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Variation of sexual and clonal reproduction in the alpine *Geum reptans* in contrasting altitudes and successional stages

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Summary

We studied the relative proportion of sexual vs. clonal reproduction in 20 populations of the alpine pioneer plant *Geum reptans* in response to altitude (low and high) and succession (early and late). Additionally, the proportion of life-cycle stages, the proportion of reproducing adults, seed size, and seed number per flower head were determined. With increasing plant size, the probability of producing both flower heads and stolons increased ($P<0.001$). Individuals of all size classes tended to produce more flower heads than stolons. Stolon production was more frequent only if plants reproduced by one reproductive mode ($P<0.05$). The significant difference among populations in sexual reproduction and of seed number per flower head was not explained by habitat type. However, clonal reproduction was higher in populations at low and high altitude compared to populations at intermediate altitude ($P<0.05$). High altitude populations were characterised by a tendency of small plants to decline and an increase in the proportion of large plants ($P<0.05$) whereas the proportion of reproducing adults did not change with altitude. This indicates not only lower recruitment but also, that after successful establishment, growth and reproduction in *G. reptans* are not generally restricted, even above 2850 m. Our results suggest that variation in the proportion of sexual and clonal reproduction in *G. reptans* is probably more shaped by individual, i.e. plastic responses to local environmental conditions than by environmental gradients.

Zusammenfassung

Wir untersuchten den relativen Anteil von sexueller vs. klonaler Reproduktion in 20 Populationen der alpinen Pionierpflanze *Geum reptans* in Abhängigkeit von Meereshöhe (tief und hoch) und Sukzessions-Stadium (früh und spät). Zusätzlich wurde der

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Anteil verschiedener Lebenszyklus-Stadien, der Anteil reproduzierender adulter Pflanzen, das Samengewicht und die Anzahl Samen pro Blüte in allen Populationen bestimmt. Die Wahrscheinlichkeit, gleichzeitig Blüten und Stolone zu bilden, nahm mit zunehmender Pflanzengröße zu ($P<0.001$). Unabhängig von ihrer Größe tendierten die Individuen dazu, mehr Blüten als Stolone zu produzieren. Die Bildung von Stolonen war häufiger, wenn Pflanzen nur eine Reproduktionsform aufwiesen ($P<0.05$). Die Populationsunterschiede im Anteil sexueller Reproduktion und in der Anzahl Samen pro Blüte konnten nicht durch unterschiedliche Meereshöhe oder Sukzessions-Stadien erklärt werden. Hingegen nahm die Häufigkeit klonaler Reproduktion in tiefen und hohen Populationen im Vergleich zu Populationen der mittleren Höhenstufe zu ($P<0.05$). Hohe Populationen zeichneten sich durch eine Tendenz zur Abnahme kleiner Pflanzen und einen höheren Anteil großer Pflanzen aus ($P<0.05$), während der Anteil reproduzierender adulter Pflanzen konstant blieb. Dies weist nicht nur auf eine geringere Rekrutierung hin, sondern zeigt, dass nach erfolgreicher Etablierung auch oberhalb von 2850 m nur wenig Einschränkungen in Bezug auf Wachstum und Überleben von *G. reptans* bestehen. Unsere Ergebnisse legen nahe, dass die Variation in der Häufigkeit sexueller und klonaler Reproduktion von *G. reptans* stärker durch individuelle, d.h. plastische Reaktionen auf lokale Umweltbedingungen als durch Umwelt-Gradienten geprägt ist.

Introduction

Prominent features of alpine ecosystems are the steep gradients of altitude and climatic conditions shaping the environment and affecting alpine plant life. The natural fragmentation of alpine habitats created by small-scale differences in relief interacting with abiotic factors may influence a species' life-history and spatial distribution. Plants capable of growing in alpine environments are usually considered to be long-lived and to rely on clonal growth (Hartmann, 1957; Billings & Mooney, 1968). Generally, the importance of clonal growth tends to increase with altitude (Bliss, 1971; Klimeš, Klimešova, Hendriks, & van Groenendael, 1997) leading to a comparatively high fraction of clonal species occurring in extremely hostile habitats like pioneer communities on screes as well as in late successional alpine grasslands (Hartmann, 1957; Stöcklin, 1992; Klimeš et al., 1997; Klimes 2003).

Clonal plants often show reduced sexual reproduction compared to non-clonal species (Crawley, 1990; Schmid, 1990; Silvertown, Franco, Pisanty, & Mendoza, 1993, Eriksson, 1997) and frequently seedling recruitment has been considered to be rare (Eriksson, 1989, 1992). Local population dynamics of many species are strongly dominated by clonal growth (Callaghan, 1976; Crawley, 1990; Eriksson, 1992; Silvertown et al., 1993) assuring population growth and species' persistence during phases lacking sexual reproduction and increasing the fitness of established genotypes. Recruitment of seedlings is often restricted to founding events, 'windows of opportunities' or is closely linked to habitat disturbances (Jelinski & Cheliak, 1992; Eriksson, 1997). Nevertheless, seedling recruitment of clonal plants is easily underestimated (Eriksson, 1989). Many studies revealed considerable genetic variation not only in clonal species in general (Ellstrand & Roose, 1987; Hamrick & Godt, 1989) but also in clonal plants from alpine habitats (Bingham & Ranker, 2000; Till-Bottraud & Gaudeul, 2002; Reisch, Anke, & Röhl, 2005). Sexual reproduction not only provides genetic variation as a basis for adaptation to long-term environmental changes but also promotes dispersal in time and space (Nathan & Muller-Landau, 2000).

Plants may vary in their allocation to sexual and clonal reproduction and an investment in clonal growth may imply a trade-off with sexual reproduction (Cody, 1966). Such trade-offs have been demonstrated for a variety of species (e.g. Law, Cook, & Manlove, 1983; Sutherland & Vickery, 1988; Ronsheim & Bever, 2000). Trade-offs also could involve structural constraints like the utilisation of the same meristems for sexual and clonal organs (Watson, 1984; Eriksson, 1985). If a particular reproductive mode is favoured in a specific environment, selection is expected to act on the relationship between sexual and clonal reproduction (Loehle, 1987). However, plants are also able to respond to changing environmental conditions by phenotypic plasticity, which may also be under selection (Sultan, 1987). The relationship between sexual and clonal reproduction may be highly plastic in response to different environments (Sultan, 2000; Fischer & van Kleunen, 2002) leading to a variable ratio between both reproductive modes.