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Life History Strategies
in *Linnaea borealis*

BY
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Abstract

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About 70% of the plant species in the temperate zone are characterised by clonal growth, clonal species are also in majority in the Arctic and Subarctic where they affect the structure and composition of the vegetation. It is therefore of great importance to increase our knowledge about clonal plants and their growth and life histories. I have investigated how ramets of the stoloniferous plant *Linnaea borealis* are affected by the naturally occurring variation in environmental factors, such as: light, nutrient and water availability. Moreover, I examined the seed set and how supplemental hand pollination affects seed set in *L. borealis*, and also investigated the significance of the apical meristem for shoot population fitness. All studies were performed under field conditions in northern Sweden in a Subarctic environment and most are experimental.

The results show that nutrient resorption from senescing leaves is not significantly affecting the growth and nutrient pools of the ramet. This implies that the growth of *L. borealis* ramets is not governed by micro-site resource availability. However, removal of light competition resulted in increased branching and number of lateral meristems produced, reduced growth, and decreased root:shoot ratio on a per ramet basis. Thus, ramets of *L. borealis* can efficiently exploit favourable light patches through plastic growth. Apical dominance exerts a significant effect on shoot population fitness and can be lost through rodent grazing. However, loss of apical dominance is dependent on the timing of grazing, if the apical meristem is removed early in the autumn the ramet can repair the loss until the next summer. If grazing occur during spring the dry weight and leaf area production is affected negatively. Seed production in *L. borealis* in the Abisko area varies between years and sites, and was unaffected by supplemental hand pollination treatment, implying that there is no lack of pollinator activity.

Keywords: *Linnaea borealis*, apex removal, apical dominance, clonal plant, hand pollination, matrix modelling, plant foraging, resorption efficiency, resorption proficiency, resource heterogeneity, shoot dynamics

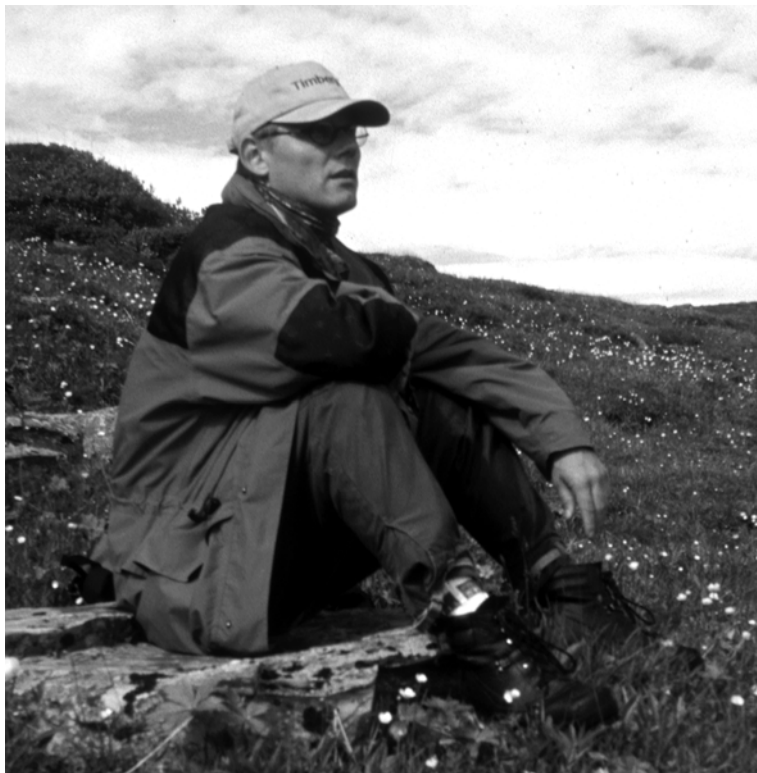
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The author on Mount Slättatjåkka, July 2000

Per angusta in augusta

This thesis is based on the following four papers, which will be referred to in the text by their Roman numerals:

- I** Niva M., Svensson B.M. and Karlsson P.S. 2003. Nutrient resorption from senescing leaves of the clonal plant *Linnaea borealis* in relation to reproductive state and resource availability. *Functional Ecology* 17: 438 – 444.
- II** Niva M., Svensson B.M. and Karlsson P.S. Effects of light and water availability on shoot dynamics of the stoloniferous *Linnaea borealis*. Submitted manuscript
- III** Niva M. and Svensson B.M. Shoot population dynamics of the stoloniferous *Linnaea borealis*: the significance of apical dominance. Submitted manuscript
- IV** Niva M. and Svensson B.M. Field experiments and observations concerning pollination and seed set in the clonal plant *Linnaea borealis*. Manuscript

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Introduction

To answer questions about why we find a plant species in a certain habitat but not in another, and why it is abundant in one place and rare in the other, we have to know how the plant is affected by, and interacts with its biotic and abiotic environment.

Clonal plants

About 70% of the plant species in the temperate zone are characterized by clonal growth (Salisbury 1942); clonal plants also dominate severely stressed habitats like the Arctic and Subarctic (Callaghan *et al.* 1992, Oborny and Bartha 1995, Jónsdóttir *et al.* 1996). Since they are so dominant, it is of great importance that we gain knowledge of the processes that determine their growth, particularly as they significantly affect the structure and composition of the vegetation. Many weeds are clonal, and so are much of the cattle's fodder, i.e., it is also of great economic importance that we increase our knowledge about clonal plants (van Groenendael and de Kroon 1990).

