CHAPTER 9

OPTIMAL ALLOCATION TO ANTI-HERBIVORE DEFENCE: IMPORTANCE OF GRAZING PRESSURE AND COMPETITION AND THE CONSEQUENCES OF CLIMATE CHANGE

Abstract   Optimal levels of anti-herbivore defence are determined not only by grazing pressure on the target plant, but also by the efficiency of the defence and by competitive interactions with neighbours. In the High Arctic on Svalbard, grazing by reindeer can be modelled without plant-to-herbivore-feedback, as reindeer population sizes are not correlated with plant growth. On the other hand, growing conditions are extreme: a short season and low temperatures inhibit optimal growth. Therefore, it is possible to model the cost and benefit of anti-herbivore defence on the competitive balance between plant species in this system. Here, I assess how the optimum allocation to defence varies in relation to grazing intensity, defence efficiency and global climate change. The model, based on a Lotka-Volterra-type competition and temperature-dependent growth indicates that competition is of considerable importance even in extreme environments. Herbivory mediates displacement of the defended plant by releasing it from competition. This process is more pronounced under high grazing pressure than under low. In other words, competition potentially magnifies the effect of herbivory. Interestingly, elevated temperatures and longer growing season have no qualitative impact on these processes, as it is especially the dominant defended plant that profits.

INTRODUCTION

Allocation of resources to anti-herbivore defence has been predicted to depend predominantly on grazing intensity, life expectancy of the consumed organ (usually the leaf), growth rate of the plant and availability of nutrients (Coley *et al.* 1985; Bryant *et al.* 1983; Herms & Mattson 1992). As pointed out by Loreau & de Mazancourt (1999), under competition the ability to exploit resources becomes much more important, especially in resource-poor environments. De Jong (1995) argued that fast growing species have no benefit from investment into anti-herbivore defence, unless grazing pressure is very high.

This study adds to these two studies a model assessing the relative importance of competition for two competing plant types, one defended, the other not, in the specific context of a terrestrial high arctic ecosystem. The reasons for restricting the approach to this extreme environment only has various reasons: 1. The optimisation of resource allocation is of vital importance for survival. Any assimilate invested into defence cannot be used for surviving the eight months long winter, soil movement, anoxic conditions etc. 2. This study ties in with other work carried out in the same system, that tries to unravel the interactions between reindeer population dynamics, parasites, vegetation and climate (Irvine *et al.* 1999; Langvatn *et al.* 1999; Van der Wal *et al.* 2000c; 2000b). 3. The arctic tundra is a very simple grazing system, in the specific case of Svalbard having only one ungulate herbivore (reindeer), the population of which fluctuates independently of plant productivity (Tyler & Øritsland 1999; see also Lee *et al.* 2000). 4. The High Arctic is predicted to experience the greatest increase in temperature due to climate change. The impact of these changes on plant performance in respect to grazing and competition are virtually unknown (but see Dormann *et al.* 2001).

The model presented addresses three specific questions:

- How are direct and indirect costs and benefits of anti-herbivore defence related to grazing intensity, i.e. when is the competitive disadvantage of slower growth rate of defended plants outweighed by the benefit of reduced grazing?

- How does the relative intensity of competition scale to that of herbivory along a grazing frequency gradient?

- How do climatic warming, longer growing seasons and higher nutrient availability affect the competitive balance of defended and undefended plant types?

METHODS

Model assumptions

The model investigates the outcome of competition between two types of plant species, differing only in their anti-herbivore strategies (and the implications of that), but not in apparency to the herbivore (e.g. as for the co-occurring cyanogenic and non-cyanogenic forms of bracken *Pteridium aquilinum*; Cooper-Driver & Swain 1976). The plants grow in a well-mixed, homogeneous patch which is small relative to the surrounding area, so that herbivores do not rely on these specific plants for their survival, thus there is no feedback from the plant population dynamics to the herbivore population dynamics (as is the case for managed livestock, as well as some reindeer populations Lee *et al.* 2000). Both species consist of ramets with constant size and weight, so that any increase in the numbers of plants is equivalent to an increase in phytomass.

The model

Competition between ramets of defended (P_D) and undefended (P_U) plant species is modeled using a Lotka-Volterra approach (Begon *et al.* 1990) of coupled ordinary differential equations:

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

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

where $P_{U/D}$ = population size of 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, plants 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 ν (randomly sampled from the interval [0.5ν; 1.5ν]). 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, not trees.

