

Optimal anti-herbivore defence allocation in *Salix polaris*: doing it the arctic way?

by Carsten F. DORMANN, Leipzig

with 4 figures

Abstract. To determine the optimal anti-herbivore defence allocation of a plant, a modelling approach is inevitable. However, models have too often been detached from field experiments and aloof of ecological knowledge. Here I present the case for combining the two approaches. Two preconditions for a simple model have to be fulfilled: 1. the investigated species should show no inducible resistance, a phenomenon often observed in temperate trees, because this requires very detailed ecological knowledge to be captured by the model, and 2. the plant species under consideration has to be flexible in its defence allocation, otherwise no optimisation can be expected under different grazing pressures. Here, I show by field experiments that these two requirements are met for *Salix polaris*, a high arctic dwarf shrub. This opens the way for a simple competition model to assess optimal defence allocation under different grazing intensities.

Keywords: competition, field experiment, grazing, induced defence, model.

Introduction

How should a plant defend itself against being consumed by herbivores? This question has occupied plant ecologists for the past few decades (summarised in CRAWLEY 1983), and has led to the identification of both general strategies that plants can adopt, and the environmental factors that effect optimal plant defence (HERMS & MATTSON 1992; HERMS 1999). However, as is often the case in ecology, field manipulations and theoretical advances have moved different directions, and while models have reached high levels of sophistication (LOREAU & DEMAZANCOURT 1999; DEMAZANCOURT & LOREAU 2000), field evidence is still weak and mostly descriptive (JONASSON et al. 1986; COLEY 1987; ZANGERL & RUTLEDGE 1996; HAZLETT & SAWYER 1998; ALMEIDA-CORTEZ et al. 1999). Here I try to relate simple modelling with field manipulations, to show that it is both feasible and fruitful.

With respect to anti-herbivore defence, two issues complicate the formulation of realistic, field-testable mathematical models: I. Do plants show “behavioural adaptations” (i.e. induced resistance, KARBAN & BALDWIN 1997)?, and II. How strong is the allocation to anti-herbivore defence controlled by their abiotic environment? If plants have “information” (sensu KARBAN et al. 1999) on grazing pressure, grazing likelihood and efficiency of defence, their allocation might be much more complex than presently modelled. Additionally, a lack of environmental control over the quantity

of anti-herbivore defence would decouple abiotic processes (e.g. resource availability, disturbance regime) from a plant's strategy against its consumer. For example, if a given species allocates similar proportions of its primary productivity when growing in nutrient-rich patches as it does when in nutrient-poor patches, then anti-herbivore defence is likely to be constant and non-optimal and therefore not suitably modelled by optimal-defence approaches.

Mathematical models are usually not concerned with a particular species, but are abstract evaluations of possibilities under specific assumptions (e.g. LOREAU & DE MAZANCOURT 1999). Tests of the assumptions, as well as the two points mentioned above, are required when relating a *general* model to a *specific* situation. It also will then become apparent if simple or complex models are needed.

The ecosystem under investigation is a dry heath in the High Arctic on Svalbard. Its extremely low productivity, paired with high grazing pressure by reindeer, make optimal defence allocation critical to survival. Moreover, anti-herbivore defence has not been investigated yet this far north, hence results serve as a new and extreme example in anti-herbivore defence literature.

This study uses data from different field experiments to test preconditions of modelling optimal defence allocation (ODA): i.e. no complication by inducible resistance and flexible defence allocation. The model itself calculates ODA as a function of the palatability of undefended neighbouring plants at a range of different defence efficiencies and grazing intensities. In a first experiment the response of the target species *Salix polaris* to simulated herbivory is investigated, addressing the issue of induced anti-herbivore defence. Then, in another field experiment the influence of environmental factors (light and nitrogen availability) on anti-herbivore defence is assessed. An extended model is used to determine ODA for *Salix polaris*.

Material and methods

Nomenclature follows RØNNING (1996).

Field experiments

The experiments were carried out in Semmeldalen, 77°90'N, 15°20'E, on Nordenskjøldsland, Spitsbergen, Svalbard. The area is a wide valley covered by polar desert and high-arctic tundra, dominated by heath with *Luzula confusa* (Hartm.) Lindeb. and *Salix polaris* Wahlenberg. This work has been carried out in a vegetation type called *Salix polaris*-heath (subtype of the *Luzula confusa*-heath, RØNNING 1996). Dominant vascular species are *Luzula confusa*, *Salix polaris*, *Poa arctica*, *Pedicularis dasyantha*, *Alopecurus borealis*, *Polygonum viviparum*, while *Ptilidium ciliare*, *Dicranum* spp., *Drepanocladus uncinatus* (= *Sanionia uncinata*), *Hylocomium splendens*, *Polytrichum* spp. and *Pohlia* spp. are the main bryophytes. Lichens (*Peltigera malcea*, *Stereocaulon* spec., very few *Cladonia* spp.) are poorly repre-

sented, due to the high grazing pressure. This vegetation has a moderate snow cover in winter, and the peaty top soil dries out over the summer. As the *Salix polaris*-heath becomes snow-free early in the season, grazing pressure by reindeer is very high in spring (June), but decreases as reindeer shift to the lush grass communities later in the season.