Clonality, or spontaneous self-cloning, is a wide-spread phenomenon in the plant kingdom, e.g. 10 out of 11 classes of vascular plants are able to proliferate vegetatively (Mogie and Hutchings 1990), it also occurs in lichens, fungi and some groups of animals. The common feature and defining principle of all types of plant clonality is the asexual, vegetative production of offspring that are genetically identical (or at least extremely similar) to each other and to the parent plant.

Clonal growth possesses many attributes which allow clonal species to efficiently confiscate space and contribute to the fitness of populations (Fagerström 1992, Wikberg 1995). Numerous aspects have received considerable attention from plant ecologists, e.g. internal transfer of resources between ramets and architectural plasticity and mobility of the genets, but also, to a lesser extent, the balance between sexual and asexual propagation and its impact on the genetic diversity of populations (Stuefer *et al.* 2002).

The physiological integration among clone modules is one of the most important aspects of clonal growth (Yu *et al.* 2002, Oborny and Kun 2002). Besides distributing resources it enables clonal fragments to have ramets specialised to acquire a locally abundant resource, the so called "division of labour" concept, reviewed by Alpert and Stuefer (1997).

"Clonal plants species can spread laterally, and as such they occupy an interesting middle position between highly mobile animals and immobile

plants" (Oborny and Cain 1997). A horizontally growing plant will face changes in resource availability; the ability to alter growth or movement in response to patch quality so that they can exploit favourable and avoid unfavourable portions of sites. Such phenotypic plasticity has been referred to as "plant foraging" (de Kroon and Hutchings 1995). Clonal growth is suggested to be adaptive under stressed conditions as in nutrient-poor and cold habitats or under shady or wet conditions, whereas under more optimal conditions non-clonal plants are favoured (Grace 1993). This is supported by results showing that populations of clonal species at the margin of their geographical range reproduce sexually to a lesser extent than populations closer to the centre of it (Dorken and Eckert 2001).

Clonal reproduction does not involve recombination and, therefore, yields offspring that are genetically identical or very similar to each other and to the plant that produced them. Because clonal offspring are also usually much larger than seeds, and lack prolonged dormancy or specialized dispersal mechanisms, it is likely that they experience reduced dispersal compared to offspring produced through sexual reproduction (Starfinger and Stöcklin 1996). High levels of clonal recruitment are, therefore, expected to strongly influence, e.g. genetic variation within and among populations (Muirhead and Lande 1997), effective population size and hence stochastic genetic processes (Orive 1993, Eckert and Barrett 1995), and to increase the species' geographical distribution (Dorken and Eckert 2001).

Resources

In habitats at high latitudes and altitudes, mineralization processes are retarded by low temperatures, leading to low nutrient availability (Körner 1999). Plants in these, and other nutrient poor habitats, may employ efficiency strategies to attain their vital activities. Such strategies may comprise increased efficiency with which nutrients are taken up from the soil via, e.g., increased root growth (Farley and Fitter 1999, McKee 2001), and by improving the availability of nutrients in the immediate vicinity of the roots by, e.g., excretion of acids (Neumann and Römheld 1999, Schulze *et al.* 2002).

The importance of an efficient utilization of nutrients by redistributing them within the plant for the production of new organs has been shown repeatedly (Field 1983, Karlsson 1994, Aerts 1996). Evergreen species combine the latter with increased longevity of leaves (Aerts 1995, Eckstein *et al.* 1999). It has been demonstrated that plants growing in infertile habitats typically retain growth-limiting nutrients for a long time (Eckstein and Karlsson 1997, Berendse 1998). One way of redistributing obtained nutrients within the plant is by the resorption of nutrients from leaves before

abscission. This has been considered either as the proportion of nutrient pool resorbed (resorption efficiency, see Aerts 1996 for a review), or as the degree to which a plant can decrease the nutrient concentration in leaves before abscission (resorption proficiency, Killingbeck 1996). As resorption is an energy-consuming process, one would expect conspecific plants to show a higher resorption efficiency and proficiency in nutrient-poor habitats than in nutrient-rich habitats, the same goes for reproductive and non-reproductive plants. Results from earlier studies are, however, far from convincing, see Aerts (1996) and Eckstein et al. (1999) for reviews.

In addition to nutrients, plants need light and water for growth, reproduction and survival. These resources are often unevenly distributed in natural environments (Silvertown 1981, Jackson and Caldwell 1993), and the ability of a plant to respond to this heterogeneity is important for its performance (Svensson *et al.* 1994). It is especially important for a laterally spreading plant as these often experience changes in resource availability as they grow. Several plant species have demonstrated an ability to concentrate resource harvesting modules in favourable patches, while avoiding adverse patches, in green-houses and garden experiments (Oborny and Cain 1997). This was suggested by van Kleunen and Fischer (2001) to be an adaptation to heterogeneity. Thus, greenhouse and garden experiments suggest that plants in natural systems have their leaves and roots concentrated to favourable patches and that this is achieved by plastic growth.