The temperature function $T(temperature)$ represents temperature-dependent growth, thus simulating winter as well as a warming climate. The actual function of *temperature* was derived by fitting two linked sinusoidal functions to temperature data from Longyearbyen, Svalbard (Audun Stien, unpublished data). This function has a parameter for the onset of spring, the onset of autumn, maximal summer temperature and minimal winter temperature. Furthermore, it assumes a 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.).

To assess the intensity of competition, competition-free populations were modelled alongside, where the competition term $(1 - ((P_U - P_D)/K))$ was replaced by (1-
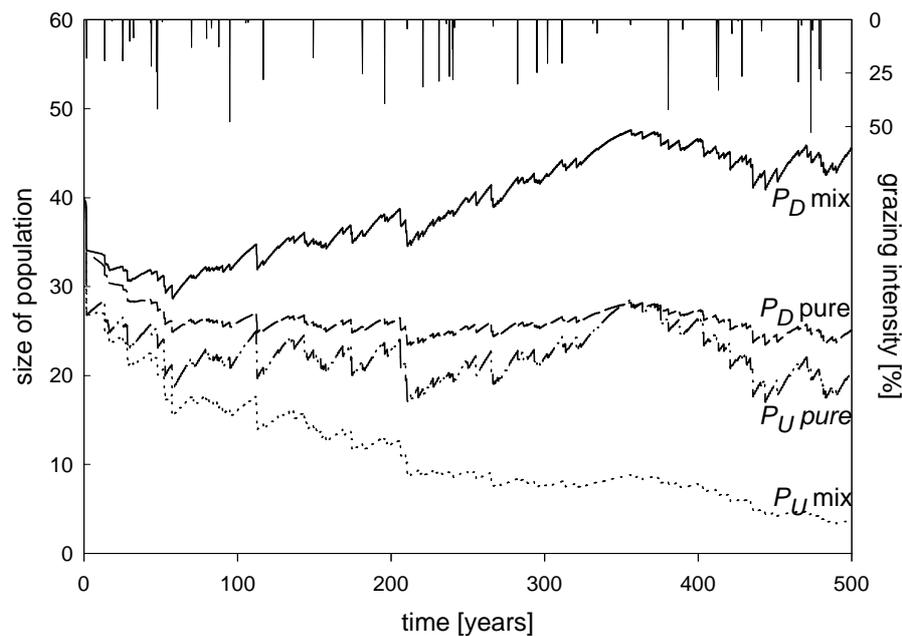
Fig. 1 Example of a model run, displaying the impact of competition in a grazed situation (difference between pure and mixed populations). Spikes at the top indicate moment and strength of grazing event. Settings: $b = 0.2$, $D^* = 0.761$, grazing frequency average = 1/10, initial value for P_D and P_U is 40.

($2P_{U/D}/K$)) (Fig. 1). For assessing competition without grazing, the grazing term was eliminated during the model runs. 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).

The effect of warming was assessed by altering the temperature function (increasing the maximum summer temperature by 5°C and the minimum winter temperature by +10°C). A four week longer season (effectively a 25% increase) was simulated by taking the onset of spring forward by two weeks, and delaying the onset of autumn by two weeks. These alterations started in year 450 and the run was continued for another 50 years. Population sizes after 500 years (means of 10 runs) were then compared to those of unaltered conditions.

Competition and herbivory indices

To compare the impact of competition and herbivory on the population size of P_D and P_U, the model was run for plant types with and without competition, each with

and without grazing, respectively. The following indices (Grace 1995; Markham & Chanway 1996) were then calculated for P_D and P_U: relative competition index (RCI) and relative herbivory index (RHI) (illustrated for P_U only).

$$RCI_{P_U} = \frac{P_U \, pure - P_U \, mix}{X} \quad \text{and} \quad RHI_{P_U} = \frac{P_U \, pure \, ungrazed - P_U \, pure \, grazed}{X},$$

where X is the bigger of the two values in the denominator (Markham & Chanway 1996). Index values range between -1 and $+1$, with positive values indicating negative net effects of competition (or herbivory) and negative values indicating positive net effects. These indices quantify the intensity of competition and herbivory at each point along the grazing frequency gradient.

