic plants have evolved a wide range of life history strategies, and (ii) there is no single life-history trait that is specific for arctic plants. However, arctic environments differ in many respects from environments of other biomes and should therefore select unique combinations of life-history traits, often shaped by the prolonged time it takes for buds to form. Consequently, although constrained by phylogeny, arctic plants should express a unique spectrum of life histories.

The overview also demonstrates that the gaps in our knowledge on arctic plants are many in respect to the framework applied here, which may hamper further analysis of life history–habitat relationships. Interesting questions to address in such an analysis would be how life-history diversity is partitioned within and among different habitats, i.e. whether the dynamic nature of the arctic habitats prevents strong life history–habitat associations

as indicated by observations in the field. A range of life-history traits like breeding system, seed bank, seed dispersability, resource storage, mode of clonal growth, degree of integration and possession of a bud bank, could be used in future studies to further explore diversity across arctic habitats. In this context access to databases such as CLO-PLA3 (Klimeš & Klimešová 1999, Klimešová & Klimeš 2006) could provide interesting information. At some stage it would be rewarding to relate plant life-history diversity to ploidy levels, which are exceptionally variable among arctic plants (Brochmann et al. 2004). At all stages in such analysis historical factors, biogeography and phylogenetic constraints need to be considered (e.g. Klimeš et al. 1997, Klimeš 2008). The ultimate goal is to identify life history syndromes or strategies. Such strategies may increase our understanding of the functional and evolutionary responses of arctic plants to climate change and other environmental changes.

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Souhrn

Práce upozorňuje na fakt, že diverzita životních cyklů rostlin v Arktidě je mnohem větší, než je obvykle prezentováno v literatuře. Je možno rozlišit tři základní typy životního cyklu, jež představují vhodný základ pro popis strategií rostlin v Arktidě: (1) jednoletky, (2) neklonální trvalky a (3) klonální trvalky. Práce shrnuje současné znalosti o průběhu životního cyklu těchto rostlin a ukazuje, že diverzita životních historií rostlin v Arktidě je značná a neexistuje žádná speciální vlastnost, charakteristická pouze pro arktické rostliny. Nicméně je třeba zdůraznit, že díky specifickým vlastnostem prostředí se u arktických rostlin nalézají unikátní kombinace vlastností životního cyklu. Naše omezené znalosti dosud brání generalizaci a poznání vztahů mezi životním cyklem arktických rostlin a vlastnostmi prostředí v různých historických, biogeografických a ekologických souvislostech. Na druhou stranu současný výzkum reakce arktických rostlin na změny klimatu přináší mnoho cenných poznatků o jejich životních strategiích.

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