The valley has a fairly stationary population of reindeer at a density of ca. 12 animals per km² (Audun STIEN, personal communication), which is high for Svalbard (VAN DER WAL et al. 2001). Reindeer are the only mammalian herbivores in the area.

Salix polaris is common throughout Spitsbergen and occurs in most habitats except wet bogs and polar desert (RØNNING 1996). It is a deciduous dwarf shrub with subterranean creeping stems and branches, and often has only shoot tips and leaves showing above ground. *Salix polaris* is the dominant vascular plant in the system, and an important food plant for reindeer (STAALAND 1985), particularly early in summer (HALLE 2000) and probably during winter (Christina SKARPE, personal communication), when animals are cratering for food under the snow.

To investigate inducible defence in *Salix polaris*, all plants in a 20 cm × 20 cm plot were subjected to simulated grazing by manually picking every other leaf, and their remaining leaves (between 100 and 300 leaves, in total c. 0.7 g) sampled after 15 minutes, 1 hour, 4 hours, 24 hours, 7 days, 30 days and 1 year (for each treatment and time period N = 10). By staggering different experimental treatments, an effect of leaf age on defence compound concentrations was avoided. The dried leaf samples were analysed for total phenolic content using the modified Prussian blue assay (HAGERMAN 1998). Further details can be found in DORMANN (2001).

To assess the flexibility of anti-herbivore defence in *Salix polaris*, a factorial experiment manipulated four levels of shading (0, 53, 72 and 83 %) and fertilisation (0, 0.5, 1.5 and 5 gN · m⁻² · 3a⁻¹) for two years (plot size 0.5 m × 1 m; 3 replicates). At the end of the experiment, leaf samples were analysed for phenolics and condensed tannins (acid butanol method, HAGERMAN 1998) as well as for nitrogen concentrations (see DORMANN 2001 for details).

Salix polaris interacts with other vegetation, especially with *Luzula confusa*. It competes for soil nutrients (DORMANN 2001), although a facilitation by its main competitor seems to be important as well (DORMANN & BROOKER 2002). Details on the mechanism of this competition, a laboratory experiment and soil nitrogen measurements are given in DORMANN (2001). The occurrence of competition allows for the following modelling approach to optimal defence in the face of competition.

Modelling optimal defence allocation

Competition between ramets of defended (P_D) and undefended (P_U) plant species is modelled using a LOTKA-VOLTERRA approach (BEGON et al. 1990), using coupled ordinary differential equations:

$$\frac{dP_U}{dt} = r_U \cdot P_U \cdot T_t \cdot \left(1 - \frac{P_U + P_D}{K}\right) - r_R \cdot T \cdot P_U - g_U \cdot P_U \quad (1)$$

$$\frac{dP_D}{dt} = r_U \cdot (1 - D) \cdot P_D \cdot T_t \cdot \left(1 - \frac{P_U + P_D}{K}\right) - r_R \cdot T \cdot P_U - g_U \cdot (1 - D^b) \cdot P_D \quad (2)$$

where $P_{U/D}$ = population size of the undefended/defended plant type

r_U = relative growth rate of undefended plant species (0.3)

T = temperature function

K = carrying capacity (100)

r_R = respiration coefficient (0.1)

g_U = grazing function for grazing on undefended plant species

D = allocation to defence [0–1]

b = efficiency of defence (lower values = higher efficiency).

In words, plant populations exhibit a sigmoidal growth curve with a maximum value of K . The defended plant grows slower than the undefended one, as a proportion of its biomass is allocated to defence, not to growth. There is no *a priori* reason however to assume a lower carrying capacity for the defended plant species. The impact of grazing is proportional to the abundance of the species, but reduced for the defended plant (by the proportion allocated to defence to the power of its efficiency; b -values above 1 are never advantageous).

