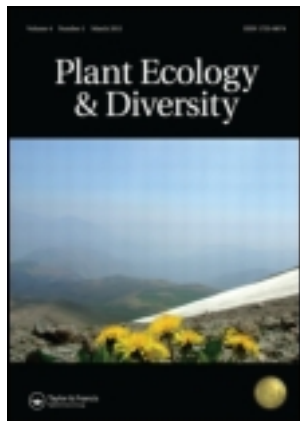


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OPINION ARTICLE

Are clonal plants more frequent in cold environments than elsewhere?

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In stressful environments, clonality provides plants with reproductive insurance and conservation of limiting nutrients. Hence, clonal growth is expected to be more frequent in floras of cold environments, such as the alpine and arctic regions, than in temperate regions. Evidence for this is largely based on comparisons of the ratio of clonal to non-clonal vascular plant species in local floras, as it is difficult to obtain reliable data that assess the extent of clonality in plant communities. Here we review, to the best of our knowledge, the most comprehensive dataset on the proportion of clonal vascular plant species in regional floras of cold environments/regions. Contrary to our expectations, the results do not show a higher proportion of clonal species in cold environments than in the reference regions. The results rather show regional differences explicable by different species pools and/or climates. More data, which take into account environmental gradients, habitat diversity and different modes of clonal growth, the relative dominance (abundance) of clonal plants, are necessary to test the hypothesis that the ratio of clonal to non-clonal vascular plants in cold environments/regions is higher than elsewhere.

Keywords: alpine floras; arctic floras; clonal growth forms; foraging for nutrients; reproductive insurance

Introduction

The ability to grow clonally enables a plant to produce genetically identical and potentially physically independent offspring by means of vegetative growth, to exploit a patchy environment, to share limited resources and information among integrated offsprings and to have multiple connections between above-ground and below-ground parts (for definition of clonality used see Figure 1) (de Kroon and van Groenendael 1997; Aarssen 2008).

The benefits of clonal growth have been demonstrated to be especially important in stressful environments. The preponderance of clonality in cold environments (alpine and arctic areas) is often used as an example (Bliss 1971; Billings 1974; Callaghan et al. 1992; Jónsdóttir et al. 1996; Körner 2003; Evette et al. 2009). The preponderance of clonality in cold environments might be achieved by increased clonality within a species (a larger proportion of clonal to seed-derived descendants) in cold in comparison with warm regions (intraspecific level) or by replacement of non-clonal species by clonal species (interspecific level), along a temperature gradient, from the warm to the cold end. Although not unique to cold regions, the following two explanations form the foundations of the reviewed paradigm: clonal growth may be interpreted as a safe alternative to risky seed production and recruitment (Callaghan and Emanuelson 1985) and as an adaptation for nutrient uptake from multiple sites occupied by a clone that can translocate and store limited resources in a system of interconnected ramets (Jónsdóttir et al. 1996).

On the intraspecific level, the fact that clones are more frequent at the margins of geographical ranges of species

(Silvertown 2008) – and latitudinal and altitudinal boundaries of plants distribution are a meeting point of such margins – can be regarded as supportive evidence for the idea that clonality contributes more to population dynamics of plants in cold regions than elsewhere. Although data on the role of clonality in population dynamics of plants can be assessed by using molecular techniques (Arnaud-Haond et al. 2007), it is impossible to separate apomixis (production of seeds without meiosis) from clonal growth using the genetic structure of populations. An apomictic seed is genetically identical with its parent, but it faces the same uncertainties in establishment as any other seed.

Here we focus on the interspecific level to evaluate if the conventional wisdom about an advantage of clonal growth results in higher representation of clonal species in comparison with non-clonal plant species in regions of extremely cold climates (i.e. where low temperature sets a limit to the distribution of vascular plants). We evaluate if the accumulated data support this idea and, finally, outline how any future assessment should be carried out to test the hypothesis of a preponderance of clonality in cold environments. Although there is clonal growth in bryophytes as well, we deal only with vascular plants in this review.

Review of literature

Despite the general opinion, we have found few supportive data in the literature for any type of preponderance of clonality in cold environments. In an analysis by Klimeš et al. (1997), preferences of clonal versus non-clonal plant species for lower versus higher temperatures were