RESULTS

Optimal defence allocation along grazing frequency gradient

Only at intermediate grazing frequencies ($\nu = 1/10$ years, Fig. 2) was allocation to defence the superior strategy ($P_D > P_U$). However, any slight deviation from optimal defence allocation (D^*) caused a marked decline in the population size of P_D and accordingly an increase in P_U (Fig. 2). At high values of D, P_D always outperformed P_U.

The absolute allocation to defence which proved optimal was strongly dependent on the grazing
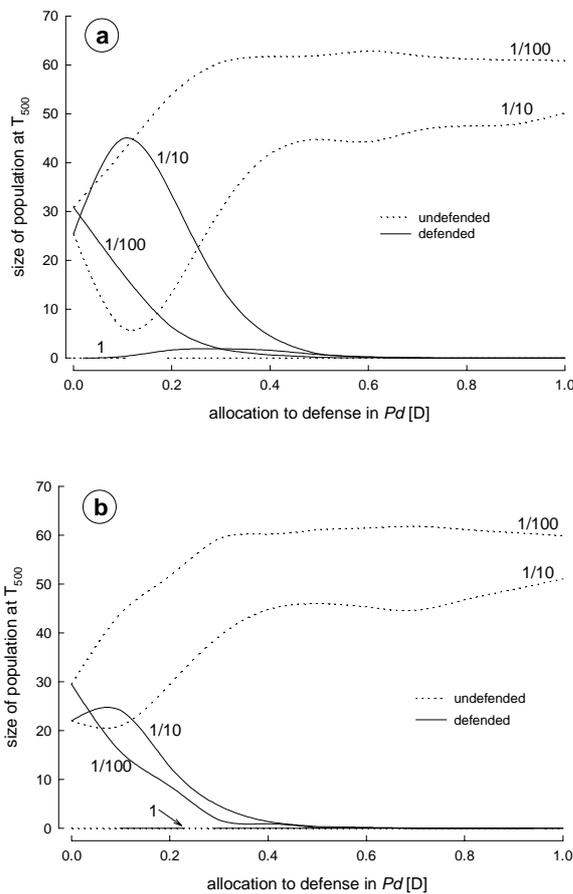
Fig. 2 Population size of undefended (dotted lines) and defended (solid) plant types for different allocation to defence (D) for the defended plant type at different grazing intensities (yearly: 1, every 10th year: 1/10; every 100th year: 1/100). **a)** $b = 0.2$. **b)** $b = 0.5$.
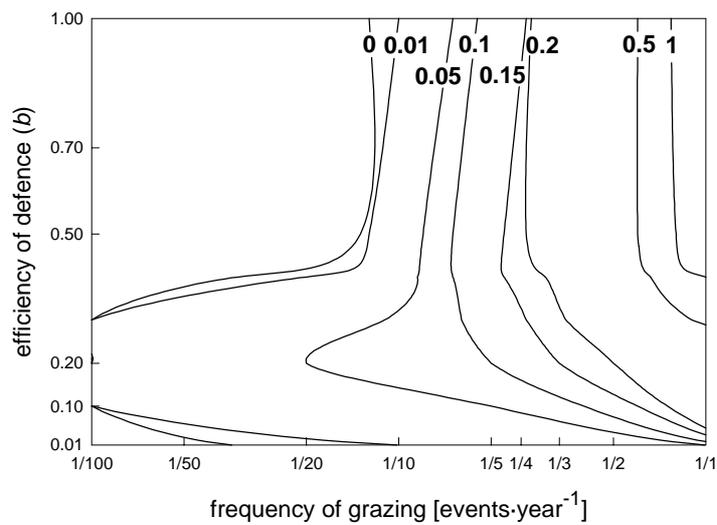
Fig. 3 Optimal allocation to defence (*D**), maximising P_D, for a range of grazing frequencies and defence efficiencies (*b*). Lines of same *D** are shown.

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

At each *b*, *D** was linearly related to grazing frequency. The values from these regressions were used to calculate the *D** for the model runs.

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. 4). 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).