Apical dominance and suppression of lateral branching is presumably an adaptation to light competition both in erect and prostrate species (Irwin and Aarssen 1996, Aarssen 1995). Moreover, apical dominance is sensitive to changes in light irradiance and spectral quality (Cline 1991). According to the 'guerrilla efficiency hypothesis' strong apical dominance is responsible for the characteristic linear growth form of a 'guerrilla strategist' (Lovett Doust 1981), by suppressing branching in primary shoots (Aarssen 1995). This growth form enables foraging in resource-poor habitats. This hypothesis also suggests increased sexual reproductive success and survival for guerrilla strategists with sustained apical dominance. 'Foraging behaviour' of clonal plants in response to water availability has not been described as much as plastic growth affected by nutrients and light. Auxins and cytokinins are the prime candidates among the endogenous growth substances for controlling plasticity in shoot form in response to small-scale variation in growing conditions (Hutchings and Mogie 1990). From the discussion above one would expect reduced fitness in guerrilla strategists when released from apical dominance.

Pollination

The origin of sexuality is often ascribed as the need for DNA repair, but it is also suggested to be an adaptation to the increasing diversity in and saturation of the biotic environment (Stearns 1987). In species that combine sexual and clonal reproduction, the latter is shown to be favoured in unsaturated environments and at the geographical margins of a species range (Eckert 2002). Nevertheless, sexual reproduction is suggested to be a significant part of many clonal plant life histories (Eriksson 1997); and the maintenance of sexual seed production has been explained by dispersal and genetic variation advantages (Starfinger and Stöcklin 1996, Muirhead and Lande 1997). However, sexual reproduction faces many problems in harsh environments like in alpine and arctic areas, e.g. pollination failure (Kudo 1993, Totland 2001), seed developmental failure (Laine *et al.* 1995, Totland and Eide 1999), failure of seed germination (Mooney and Billings 1961, Amen 1966), and low seedling survival rate (Stöcklin and Bäumler 1996, Weih and Karlsson 1999). Pollination success may be lowered by pollen limitation, which is shown to be quite frequent in plant populations (Burd 1994, Larson and Barrett 2000), and low pollinator activity, which seems to be a problem for early flowering species in cold environments, but not for late flowering species (Kudo 1993, Molau 1993). Also population density and size can be of importance: small populations may have reduced fecundity (Byers 1995, Charpentier *et al.* 2000). For self-incompatible species the effective population size is of importance (Eriksson and Bremer 1993).

From the above one can assume that horizontally spreading species in harsh environments may have reduced seed set due to low pollinator activity and partner limitation.

Aims and hypotheses of this thesis

The general aim of this thesis was to examine how a few environmental factors and life history traits affect the shoot population dynamics of a stoloniferous plant, *Linnaea borealis* L. (Linnaeaceae). I wanted to reveal proximate causes explaining ramet architecture and distribution observed on mountain birch (*Betula pubescens* ssp. *czerepanovii*) forest floors.

Specifically, I examined the significance of resorption from senescing leaves for growth and nutrient pool sizes of *L. borealis* ramets, and its variation with reproduction and soil nutrient availability (I). Further, I assessed the effect of light and water availability on ramet growth patterns (II) and the significance of apical dominance for ramet fitness (III). Finally, I examined spatial and temporal seed set variation and their plausible causes (IV). The study in paper IV was performed during several years to include

yearly variation; the studies in papers **II** – **IV** were done at three sites with varying forest floor vegetation and canopy closure, the variation between sites were analysed in papers **II** and **IV**.

Examining these topics I put up the following hypotheses:

- Resorption from senescing leaves is increased on reproductive compared to non-reproductive ramets to compensate for reproductive investment. Resorption is also sensitive to soil nutrient availability, so that it is reduced when availability is high; and finally, resorption is increasing growth and nutrient pools in ramets of *Linnaea borealis*. These hypotheses were tested in paper **I**.
- Branching increases, and average internode lengths are reduced, when light availability is increased; further, internode lengths are increased when ramets experience drier conditions. The surrounding environment will affect the response of the plant. Paper **II**.
- Fitness, measured as long term population growth rate (λ) will be reduced when apical dominance is released, and so will other fitness related measures. Paper **III**.
- Seed set will increase with supplemental hand pollination. Paper **IV**.

Study species and sites

Linnaea borealis

Linnaea borealis L. (Linnaeaceae, previously Caprifoliaceae, Backlund and Pyck 1998) has a circumpolar distribution. In Sweden it is common from the province of Småland and northwards; it is a typical species of coniferous forests but thrives in considerable amounts in mountain birch forests too (Hultén 1960).