The grazing function g_U is modelled as a grazing pulse of random intensity (0 to 50% of the population removed, average = 25%) and predetermined frequency v (randomly sampled from the interval [0.5 v ; 1.5 v]). Altering the quantity of grazing off-take produces qualitatively the same results (data not shown). Plants have no “safe size” where they are not eaten any more, i.e. they are shrubs, herbs or grasses but not trees.

The temperature function T (*temperature*) represents temperature-dependent growth, the model can thus be used to simulate both summer and winter conditions. The actual function of *temperature* was derived by fitting two linked sinusoidal functions to temperature data from Longyearbyen, Svalbard (Audun S_{TIEN}, unpublished data). Furthermore, it assumes that the temperature response of plant growth follows a Gaussian function $T = e^{-0.5 \left(\frac{temp - 20}{10}\right)^2}$. The relative growth rate r_U is set to be 0.3 at 20°C. Respiration is 10% per time step, also adjusted by the temperature function, with a minimal value of 0.05 to simulate a build-up of costs over the winter.

Grazing pressure is kept independent of species abundance, e.g. a grazing event would reduce P_U by $0.2 \cdot P_U$ and P_D by $0.2 \cdot (1 - D^b) \cdot P_D$. Herbivore grazing pressure is assumed to be unrelated to the abundance of either plant species, but rather governed by extrinsic factors (predation, winter survival, parasites, etc.).

The model was run for 450 years after an initiation period of 50 years, with initial values for $P_D = P_U = 40$. Optimal defence allocation (D^*) was

calculated iteratively by maximising population size of P_D after 500 years (mean of three runs). Further results and properties of this model can be found in DORMANN (2003).

Results

Inducible defence experiment

Total phenolic concentrations were significantly increased only 15 minutes after leaf removal (TUKEY'S HSD test, $P > 0.05$; Fig. 1). This difference vanished after one hour, and was curiously reversed after four hours. 24 hours after simulated herbivory, phenolic concentrations were higher than in controls again, but at even longer time periods, no further differences could be detected. The striking differences between controls of different sampling times are not explained by seasonal variation (no significance of Julian date of sampling as covariate, $P > 0.2$). In the leaf removal plots, phenolics showed a slow but steady decline with re-sampling interval. As it is the variation in the controls that leads to significant differences after 15 minutes and 4 hours, these results have to be treated carefully. The difference between controls was also almost double that of effects of simulated herbivory (Fig. 1). This indicates that all differences detected are due to variation in the control group, rather than the treatment, and hence, that there is no detectable effect of simulated herbivory on leaf phenolic concentrations.

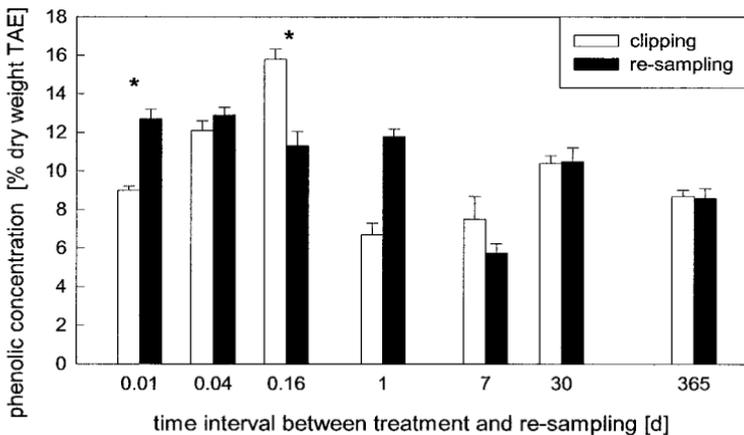


Fig. 1. Total phenolic concentrations of *Salix polaris* leaves (in tannic acid equivalents, TAE) at different intervals after simulated grazing (black bars) compared to controls (white). Note that time axis is on \log_{10} -scale. Asterisks indicate significant difference between simulated grazing and control (TUKEY'S hsd).