Intensity of competition and herbivory
along a grazing frequency gradient

To separate effects of competition and herbivory, the model was run for species in pure and mixed stands, with and without grazing. The idea here is that this allows to determine the effect of competition in an ungrazed situation but with values for *D*
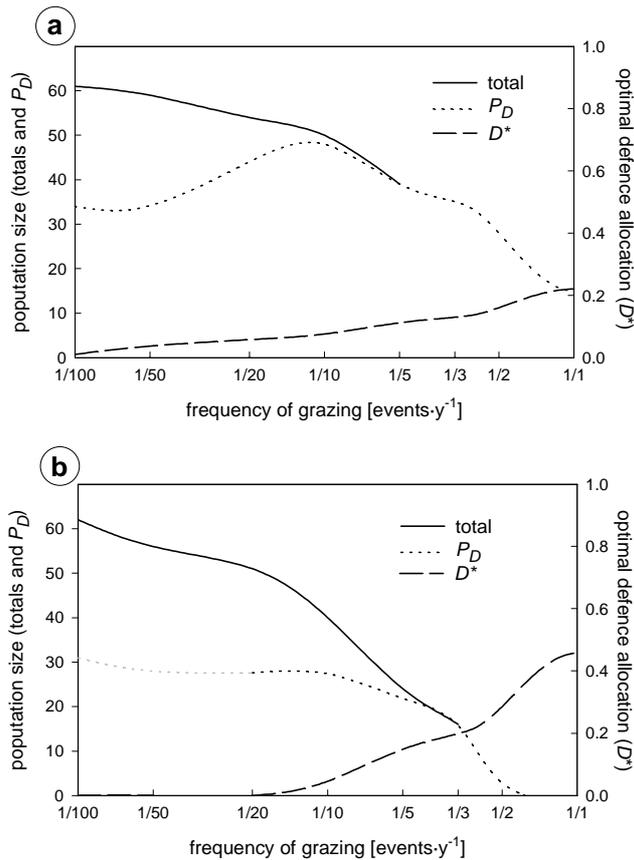
Fig. 4 Relative contribution of the defended plant type (P_D: dotted line) to the total plant population size (solid line), and optimal defence allocation (D^*) along a gradient of grazing frequency. Note that at some grazing frequency the entire population is made up of the defended plant type. **a)** $b = 0.2$, **b)** $b = 0.5$. Note that $D^* = 0$ for grazing frequencies less than 1/20 years (line of P_D in grey).

derived from the grazed scenario. The difference in RCI from grazed and ungrazed situations can then be attributed to the effect of grazing on competition.

Without grazing (grey lines in Fig. 5a), undefended plants grow better in mixture with the defended than in pure stands. This is because D^* increases with grazing intensity, thus reducing the competitive ability of the defended plant under no-grazing conditions, leading to an increased dominance of the undefended plant species (compare grey lines in Fig. 5 a and b).

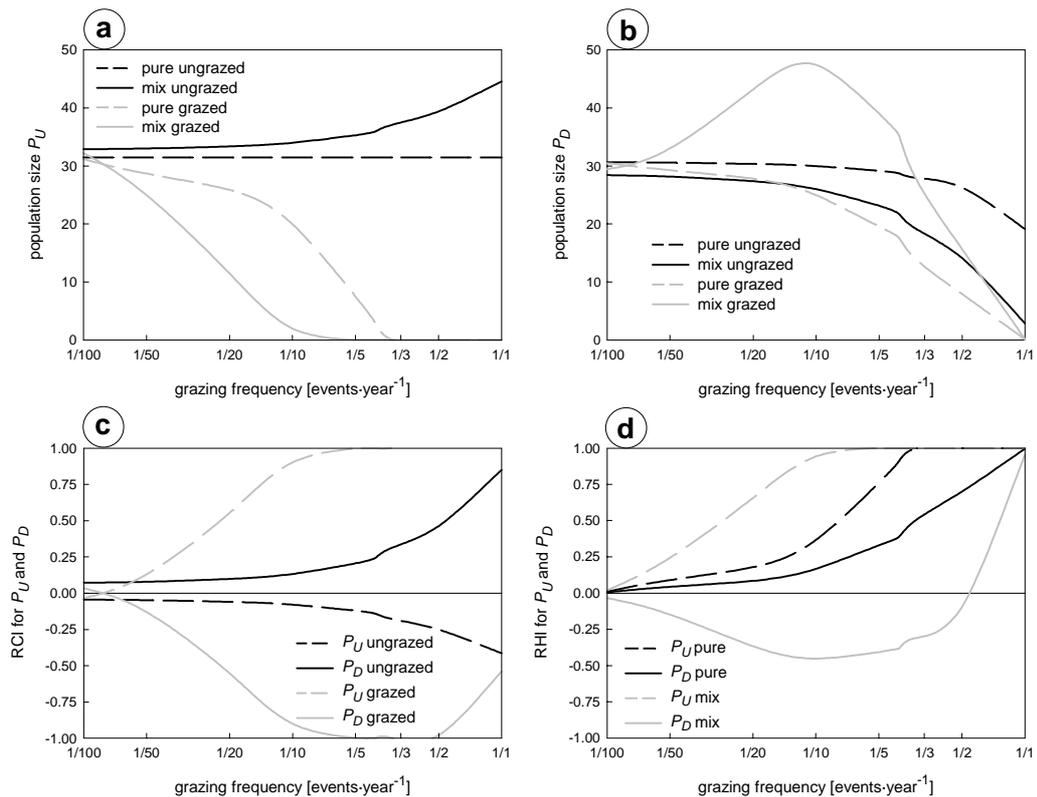This picture is inverted under grazing (black lines in Fig. 5ab). The population size of undefended plants in pure stands decreases with increasing grazing frequency (Fig. 5a, solid black line), as does that of the defended plants (Fig. 5b, solid black line), although more slowly. When the two plant types grow in mixture (broken black line), the decrease is much more rapid for P_U, while P_D profits from the release from competition by P_U over intermediate grazing frequencies.