This favourite of Carl von Linné is a slender, evergreen dwarf shrub with a long, creeping main axis bearing two kinds of erect, short shoots, which according to their function may be called assimilation (sexually non-reproductive) and flowering (sexually reproductive) shoots, respectively. The shoots are 4 – 6 cm high, and the inflorescence can be up to 15 cm (Hagerup 1915, Hultén 1960). Growth of the main stolon is by means of yearly segments. A third prostrate kind of shoot is the rejuvenating shoots or branches (vegetatively reproductive). These form new ramets with the potential to become independent of the mother ramet (Fig. 1, Wittrock 1878 – 1879). On average, 1 – 2% of all ramets produce flowering shoots in a year (Eriksson 1988, M. Niva unpublished), inflorescences bear two whitish-pink nectariferous flowers, each with one fertile ovule. Floral scent is described as

almond-like and consists of four benzenoid compounds: 1,4-dimethoxybenzene, anisaldehyde, 2-phenylethanol, and benzaldehyde, and one nitrogen-containing compound, nicotinaldehyde (Bergquist 2000). Main pollinators of *L. borealis* in the Abisko area are small flies, e.g. Syrphidae, and bumblebees, *Bombus* spp. (Bergquist 2000, M. Niva, pers. obs.); germinability of seeds under laboratory conditions is 100% (Hagerup 1915, M. Niva unpublished). Seedlings are not considered to be common in natural populations, and I have never seen seedlings in the Abisko area.

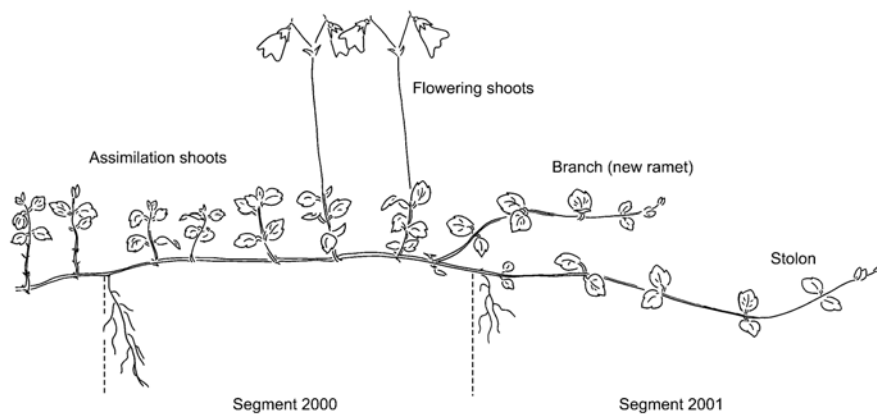


Figure 1. A ramet of *Linnaea borealis* with three types of lateral shoots: assimilation shoot, flowering shoot, and branch. The annual growth of the stolon is by means of segments; during the first year the segment does not normally produce lateral shoots. Roots grow from nodes separating segments. Leaves stay green for 12 – 14 months. Drawing by B.M. Svensson

Study sites

The studies included in this thesis have been carried out in the Abisko area (68°15 – 20'N, 18°45'E – 19°15'E, c. 400 m above sea level) on the south side of Lake Torneträsk in Swedish Lapland (Fig. 2). The study area belongs to the forest tundra ecotone (Hustich 1979), and has a subarctic climate (Andersson *et al.* 1996) with a mean annual temperature of -0.8 °C (1961 – 1990) and c. 300 mm of annual precipitation; summer mean temperatures are: June 8.4 °C, July 11.0 °C, and August 9.7 °C. Below the tree line (c. 650 m.a.s.l.) the vegetation is characterised by woodlands dominated by mountain birch *Betula pubescens* ssp. *czerepanovii* (N.I. Orlova) Hämet-Ahti. Several woodland types can be recognised, which are composed of different sets of species (Sonesson and Lundberg 1974). A main distinction can be made between relatively dry heath birch forests (Open site (**OS**)) in

papers II – IV) and moist meadow birch forests (papers I and III, and Closed site (CS) and Intermediate site (IS) in papers II – IV). OS has low, *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher-dominated forest floor vegetation with a mean cover-weighted height of 6.8 cm, and a tree canopy cover of 11%. At CS the tree canopy cover is 74% with forest-floor vegetation dominated by *Deschampsia flexuosa* L., *Vaccinium* spp. and *Juniperus communis* L. with a mean vegetation height of 14.1 cm. IS has a similar mean vegetation height to OS, but here *L. borealis* dominates the forest floor together with *Cornus suecica* L., *Vaccinium* spp. and *D. flexuosa*. The tree canopy cover is, however, more similar to CS with a canopy cover of 67%. Mountain birch is the dominating tree species at all sites.