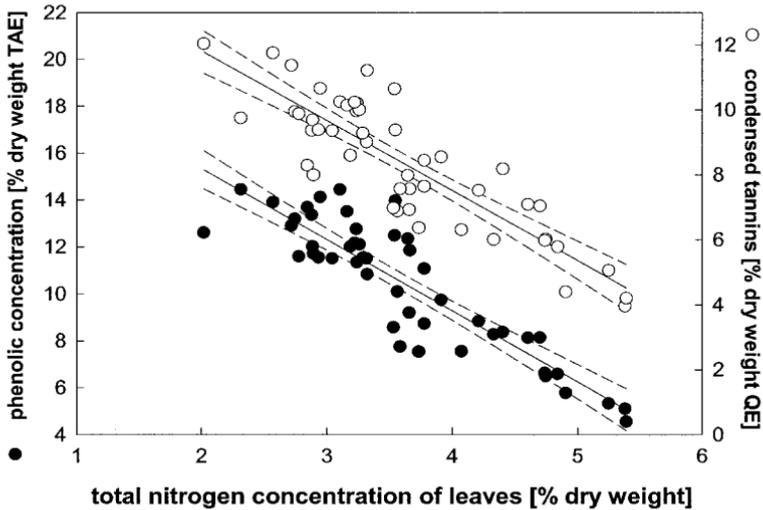


Fig. 2. Correlation of phenolic and condensed tannin concentration on leaf nitrogen concentration in 2000. Regression equation for the indicated line (and 95 % confidence limits) is $y = 21.41 - 3.03 \cdot x$, $R^2 = 0.791$ for phenolics and $y = 16.12 - 2.15 \cdot x$, $R^2 = 0.749$ for condensed tannins.

Fertilisation-shading experiment

Manipulating shading increased nitrogen concentrations in *Salix polaris* leaves. Carbon-based defence compounds decreased as a function of nitrogen content (Fig. 2). Levels of anti-herbivore defence were generally high, with phenolics at c. 12 % dry weight tannic acid equivalents (TAE) and condensed tannins at c. 10 % dry weight quebracho equivalents (QE; Fig. 2). Shading consistently increased nitrogen concentrations over all treatment levels, indicating a non-linear reduction of phenolics and condensed tannins with increased shading. Surprisingly, fertilisation had no detectable impact (data included in Fig. 2). The similarity between the responses of phenolics and condensed tannins is reflected in a very high correlation ($r = 0.871$, $P < 0.001$; Fig. 2).

Modelling optimal defence allocation

The absolute allocation to defence which proved optimal was strongly dependent on the grazing function. Fig. 3 shows the dependency of D^* on b and grazing frequency. The absolute level of optimal defence was low ($D^* < 0.2$) for all grazing frequencies up to once per three years and all defence efficiencies (Fig. 3). The relationship between D^* and grazing frequency was fairly constant for all defence efficiencies greater than 0.5 (Fig. 3). Highly efficient defence (e.g. $b = 0.01$) did not require high allocations to deter herbivores (Fig. 3).

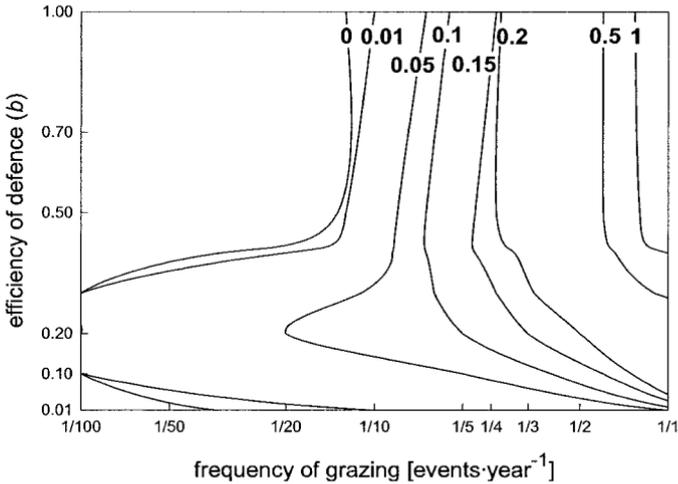


Fig. 3. Optimal allocation to defence (D^*), maximising P_D , for a range of grazing frequencies and defence efficiencies (b). Lines of same values of D^* are shown.

Total population size ($P_D + P_U$) decreased with increasing grazing frequency. The proportion P_D of the total, however, increased steadily. For P_D to withstand yearly grazing events, b has to be < 0.2 (Fig. 4a). With low defence efficiencies (e.g. $b = 0.5$), $D^* = 0$ until grazing frequency exceeds once in every 20 years; until then $P_D = P_U$ (Fig. 4b).