The competition and herbivory indices calculated for these four scenarios are presented in figure 5c and d. The black lines present the index calculated without the inclusion of herbivory (Fig. 5c) or competition (Fig. 5d), respectively. The undefended plant type dominates the defended one (negative values for P_U, positive

Fig. 5 Population size of **a)** undefended and **b)** defended plants along a grazing frequency gradient. Populations with (mix, solid lines) and without (pure, broken lines) competition, with (grey lines) and without grazing (black lines) are shown. **c)** Relative competition index (RCI) for undefended (P_U, broken lines) and defended (P_D; solid lines) plant types with (grey lines) and without grazing (black lines). **d)** Relative herbivory index (RHI) with (grey lines) and without competition (black lines).

ones for P_D) without grazing. With grazing (grey lines) this is altered and now the defended type profits from the mixed stands, as grazing leads to a reduction in competition from the undefended (and therefore heavily grazed) plant type (Fig. 5c). It is only when $P_U = 0$ (at grazing frequencies > 1/3) that the RCI for P_D starts to rise again.

For the impact of herbivory, this picture is less complex (Fig. 5d). In pure stands (black lines), grazing obviously affects undefended plants more than defended ones. When plants co-occur (grey lines), herbivory has a positive effect on defended plants as it takes its toll on the population of the undefended plant type, thereby reducing competition.

In other words this means that competition is the more important factor for the defended plant, while herbivory rules the undefended one. Most importantly,

Table 1 Absolute and relative (% in parentheses) changes of the population size relative to unaltered climate of undefended and defended plants simulating warming (summer +5°C, winter +10°C), longer seasons (+25%, i.e. earlier spring and later autumn), and their interaction for 50 years. Grazing frequency refers to a grazing event with average frequency of once every 100, 50, 20, 10, 5, 4, 3, 2 or 1 year. -- indicates that calculations were not performed as the population size was < 1.

	grazing frequency	1/100	1/50	1/20	1/10	1/5	1/4	1/3	1/2	1
warming	PU	0.74	1.25	1.36	0.42	0.02	0.00	0.00	0.00	0.00
		(2.29)	(5.00)	(11.85)	(21.31)	--	--	--	--	--
	PD	0.79	2.74	3.20	5.05	6.46	6.23	6.44	3.99	0.05
		(2.67)	(8.28)	(7.41)	(10.64)	(16.54)	(17.72)	(23.15)	(25.51)	--
longer season	PU	-0.94	-0.04	0.27	-0.68	0.00	0.00	0.00	0.00	0.00
		(-2.91)	(-0.15)	(2.38)	(-34.6)	(-8.06)	(1.48)	--	--	--
	PD	0.35	0.37	-0.14	-1.03	0.75	-0.99	0.15	0.94	0.03
		(1.19)	(1.11)	(-0.33)	(-2.18)	(1.92)	(-2.82)	(0.52)	(6.02)	--
both	PU	-0.41	1.99	1.43	0.05	-0.02	0.00	0.00	0.00	0.00
		(-1.27)	(7.95)	(12.43)	(2.54)	--	--	--	--	--
	PD	1.15	2.71	3.78	2.96	3.83	-0.78	4.92	3.37	0.05
		(3.92)	(8.21)	(8.74)	(6.24)	(9.80)	(-2.23)	(17.66)	(21.55)	--

however, is the way that herbivory puts the undefended plant at a selective disadvantage, thereby inverting its competitive dominance into becoming highly susceptible to competition by the defended plant.