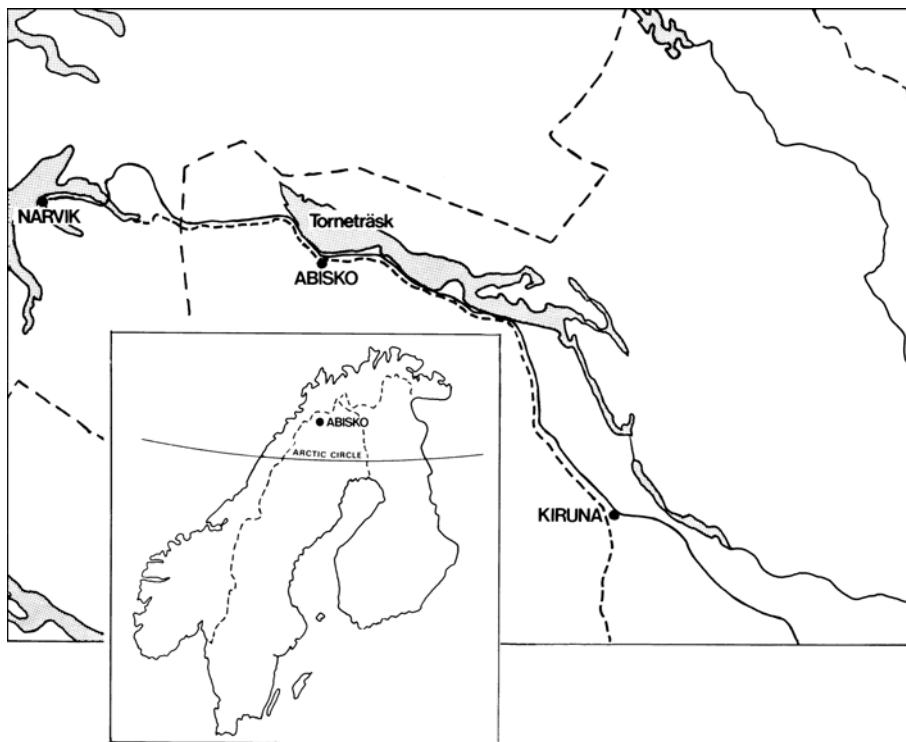


Figure 2. Scandinavia with the location of Abisko on the south side of Lake Torneträsk (Modified after Bernhard 1985).

Methods

Experimental studies

To assess the significance of nutrient resorption from senescing leaves for ramet growth and nutrient pool size, I compared segment dry weights and nutrient pool sizes of ramets who could resorb from senescing leaves with ramets that were defoliated (**I**). To eliminate differences in carbon gaining possibilities between groups, I shaded the leaves on non-defoliated ramets.

Variation in nutrient resorption efficiency and proficiency in relation to soil nutrient availability was studied comparing a non-treated control group of ramets with a fertilized group of ramets (**I**). Fertilization was done using slow-releasing fertilizer sticks placed adjacent to the root nearest to the stolon apex.

A light competition free patch as an example of a favourable micro site, and a substrate shift from forest floor litter to non-water holding wooden ledges as an example of an adverse micro site, were used to investigate the plasticity of ramet growth (**II**). To assess the importance of contrast between manipulated patch and the surrounding matrix, three sites with varying forest floor vegetation height and canopy closure were used in the study. To increase light availability for *L. borealis* ramets, patches on the forest floor were mown, these were 40 × 40 cm in size, i.e. similar to vegetation free patches occurring in the forests. To reduce water availability main stolons of *L. borealis* were set to grow up on wooden ledges, 2.5 × 1.0 × 40 cm (w × h × l). Growth responses in *L. borealis* were measured as the number of lateral shoots developed, internode lengths, ramet dry weight and leaf area, during two growth seasons after manipulation.

The significance of apical dominance for ramet fitness related traits, and the effect of developing leaves, were studied by cutting off the apical meristem on ramets at three different times (**III**). One group was left untreated, one group had their apices cut off in late August the year before harvest, one group had apex removed in late May the year of harvest, and the last group had apex removed in early July, nearly two months before harvest in late August. Number of meristems and branches were noted, and leaf area and dry weight were measured on a per ramet basis.

Plausible explanations to seed set variation between years were explored by means of supplemental hand-pollination (**IV**). To investigate possible pollinator shortage I hand-pollinated flowers with pollen collected from the local population. Effects of the treatments were measured as seed set and weight.

Self-compatibility was controlled by comparing seed set on caged inflorescences, hand-pollinated with self-pollen and non-self pollen (IV).

Demographic study

I followed 30 ramets of *L. borealis* at each of the three sites described above: CS, IS, and OS (paper III) for four years. Ramets were not physically connected with each other and were separated by at least 2.5 metres, it was however not possible to determine if they belonged to the same genet or not. Each year during the last week of July, the survival and fecundity of individual ramets were recorded. We define survival as the continuation of a shoot and fecundity as the production of a new apex. From these data life-cycle graphs were constructed (Fig. 3); the stages were: main stolon, assimilation shoot, flowering shoot, and branch. Nine matrices were constructed; one for each yearly transition and site.

Matrix analyses

In examining shoot population dynamics on *L. borealis* and its relation to apical dominance (III), I regarded the ramet with its shoots as the study unit, which is initiated, growing and dying (Eriksson 1988, Svensson and Callaghan 1988). All transitions between stages are described by the entries a_{ij} in a square matrix (**A**). The population grows by $n(t + 1) = \mathbf{A} n(t)$ where n is a column vector describing the distribution of ramets in the different stages. The population growth rate is described by the dominant eigenvalue λ of **A** (Lefkovich 1965). Sensitivity of λ to particular transitions was estimated using sensitivity and elasticity analyses (Caswell 2001). Standard errors (S.E.) of λ s were estimated using a bootstrap resampling method (Caswell 2001); entries from the original nine matrices were randomly resampled 10,000 times.

Nutrient analyses

To determine segment pools of nitrogen (N) and phosphorus (P) I analysed five ramet fractions for total N and P concentrations on a dry weight basis (paper I). Fractions were digested according to the Kjeldahl procedure, using concentrated sulphuric acid. N and P concentrations were determined using a flow injection analysis system. Nutrient pools were calculated using mean N and P concentrations ($n = 5$) multiplied by the mean dry weight of all samples ($n = 15$). The standard error of mean ramet nutrient pools was calculated according to Hansen *et al.* (1965).