Discussion

Problem 1: Induced resistance

Apparently *Salix polaris* displays no consistent change in its chemical defence after simulated herbivory (Fig. 1). This is in line with the findings of CHAPIN et al. (1985), who found no delayed inducible resistance (DIR) in five sub-arctic tree species. In contrast, HÄUKIOJA and co-workers (HÄUKIOJA & HÄNHIMÄKI 1985; HÄUKIOJA & NEUVONEN 1985; HÄUKIOJA et al. 1985; HÄUKIOJA 1991) detected DIR in *Betula pubescens* as a response to attack by the moth *Epirrita autumnata*, suppressing larval growth and herbivore performance in subsequent years. While insects seem to respond strongly to specific chemical compounds (TÄHVÄNÄINEN et al. 1985), and resistance can therefore be acquired at comparatively low cost to the plant, deterrence of mammalian herbivores seems to be a matter of *quantitative* defence with phenolics, tannins or fibres (EDWARDS et al. 1986; HARBORNE 1991, 1997). Their production costs are considerably higher, and efficacy is often lower (see BERGELSON & PURRINGTON 1996 and references within). To produce a benefit for the plant, investing in carbon-based inducible defence might therefore be too expensive in low productivity environments (DE JONG 1995).

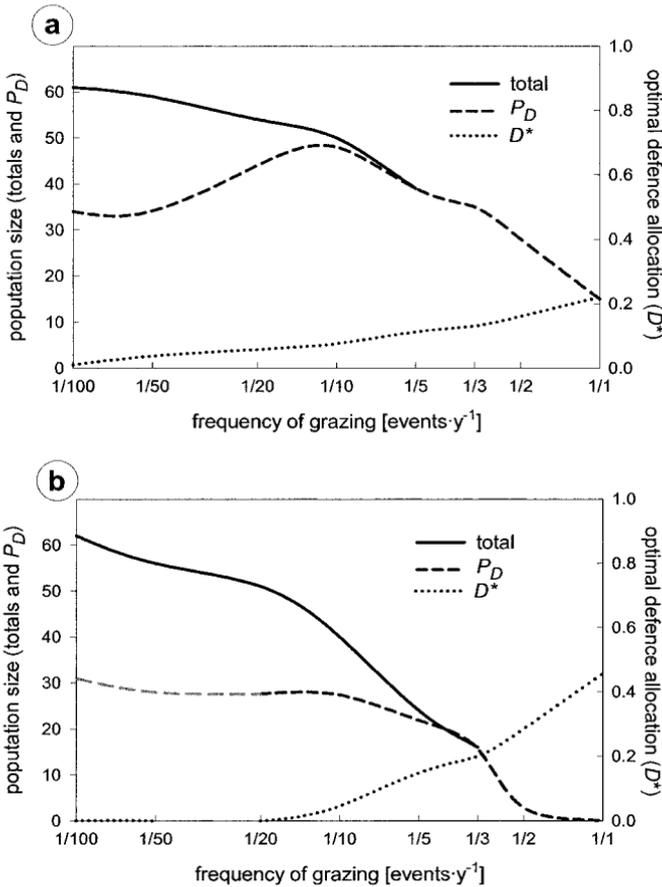


Fig. 4. Relative contribution of the defended plant type (P_D : dashed line) to the total plant population size (solid line), and optimal defence allocation (D^* : dotted line) along a gradient of grazing frequency. Note that at some grazing frequency all plants are undefended. **a)** $b = 0.2$, **b)** $b = 0.5$ (Note that $D^* = 0$ for grazing frequencies less than 1/20 years: line of P_D in grey).

Problem 2: Environmental control over anti-herbivore defence

Resource availability, in particular of those resources that affect nitrogen concentration in the leaves (i.e. shading), affects the quantity of anti-herbivore defence (Fig. 2). In this case the results are supportive of the carbon-nutrient-hypothesis (BRYANT et al. 1983), but in a more general context, they illustrate the effect of environment on defence allocation. This means that *Salix polaris* is capable of adjusting its defence allocation in response to abiotic conditions. Another case in which source-sink relations have an impact on defence chemistry is after exclusion of reindeer: *Salix polaris*' leaf

phenolic concentrations are *higher* inside enclosures (DORMANN & SKARPE 2002). This is due to a higher leaf biomass compared to the "normal" (= grazed) situation, leading to higher availability of assimilates relative to nitrogen (BRYANT & REICHARDT 1992). This surplus carbon can then be invested into carbon-based secondary compounds (MOLE et al. 1988). In the Salicaceae, tannins are the most important type of defence (JUNG et al. 1979). Interestingly, the concentrations of condensed tannins were *not* different inside or outside enclosures, indicating that *Salix polaris* does not invest surplus C into defence targeted at mammals only (ZUCKER 1983), but rather in phenolics, which serve a wider range of purposes (anti-fungal, UV-B protection HARBORNE 1997).

These experiments indicate that *Salix polaris* is a species which responds flexibly, adapting its secondary chemistry according to environmental conditions, but lacking "behavioural" responses such as delayed inducible resistance.