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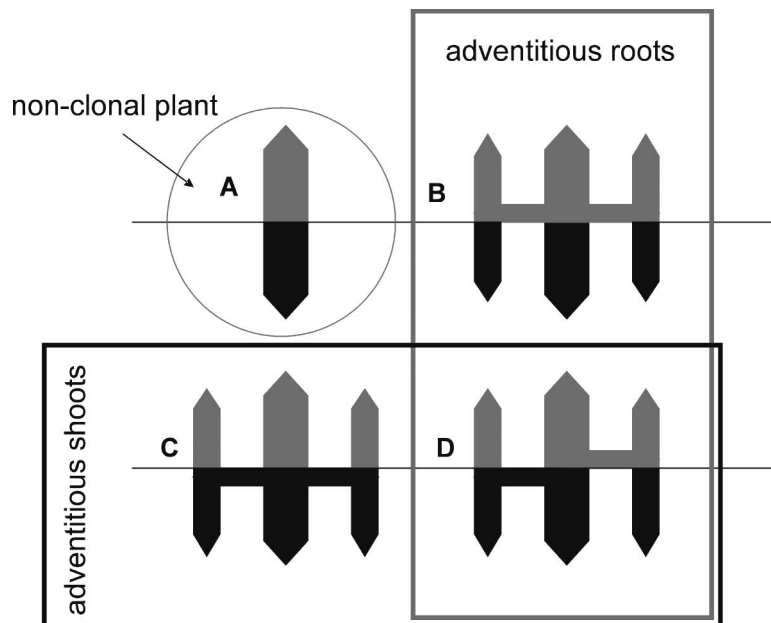


Figure 1. Delimitation of clonality according to basic types of root–shoot connections in plants (adapted from Groff and Kaplan 1988). Grey: shoots, black: roots. Non-clonal plant (A) consists only from primary shoot growing from the shoot pole of the embryo and primary root growing from the root pole of the embryo. Clonal plants are plants in which the primary shoot is replaced either by axillary shoots in rhizomatous and stoloniferous species (B, D), or by adventitious shoots (C, D) in root-sprouting plants. The production of adventitious roots or shoots provides plants with the ability to have multiple connections between above-ground and below-ground parts (rooting units sensu Aarssen 2008).

interpreted as a proof for higher proportion of clonal plants in cold environments than in warm ones. However, the analysis by Klimeš et al. (1997) was restricted to the flora (using the CLO-PLA database for delimitation of clonal plants) of Central Europe, where nearly all annuals and trees are non-clonal plants. Consequently, the significant but small difference in distribution of clonal versus non-clonal species according to their preference for temperature assessed indirectly, by using Ellenberg indicator values (10-degree scale, Ellenberg 1979) might have been due to the fact that not only annuals but also trees prefer warmer habitats, and trees by definition do not grow above the alpine treeline. Jónsdóttir et al. (1996) compared lists of growth forms reported from the county of Durham, England, and the Torneträsk region, Sweden, and demonstrated a preponderance of clonal species in the Swedish subarctic site. Their growth forms were delimited according to their above-ground morphology (e.g. multi-stemmed perennials vs. single-stemmed perennials), but an analysis of below-ground structures through which clonality is usually achieved in herbs was not undertaken.

A contrary opinion on the proportion of clonal species in cold environments was provided by Söyrinki (1938), who concluded that the preponderance of clonal over sexual multiplication in alpine regions was due to the dominance (abundance) of clonal plants and not to the prevalence of clonal species. Out of a total of 197 species, 52% had some ability to produce vegetative offspring in the alpine zone

of the Scandinavian mountains, and these species usually included community dominants.

A surprisingly low proportion of clonal plant species (delimited by the ability to produce either adventitious roots or shoots) in the flora of eastern Ladakh, Trans-Himalaya, in comparison with the flora of the Czech Republic was reported by Klimeš (2003). Only 30% of the plants occurring at an altitude of about 4000 m a.s.l. in Ladakh were clonal, and their proportion declined towards higher altitudes. All species growing at the highest altitudes (ca. 6000 m a.s.l.) were non-clonal.

From the above it follows that the proportion of clonally growing species in cold environments, or the proportion of clonally growing species in comparison with non-clonal species in a region, have been repeatedly studied; however, due to different definitions of clonality, a cross-region comparison cannot be made. Are we able to find additional data to enable the comparison of the proportion of clonally growing species across different regions?

A comparison of data on the proportion of clonal species in the floras of cold regions

Clonality is an architectural trait that characterises the growth form of a plant. Although growth form classification has a long tradition (e.g. Raunkiaer 1910; Barkman 1988; Halloy 1990), it does not allow a delimitation of clonality, as its application is largely restricted to the

above-ground architecture of plants (e.g. Komárková and McKendrick 1988; Pokarzhevskaya 1995). Consequently, the comparison of floras for clonality should use data from studies that report directly on clonality and the vegetative multiplication of plants. Unfortunately, even such studies distinguish several categories of clonal growth, and therefore they are not readily comparable (Hess 1909; Söyrinki 1938; Hartmann 1957). Nevertheless, some of the distinctions defined between clonal and non-clonal plants are identical (see references in Table 1).