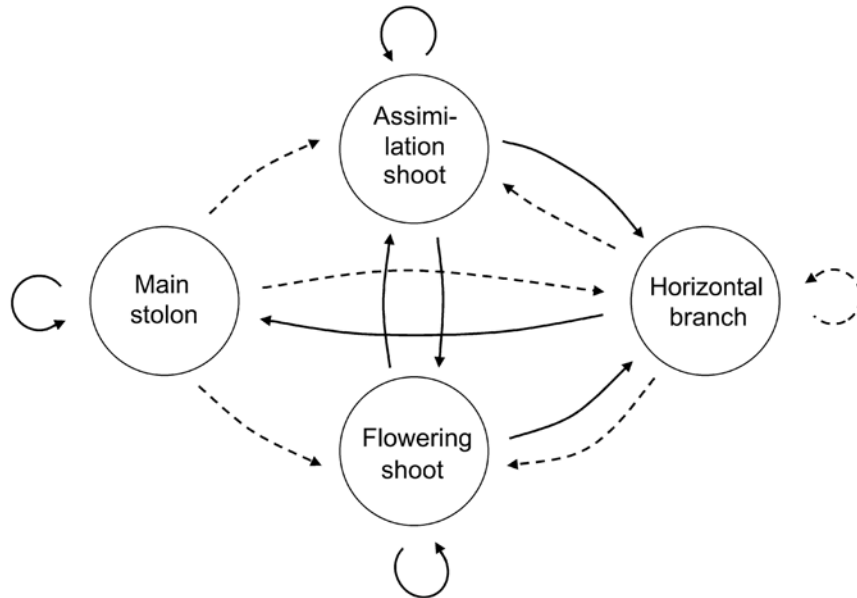


Figure 3. Life cycle graph for *Linnaea borealis*. Broken lines indicate the formation of a new apex (i.e. fecundity), and solid arrows indicate the continued growth of the apex (i.e. survival). Transition period is one year.

Statistical analyses

Statistical significant differences between two λ s derived from the transition matrices were determined using nonparametric randomization tests (paper **III**; Manly 1997, Caswell 2001). Ramets with their histories were randomly permuted 10,000 times between two groups, from which transition matrices were constructed and λ s calculated; the sample sizes were kept fixed.

Generalized linear models (GLM) were used to analyse response variables in the form of counts and proportions (papers **II** – **IV**; McCullagh and Nelder 1989, Olsson 2002). GLMs are generalizations of classical linear models (LM); in GLM the response variable \mathbf{y} is permitted to be of any distribution of the exponential family. Further, by using GLM the linear predictor $\boldsymbol{\eta} = \mathbf{X}\boldsymbol{\beta}$ is modelled as a function of the mean $g(\boldsymbol{\mu}) = \mathbf{X}\boldsymbol{\beta}$, instead of as in LM where the mean is modelled, $\boldsymbol{\mu} = E(\mathbf{y})$. Link functions $g(\cdot)$ used in this thesis are the canonical links for Poisson, negative binomial, binomial, and normal distributions. For Poisson and neg. binomial $g(\boldsymbol{\mu}) = \log(\boldsymbol{\mu})$, for binomial distributions $g(\boldsymbol{\mu}) = \log(p/(1 - p))$, and for normal distribution $g(\boldsymbol{\mu})$

= μ . Parameters were estimated using the maximum likelihood method. In GLM an adjustment term, an offset, can be used when modelling rate data; this term will be added to the linear predictor. Models' fit to data were explored using analyses of residuals and influential observations. Post-hoc test between groups within a factor were done using least square parameter mean of groups, which is not a multiple comparison-test. Multiple comparison-tests for GLM have just recently become available in the advanced statistical software R (version 1.7.1; multcomp-package), but is not yet available for SAS, which is used for all GLM-analyses in this thesis. I have therefore used sequential Bonferroni tests to compare component means (Rice 1989).

Results and discussion

Sexually reproductive and non-reproductive ramets of *Linnaea borealis* were of similar size regarding dry weight, leaf area and number of lateral shoots, but non-reproducing ramets were slender than the sexually reproductive ones. This, together with the fact that non-reproductive ramets are found in more shaded micro-sites coincide with my result that increased light reduces ramet lengths. However, I have not been able to show that light increases flowering in *L. borealis*; which also Eriksson (1988) failed to do. Nevertheless, increased flowering under favourable light conditions is known from other species, e.g. Evans (1991). One can speculate that the increased visibility of flowers to pollinators has a selective advantage, and that this is affecting pollinator visitation rates (Lortie and Aarssen 1999). Increased temperature at patches of high irradiation may also be advantageous, as low temperatures have been shown to reduce fecundity in a mountain area (Totland 2001); I suggest this to partly be responsible for seed set variation between years in the Abisko area, although I do not have results supporting it.