Optimal defence allocation in high-arctic *Salix polaris*

The investment in anti-herbivore defence is only worthwhile if the costs (in the form of growth reduction due to re-directed resources) are less than the benefits (the reduction in tissue consumed by the herbivore). Optimising the percentage of biomass allocated to defence when growing in competition with a non-defended plant will necessarily yield different ODAs under different grazing intensities and defence efficacies (Fig. 3). For the example depicted in Fig. 4, *some* defence is always superior to none, if the grazing pressure exceeds a certain threshold. Only at very low grazing frequencies is no defence optimal. This threshold will vary with defence efficacy, for which no data are available. The *b* in the equation is a "relative defence efficacy": for example, if the substance produced as anti-grazing chemical has additional functions, the value of *b* is lower. If the turnover of this substance is high (e.g. toxic peptides), its *b*-value increases (HARBORNE 1991; BERGELSON & PURRINGTON 1996).

The classical case of defended versus undefended plant competition is that of shrubs versus graminoids (e.g. in the South American and African grasslands). The observed pattern here are a dominance of grasses at high grazing intensities (for possible reasons and review see DRENT & VAN DER WAL 1999), which is opposite to that which would be predicted by this model. This illustrates two important shortcomings: mechanical damage by trampling and by removal of leaf and shoot buds may play a major role in the impact of herbivores, and hence explain the existence of plant growth beyond the maximum tolerable grazing pressure for shrubs (the right end of Fig. 4). The model is thus limited in its applicability to comparisons within plant functional types.

In the dry heath studied, *Salix polaris* is the dominant vascular plant. Reindeer graze all plant species at some point during the season, and only the highly tannin-defended evergreen ericaceous shrub *Empetrum hermaphrodi-*

tum and *Cassiope tetragona* escape intense consumption. However, their resource allocation to defence is considerable, thereby presumably leading to lower growth rates and low abundances. Deciduous dwarf shrubs such as *Vaccinium gaultherioides* and *Betula nana* are extremely rare on Svalbard (*Vaccinium* rare and *Betula* absent from the study area; personal observation), a factor apparently unrelated to their defence allocation (*Betula* lower than *Salix*, *Vaccinium* higher). Morphological plasticity and tolerance to icing and mechanical damage are at least as important for arctic shrubs as optimal defence allocation (C_{RAWFORD} 1989; B_{RET-HARTE} et al. 2001).

Anti-herbivore defence and productivity

Arguments for and against high defence investment in unproductive environments have been put forward: because of the extremely low growth rates, any loss of tissue to herbivores is equivalent to many years of growth, and plants should therefore invest strongly into anti-herbivore defence (C_{OLEY} et al. 1985; D_{E JONG} 1995). On the other hand, if plants are able to deplete resources (i.e. densely vegetated but resource-poor environments such as the dry heath investigated here), resource supply might be entirely unrelated to defence investment, and hence optimal defence investment be independent of productivity (L_{OREAU & DE MAZANCOURT} 1999). Moreover, if the defence efficiency is low, defence might be a detrimental investment (J_{OKELA} et al. 2000).

So far, data are too sparse to detect pattern in the allocation to defence along productivity gradients. It rather seems that the type of herbivory and the diversity of herbivores are more important in determining quantity and quality of defence than the productivity of the system (C_{OLEY & AIDE} 1991; P_{RICE} 1991).

Conclusions

As with most woody species in temperate or tropical areas, *Salix polaris* is chemically defended against herbivory. The environmental drivers of the allocation to defence are related to the balance of carbon and nitrogen, and there is no convincing evidence for inducible resistance. Compared with undefended plants in its neighbourhood, a defended plant will almost always win in competition, as grazing will shift towards the undefended neighbour (L_{OU DA} et al. 1990). At extremely low grazing intensities or low defence efficiencies, the reduction in growth due to the diversion of resources would make anti-herbivore defence obsolete. More field experiments are needed to provide conclusive evidence of the role played by growth rate, ecosystem productivity and herbivore identity/diversity.

Acknowledgements. Christina S_{KARPE} and Audun S_{TIEN} for allowing me to use their data; Sarah W_{OODIN} for various discussions on these issues; Phil L_{AMB DON} for correcting my English; Aberdeen Research Consortium for funding; and everybody, who helped in the field.