We compared the proportion of clonal species, using the definition presented in Figure 1, in regional floras, for different cold versus reference regions. Altogether, we report data on clonal growth from two arctic and four alpine regions (Table 1) and two adjacent reference regions: the Czech Republic for mesic alpine and arctic areas (Caucasus, Scandes, Alps, Svalbard and Taimyr), and Kazakhstan for arid mountains such as Ladakh (Table 1, Figure 2). The data were split according to moisture availability, as clonality is known to be more common in wet habitats (Klimeš et al. 1997; Sosnová et al. 2010). The collection of compared datasets represented all sources available to date.

Our simple comparison provides no evidence that clonality, in terms of the ratio of clonal to non-clonal taxa, differs between arctic-alpine and reference regions (Figure 3). On the other hand, there are indications that areas with different species pools and/or climates (mesic versus arid) differ in clonality. The proportion of clonal plants in arctic and European mountains was found to be 60–90%, which is more than in the Czech Republic (65%). However, in the arid Trans-Himalaya, non-clonal plant species prevailed over clonal ones. Two datasets, those

for the Scandinavian mountains and for the Alps, include the highest proportion of clonal species, about 90%. Both include alpine grasslands and/or shrublands, where the proportion of clonally growing plants is the highest, similarly to grasslands in the low-altitude temperate zone (Tamm et al. 2002), whereas other surveys contain open vegetation of the nival zone (Caucasus) or the high arctic (Svalbard, Taimyr) (Table 1).

Hartmann (1957) noticed the decreasing proportion of clonal plants towards open communities in his study in the Central Alps. He explained it by reduced competition in pioneer communities that allows generative reproduction, but in places, where plant cover becomes denser, clonal propagation is more successful than generative regeneration, and non-clonal species become underrepresented.

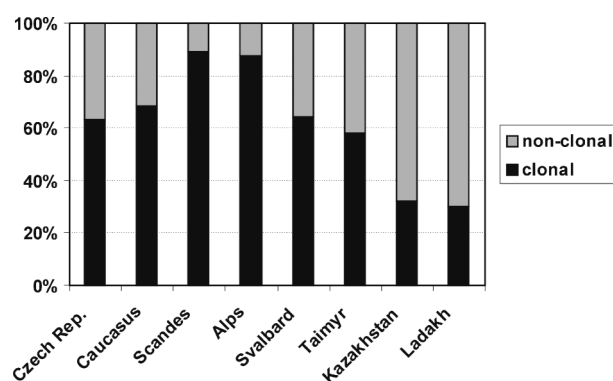


Figure 3. Proportion of clonal (black) and non-clonal (grey) plant species in floras from cold and reference regions. For characteristics of datasets, see Table 1. Clonal plants were defined as those without a persistent main root and with the ability to form adventitious roots or shoots.



Figure 2. Localisation of the studied cold and reference regions (see Table 1 for details). 1, Czech Republic; 2, Caucasus; 3, Scandes; 4, Alps; 5, Svalbard; 6, Taimyr; 7, Kazakhstan; 8, Ladakh.

Table 1. Data on clonality in arctic, alpine and reference regions compiled from cited literature. Arctic and alpine zones are defined as areas between the potential climatic tree-line and the permanent snow line.

Region (see Figure 2)	Type, latitude, altitude mean annual temperature*	Vegetation	Number of species	Reference
(1) Czech Republic	reference region, 50° N, 250–1600 m a.s.l., –0.4 – +10 °C	Temperate forests and anthropogenic habitats	2700	Klimešová and Klimeš (2008)
(2) Caucasus	alpine, 43° N, 3500–4000 m a.s.l., –6.1 °C	Subnival communities	89	Nakhutsrishvili and Gamtsemlidze (1984)
(3) Scandes	alpine, 62° N, 900–1100 m a.s.l., 0.65 °C	Alpine grasslands and shrubland	81	Rush et al. (2011)
(4) Alps	alpine, 47° N, 2400–3000 m a.s.l., –3 – –8 °C	Alpine grasslands and subnival communities	213	Hartmann (1957)
(5) Svalbard	arctic, 78° N, 0–450 m a.s.l., –2 °C	Tundra	78	J. Klimešová unpubl.
(6) Taimyr	arctic, 73–77° N, 0–100 m a.s.l., –13 °C	Tundra	43	Polozova (1981)
(7) Kazakhstan	reference region, 40–54° N, 100–500 m a.s.l., 0.5–12 °C	Steppes, semi-deserts and deserts	170	Baitulin (1979)
(8) Ladakh	alpine, 33° N, 4100–5900 m a.s.l., –8.2 °C	Cold deserts and subnival communities	540	Klimešová et al. (2011a)

*From www.worldclim.org

However, this idea was not supported by a case study from the Alps on the demography of *Poa alpina* L. The establishment by vegetative regeneration (by means of plantlets produced in inflorescences) of the species along a successional gradient in glacier foreland was restricted to the early stages with open vegetation, while regeneration by seed occurred along the whole gradient (Winkler et al. 2010).