Resorption of nitrogen and phosphorus from senescing leaves did not affect growth and nutrient pools of ramets. This fails to support my hypothesis. However, it coincides with the findings of Eckstein *et al.* (1999) that resorption strongly affects mean residence time of nutrients in a plant like *L. borealis* only if it exceeds 70–80%. Further, the result supports the conclusions of Chapin (1980) and Aerts (1996) that evergreens have adapted to nutrient-poor habitats by developing long-lived nutrient-poor leaves, and not by having high nutrient resorption from them. The negative correlation between nutrient residence time and nutrient use efficiency has been shown before, e.g. by Eckstein and Karlsson (1997) and Vásquez de Aldana and Berendse (1997). The lack of a significant effect of resorption on the

performance of ramets was also illustrated by the resorption consistency in relation to reproductive state and soil nutrient availability, which contradicts my hypothesis. Nordell and Karlsson (1995) observed decreased nitrogen concentrations in senesced mountain birch leaves on sites with low soil fertility; and Eckstein and Karlsson (1997) got similar results investigating 14 species in the Subarctic; however, these two studies are exceptions. Aerts (1996) showed in a meta-analysis that in more than half of the performed studies there were no effects seen on nutrient resorption by enhanced nutrient supply. My results imply that the performance of *L. borealis* ramets is not dependent on resorption from senescing leaves but is adapted to nutrient-poor habitats via low leaf N concentrations and low leaf turn-over rates. They also suggest that plant nutrient economy in well physiologically integrated plants should be studied considering the whole clonal fragment and not just a few segments as the performance is not governed by the conditions at the micro-site.

Although nutrient pools and growth of *L. borealis* ramets were not significantly affected by denied nutrient resorption from senescing leaves, their growth was shaped by micro-site light conditions in accordance with my hypothesis. When ramets grow into areas with increased light availability branching increased and internode lengths were reduced, resulting in an increased number of active meristems in these micro-sites. This ability to respond in an effective way to micro-site conditions by plastic growth has been shown many times in greenhouse and garden experiments (e.g., Dong and Pierdominici 1995, Kleijn and van Groenendael 1999; for review see Hutchings and de Kroon 1994), but never in natural systems. Patch exploitation is important as it enables ramets to exploit favourable micro-sites, which increases plant and population performance (Birch and Hutchings 1994, Svensson *et al.* 1994). A synergistic effect between reduced light competition and the surrounding light environment shows that the contrast between patches must reach a certain magnitude for plants to recognise it, proving that studies should also be performed in natural systems to ensure that relevant conditions are able to reproduce the phenomenon seen in these controlled experiments.

Contrary to my expectation, reduced water availability did not increase internode lengths of *L. borealis* ramets. Reasons for the lack of response can be several; a plausible one is that the treatment was not perceived as particularly adverse by the ramet. As implied by earlier results, *L. borealis* is a well physiologically integrated plant. For example an acropetal transport of water up to 1.5 m has been shown (Sandring 2000). Together these results confirm the idea that horizontally growing plants can respond to certain resource heterogeneity in natural systems in an effective manner via

branching and internode length reduction, which improves the plants' performance.

Branching, i.e. vegetative reproduction, is under the control of apical dominance (Lortie and Aarssen 2000). Both the long-term study of shoot dynamics of *L. borealis* and the field experimental study showed that this control is of significance for ramet fitness, measured both as long-term population growth rate and as fitness related measures such as dry weight. Elasticity analysis of the survival of the apical meristem of the main shoot showed that this contributed 36% to the fitness of the shoot population. This is according to my hypothesis and the 'guerrilla efficiency hypothesis' by Aarssen (1995). The guerrilla efficiency hypothesis predicts suppressed branching and promoted horizontal growth for efficient foraging in resource-impooverished habitats. My results imply that apical dominance in *L. borealis* has adaptive significance. A population growth rate of $\lambda = 1.19$ implies that shoot populations of *L. borealis* in the Abisko area are thriving; however, there was large spatial and temporal variation.

The same was true for seed set; this varied between 24 and 60% with a mean of 40%. This is comparable to results from eastern Canada (Helenurm and Barrett 1987), but much higher than what has been reported from small populations in Scotland (Wilcock and Jennings 1999). Supplemental hand-pollination resulted in a small insignificant increase of seed set. Thus, populations of *L. borealis* in Abisko do not suffer from small pollen loads.

Conclusions

Contrary to my expectation, I could not detect any increase in growth and nutrient pools on ramets of *L. borealis* due to resorption from senescing leaves. Nor was resorption affected by investments in sexual reproduction or soil nutrient availability. The clonal fragment is considered the relevant unit to study resource economy in this species.

Nevertheless, the growth of the ramet was shown to be able to respond in an efficient way to micro-environmental changes in light availability. When neighbours were removed, ramets of *L. borealis* had shorter internode lengths and branched more frequently, all in accordance with my hypotheses. The magnitude of the response was dependent on the light conditions in the surrounding environment, so that the response to increased light availability was larger in the darker habitats. However, reduced water availability did not affect the growth of the ramet as expected.

Fitness measured as long-term population growth rate (λ) was reduced when ramets experienced reduced apical dominance before summer growth, other fitness related measures were also reduced. The importance of apical dominance was also indicated by obtaining the highest elasticity values of

the ramet life cycle for the main shoot. This is all in accordance with my hypothesis.