References

- Almeida-Cortez, J. S., Shipley, B. & Arnason, J. T. (1999): Do plant species with high relative growth rates have poorer chemical defences? – *Funct. Ecol.* **13**: 819–827.
- Begon, M., Harper, J. L. & Townsend, C. R. (1990): *Ecology*. – 2nd edition, Blackwell, Cambridge. 1024 pp.
- Bergelson, J. & Purrington, C. B. (1996): Surveying patterns in the cost of resistance in plants. – *Am. Nat.* **148**: 536–558.
- Bret-Harte, M. S., Shaver, G. R., Zoerner, J. P., Johnstone, J. F., Wagner, J. L., Chavez, A. S., Gunkelman, R. F., Lippert, S. C., & Laundre, J. A. (2001): Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. – *Ecology* **82**: 18–32.
- Bryant, J. P., Chapin, F. S. & Klein, D. R. (1983): Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. – *Oikos* **40**: 357–368.
- Bryant, J. P. & Reichardt, P. B. (1992): Controls over secondary metabolite production by arctic woody plants. – In: Chapin, F. S., Jefferies, R. L., Reynolds, J. F., Shaver, G. R. & Svoboda, J. (eds.): *Arctic Ecosystems in a Changing Climate – An Ecophysiological Perspective*, pp. 379–390. – Academic Press, San Diego.
- Chapin, F. S., Bryant, J. P. & Fox, J. F. (1985): Lack of induced chemical defense in juvenile Alaskan woody plants in response to simulated browsing. – *Oecologia* **67**: 457.
- Coley, P. D. (1987): Interspecific variation in plant anti-herbivore properties: the role of habitat quality and rate of disturbance. – *N. Phytol.* **106** (Suppl.): 251–263.
- Coley, P. D. & Aide, T. M. (1991): Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. – In: Price, P. W., Lewinsohn, T. M., Fernandes, G. W. & Benson, W. W. (eds.): *Plant-Animal Interaction: Evolutionary Ecology in Tropical and Temperate Regions*, pp. 25–49. – John Wiley & Sons, New York.
- Coley, P. D., Bryant, J. P. & Chapin, F. S. (1985): Resource availability and plant antiherbivore defense. – *Science* **230**: 895–899.
- Crawford, R. M. M. (1989): *Studies in plant survival: Ecological case histories of plant adaptation to adversity*. – Blackwell, Oxford. 296 pp.
- Crawley, M. J. (1983): *Herbivory. The Dynamics of Animal-Plant Interactions*. – Blackwell, Oxford. 436 pp.
- De Jong, T. J. (1995): Why fast-growing plants do not bother about defense. – *Oikos* **74**: 545–548.
- De Mazancourt, C. & Loreau, M. (2000): Effect of herbivory and plant species replacement on primary production. – *Am. Nat.* **155**: 735–754.
- Dormann, C. F. (2001): *Global Change, Herbivory and Arctic Plants*. – PhD thesis, University of Aberdeen, Scotland. <http://www.ufz.de/spb/aloe/dormann/Dormann.htm>
- (2003): Herbivore mediated competition between defended and undefended plant species: a model to investigate consequences of climate change. – *Plant Biology*, in press.
- Dormann, C. F. & Brooker, R. W. (2002): Facilitation and competition in the High Arctic: the importance of experimental approach. – *Acta Oecol.*, in press.
- Dormann, C. F. & Skarpe, C. (2002): Flowering, growth and defence in the two sexes: consequences of herbivore exclusion on *Salix polaris*. – *Funct. Ecol.* **16**: 649–656.
- Drent, R. H. & van der Wal, R. (1999): Cyclic grazing in vertebrates and the manipulation of the food resources. – In: Olff, H., Brown, V. K. & Drent, R. H. (eds.): *Plants, Herbivores, and Predators*, pp. 271–299. – Blackwell, Cambridge.
- Edwards, P. J., Wratten, S. D. & Greenwood, S. (1986): Palatability of British trees to insects: constitutive and induced defences. – *Oecologia* **69**: 316–319.
- Hagerman, A. E. (1998): *Tannin Analysis*. – <http://www.muohio.edu/~hagermae/handbook/>