Körner (2003), citing Hartmann (1957), also noted that there was an abundance peak of clonal growth in the lower alpine belt, followed by a reduction in frequency of clonal species at higher elevations. An alternative point of view can be that cold environments are not especially suited for clonal plants, but they are more hostile for certain non-clonal ones. With increasing altitude, first annuals and trees are lost from the species pool, then clonal perennials and finally non-clonal perennials.

Foundations of a paradigm reconsidered and future directions

The foundations of the paradigm concerning the preponderance of clonality appear general, and not restricted to cold climate. Reproductive insurance applies to environmental stress in general and, equally, the existence of a plant foraging strategy for nutrients occurs in all environments characterised by nutrient limitation.

The most pronounced example of reproductive insurance by clonal growth occurs in aquatic habitats, where plants may spread via clonal propagation as vegetative growth could be very vigorous and plants can become fragmented and transported via water current and easily re-root (in the case of rooting species); however, flowering can be very rare (Sculthorpe 1967). Cold environments differ from the above. Although generative regeneration is scarce

at high altitudes or latitudes (Cooper et al. 2004; Alsos et al. 2007; Steltzer et al. 2008), the vegetative growth of plants and hence clonal growth is limited as well (Bell and Bliss 1980; Alexandrova 1983). For example, *Carex curvula* All., an alpine clonal sedge, spreads ca. 1 mm per year laterally (Steinger et al. 1996). Rather, high-altitude and high-latitude plants rely on longevity, while successful establishment either from seeds or by clonal propagation is a rare event (Bell and Bliss 1980; Marcante et al. 2009; Douhovnikoff et al. 2010). Therefore not clonality, but more generally perennality could be viewed as providing reproduction insurance in cold environments.

Foraging for nutrients over the area over which a clone extends and perennial connection between ramets (integrator) is favourable in all nutrient-poor habitats (Jónsdóttir and Watson 1997), as shown by the study of the spatially extensive clones of *Carex bigelowii* Torr. ex Schwein. in the Swedish subarctic (Jónsdóttir and Callaghan 1988). However, long internodes are rarely produced in the skeletal soils of cold environments, and once established the long internodes can be damaged by frost heave, solifluction and unstable substrate on screes (Hess 1909; Jonasson and Callaghan 1992; Klimeš 2008). Consequently, one could rather expect a lower number of rhizomatous and root-sprouting plants in cold environments than elsewhere (see Klimešová et al. 2011b) and therefore different spectra of clonal growth organs in those areas in comparison with reference regions.

Is there enough evidence to reconsider the paradigm on the preponderance of clonally growing species in cold regions? Although the foundations of the paradigm could be questioned (see above), we certainly need better comparative data from a variety of alpine and arctic environments to offer an alternative.

A consideration of the distribution of clonal plants in different habitats and their plant communities, as opposed to that in entire regional floras, would likely to yield a refined ecologically meaningful understanding. For example, shallow waters, which host the highest proportion of clonal plants in temperate regions (Sosnová et al. 2010), are either missing at high altitudes and latitudes or are devoid of higher plants (Glooschenko et al. 1993; Klimešová et al. 2011a). Land use history may also be a factor to consider. For example, in hay meadows, no differences in the proportion of clonal to non-clonal plants were found along an altitudinal gradient spanning more than 1000 m in the Swiss Alps (Wellstein and Kuss 2011).

To accept or reject the hypothesis that environmental filters operating in cold environments select more for plants capable of clonal multiplication than in adjacent milder environments, one should compare the clonal traits of the species pool from which the flora of a cold region is derived and the flora of cold region itself, ideally across different plant communities. To interpret the comparison of rather remote regions, e.g. the Czech Republic and Svalbard, as was done in our simple analysis (Table 1), is problematic since the flora of the Czech Republic is by no means a direct source of species for the Svalbard flora and cannot be a norm for the proportion of clonal species.

To conclude, we highlight that clonal growth is not particularly enhanced in comparison with generative reproduction in cold environments, and for reproductive insurance perennality is sufficient. Moreover, cold environments are less suited for some types of clonal growth, such as below-ground rhizomes and roots with adventitious shoots, due to undeveloped substrate and its instability (cryoturbation and mass movement). The proportion of clonal species in a flora could also be affected by the fact that some specific habitats are absent, rare or without plants in cold regions (e.g. wetlands).

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