Seed set was not affected significantly by supplemented hand-pollination, indicating sufficient pollinator visitation frequencies in the investigated populations at Abisko. The short-fall of seed set is tentatively explained with resource limitations.

Finally, some areas that I find very interesting and like to see investigated further. (i) Division of labour has only been described in garden and greenhouse experiments, it would be interesting to quantify its significance under field conditions. (ii) Guerrilla and phalanx efficiency theories should be tested thoroughly under field conditions, perhaps using plant hormones to neutralize apical dominance. (iii) Quantification of the advantages of placing flowers in patches of low surrounding vegetation for low-statured species on the forest floor would be very interesting. Also exciting would be to (iv) investigate if the observed variation in pistil length has any reproductive significance for *L. borealis*.

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Populärvetenskaplig sammanfattning

Bakgrund

Ungefär 70 % av växtarterna i den tempererade zonen kan reproducera sig vegetativt, d.v.s. klonalt. Klonal reproduktion hos växter är också mycket viktig i kalla miljöer som t.ex. i fjällen. Klonala växters dominans påverkar vegetationens diversitet och dynamik, dessutom är många ogräs och många av betesväxterna klonala. Det är därför viktigt ur både ekologisk och ekonomisk synvinkel att vi ökar vår kunskap om vad som karaktäriserar dessa växters tillväxt och liv, deras livshistorie-egenskaper.

Jag har studerat den klonala linnean (*Linnaea borealis*). Genom flera fältexperiment och en noggrann beskrivning av förgrening, tillväxt och överlevnad (skottdynamik) hos revor av linnean vill jag förklara en del av vad som bestämmer dess utbredningsmönster på marken.

Metodik

Alla mina studier är gjorda i fjällbjörksskogarna omkring Abisko i norra Lappland. I avbladnings- och gödslingsförsök har jag studerat betydelsen av näringsupptag från gamla blad för revornas tillväxt och näringspooler och relaterat detta till deras sexuella reproduktion och näringstillgången i marken. Genom att förändra ljus- och vattentillgången för revorna har jag studerat linnearevors förmåga att reglera tillväxten så att de optimalt utnyttjar resursrika fläckar i skogen. Jag har även studerat hur betydelsefull revspetsen är för överlevnad och tillväxt av revan och dess skott, d.v.s. dess fitness och relaterat detta till bete av t.ex. fjälllämmel. Med handpollineringsförsök har jag undersökt en möjlig orsak till den stora variationen i frösättning som finns hos linnean i Abiskoområdet.

Resultat och slutsatser

Ungefär hälften av bladets fosfor och mindre än en tredjedel av bladets kväve dras tillbaka till perenna delar av linnearevan innan bladet fälls, detta sker växtsäsongen efter att bladet bildats. Både fosfor och kväve anses vara begränsande för tillväxten hos växter i näringsfattiga områden. Linneans återupptag från gamla blad är för litet för att märkbart påverka tillväxten eller näringspoolerna hos revan, särskilt som dessa är sammankopplade i stora system av revor, s.k. klonfragment. Mina resultat överensstämmer med

resultat från tidigare gjorda studier. Dessa har konstaterat att städsegröna växter inte har anpassat sig till näringsfattiga miljöer genom ett stort återupptag från gamla blad utan genom att ha näringsfattiga delar som de behåller länge.

Linnearevor som växer in i en fläck med goda ljusförhållanden i skogen producerar fler grenar i dessa ljusa fläckar än på fläckar med sämre ljusförhållanden. Längdtillväxten reduceras också något vilket betyder att den ljusabsorberande delen av revan får fler tillväxtmöjligheter på dessa fläckar. En förändring av fördelningen av tillväxtresurserna sker också hos revor på dessa fläckar. Revorna producerar mer ovanjordiska delar i förhållande till rötter. Detta resultat antyder att revor kan specialisera sig på att ta upp de resurser som finns mest lättåtkomliga, andra delar av klonfragmentet måste då specialiseras för att ta upp andra nödvändiga resurser, t.ex. vatten och näring. Resultat som dessa har tidigare visats i växthus och experimentträdgårdar, mina resultat konfirmerar antaganden från dessa försök om att växter kan exploatera resursrika fläckar effektivt.

Skottdynamiken och därigenom revans fitness försämras av förlust av övervintringsknoppen i revspetsen hos linnean, som kan ske t.ex. genom smågnagares bete. Vid simulerat bete innan sommartillväxten minskade både producerad bladyta och biomassa. Men om betessimuleringen skedde tidigt under föregående höst så repareras skadan så att fitnessen inte försämras. Enligt tidigare studier sker det svåraste betet av linnearevor under hösten och vintern och linneans tillväxt reduceras av detta.

Den genomsnittliga frösättningen hos linnean är 45 % och kan inte höjas genom tillförsel av mer pollen. Detta tyder på att linneans frösättning inte är begränsad av låg aktivitet hos dess pollinatörer, små flugor och humlor. Jag har också visat att linnean inte bildar några frön om den bara får pollen från sig själv, d.v.s. den är självinkompatibel. I vissa små populationer av linnea i Skottland finns bara ett enda individ och där sätts inga frön. Jag har med mina resultat visat att de undersökta linneapopulationerna i Abisko-området alltså består av flera individ.

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