- Halle, Y. (2000): Forage selection of vascular plants in different spatial and temporal scales by Svalbard reindeer (*Rangifer tarandus plathyrinchus* Vrolik). – M.Sc. thesis, University of Oslo, Norway.
- Harborne, J. B. (1991): The chemical basis of plant defense. – In: Palo, R. T. & Robbins, C. T. (eds.): *Plant Defenses Against Mammalian Herbivory*, pp. 45–59. – CRC Press, Boca Raton, Florida, USA.
- (1997): Plant secondary metabolism. – In: Crawley, M. J. (eds.): *Plant Ecol.*, pp. 132–155. – Blackwell, Oxford.
- Haukioja, E. (1991): Induction of defenses in trees. – *Ann. Rev. Entomol.* **36**: 25–42.
- Haukioja, E. & Hanhimaki, S. (1985): Rapid wound-induced resistance in white birch (*Betula pubescens*) foliage to the geometrid *Epirrita autumnata*, a comparison of trees and moths within and outside the outbreak range of the moth. – *Oecologia* **65**: 223–228.
- Haukioja, E. & Neuvonen, S. (1985): Induced long-term resistance of birch foliage against defoliators – defensive or incidental. – *Ecology* **66**: 1303–1308.
- Haukioja, E., Suomela, J. & Neuvonen, S. (1985): Long-term inducible resistance in birch foliage – triggering cues and efficacy on a defoliator. – *Oecologia* **65**: 363–369.
- Hazlett, D. L. & Sawyer, N. W. (1998): Distribution of alkaloid-rich plant species in shortgrass steppe vegetation. – *Conservation Biology* **12**: 1260–1268.
- Hermes, D. A. (1999): Physiological and abiotic determinants of competitive ability and herbivore resistance. – *Phyton-Ann. Rei Bot.* **39**: 53–64.
- Hermes, D. A. & Mattson, W. J. (1992): The dilemma of plants: to grow or defend. – *Quart. Rev. Biol.* **67**: 283–335.
- Jokela, J., Schmid-Hempel, P. & Rigby, M. C. (2000): Dr. Pangloss restrained by the Red Queen – steps towards a unified defence theory. – *Oikos* **89**: 267–274.
- Jonasson, S., Bryant, J. P., Chapin, F. S. & Andersson, M. (1986): Plant phenols and nutrients in relation to variations in climate and rodent grazing. – *Am. Nat.* **128**: 394–408.
- Jung, H.-J. G., Batzli, G. O. & Seigler, D. S. (1979): Patterns in the phytochemistry of arctic plants. – *Biochem. Syst. Ecol.* **7**: 203–209.
- Karban, R., Agrawal, A. A., Thaler, J. S. & Adler, L. S. (1999): Induced plant responses and information content about risk of herbivory. – *Trends Ecol. Evol.* **14**: 443–447.
- Karban, R. & Baldwin, I. T. (1997): *Induced Responses to Herbivory*. – Univ. of Chicago Press, Chicago. 319 pp.
- Loreau, M. & de Mazancourt, C. (1999): Should plants in resource-poor environments invest more in antiherbivore defence? – *Oikos* **87**: 195–200.
- Louda, S. M., Keeler, K. H. & Holt, R. D. (1990): Herbivore influences on plant competitive interactions. – In: Grace, J. B. & Tilman, D. (eds.): *Perspectives on Plant Competition*, pp. 413–444. – Academic Press, London.
- Mole, S., Ross, J. A. M. & Waterman, P. G. (1988): Light-induced variation in phenolic levels in foliage of rain-forest plants. I. Chemical changes. – *J. Chem. Ecol.* **14**: 1–19.
- Price, P. W. (1991): Patterns in communities along latitudinal gradients. – In: Price, P. W., Lewinsohn, T. M., Fernandes, G. W. & Benson, W. W. (eds.): *Plant-Animal Interaction: Evolutionary Ecology in Tropical and Temperate Regions*, pp. 51–69. – John Wiley & Sons, New York.
- Rønning, O. I. (1996): *The Flora of Svalbard*. – 3rd edition, Norsk Polarinstitut, Oslo.
- Staaland, H. (1985): Svalbardsreinens ernæring. – In: Øritsland, N. A. (ed.): *Svalbardreinen og dens Livsgrunnlag*, pp. 97–128. – MAB, Norsk Polarinstitut, Oslo.
- Tahvanainen, J., Julkunen-Tiitto, R. & Kettunen, J. (1985): Phenolic glycosides govern the food selection pattern of willow feeding leaf beetles. – *Oecologia* **67**: 52–56.
- van der Wal, R., Brooker, R. W., Cooper, E. J. & Langvatn, R. (2001): Differential effects of reindeer on high Arctic lichens. – *J. Veg. Sci.* **12**: 705–710.

Zangerl, A. R. & Rutledge, C. E. (1996): The probability of attack and patterns of constitutive and induced defense: a test of optimal defense theory. – *Am. Nat.* **147**: 599–608.

Zucker, W. V. (1983): Tannins: Does structure determine function? An ecological perspective. – *Am. Nat.* **121**: 335–365.

Address of the author:

Dr. Carsten F. DORMANN, Applied Landscape Ecology, Centre for Environmental Research Leipzig–Halle, Permoserstr. 15, D-04318 Leipzig. E-mail: dormann@alok.ufz.de