Effect of altered environment

When modelling plant response to altered environment, plant allocation to defence was kept constant, i.e. at the same value obtained for D^* in the unaltered conditions. This is because allocation pattern probably evolved over longer time scales than the modelled 50 years of environmental change. Hence quick re-adaptation to the new environmental conditions is unlikely.

Warming by 5°C in the summer and 10°C in winter over 50 years caused slight to pronounced absolute increases in P_D, while it had no effect on the absolute population size of P_U (Table 1). P_D profited most from elevated temperatures at lower grazing intensities, although the absolute changes were small. Longer seasons

led to no important absolute difference for either plant type (Table 1). Interaction of warming and longer season caused slight counteracting effects for P_D at intermediate grazing frequencies.

Changes in environmental conditions had no effect on important effect on competition and herbivory indices, as the defended plant type could profit more than the undefended, and for both types changes were relatively small (data not shown).

Increased nutrient availability will lead to a higher value of K, which has no qualitative consequences for species abundances or interactions using this type of model. Moreover, it is not known how a, say, 15% increase in nutrient availability would translate in terms of K, thus no such calculations were performed.

DISCUSSION

The optimal investment into anti-herbivore defence in face of competition depends obviously on grazing pressure (frequency and intensity) and defence efficiency. For low defence efficiencies and grazing pressure, no defence is the best strategy (Fig. 4b), but with higher grazing pressure, optimal defence allocation (D^*) increases as well. Plant populations are then dominated by the defended type, and will eventually only contain this plant type. At high defence efficiency, D^* exceeds 0 even at very low grazing frequencies. By definition, allocation to defence is the superior strategy as soon as $D^* > 0$. It is striking, however, that this is the case for all investigated grazing frequencies (at $b = 0.2$), i.e. that simple re-growth after grazing is never an optimal strategy.

Herbivory plays a major role in shaping the outcome of competition between the defended and undefended plant type (P_D and P_U, respectively). Without grazing, P_U obviously always outcompetes P_D. When grazed, this situation is inverted. Surprising is the strength of competition acting on P_D in the grazed situation (Fig. 5c), which arises from the fact that P_D greatly profits from the presence of undefended plants, being released from competition.

The inversion of competitive outcome by grazing is intrinsic in the model structure, as well as having been shown repeatedly in the field (e.g. Reader 1992; see Crawley 1997 for overview). It has been argued however, that in harsh environments plant-plant competition would not act and therefore not be important for structuring the community (Grime 1979). This was rejected by the model-based

work of Chesson & Huntly (1997), who found that in extreme environments the balance between surviving and dying is more fragile, thus competition would not have to be strong to drive one species to extinction. Explicitly modelling the determinant of severity, i.e. in this case temperature, the data presented here supports their findings. Despite total plant population size being far from carrying capacity (usually at less than 60% of *K*), competition is a major determinant of population size. Evolutionary pressure on the realisation of *D**, reducing competition along the way, is thus high, even at grazing frequencies of only once every 20 years.

Climate changes – but without

The simulated potential effects of global climate change on this herbivory-competition-complex are relatively small. Increased growth of plant populations is particularly noticeable in the defended plant type, while the undefended hardly responds. No change in competitive balance could be observed. It thus seems, that changes in herbivore density (and thus grazing pressure) are much more likely to cause changes in plant community composition then direct effects of climate changes. How reindeer density on Svalbard will change with increasing temperature can only be speculated, as correlations between reindeer population growth and North-Atlantic Oscillation anomalies are based one twenty year study of an introduced population (Aanes *et al.* 2000).

Several parameters have not been changed, e.g. relative growth rate, carrying capacity, respiration constant, shape of competitive interaction and random function of grazing intensity and frequency. Their alterations have no qualitative effect on the outcome of the model, i.e. lead only to different scales of the axes. The model assumes no trade-off between anti-herbivore defence and re-growth after grazing other than a proportional reduction in realised growth. It has been argued that this trade-off exists, but supportive data are limited to one study (Van der Meijden *et al.* 1988). De Jong (1995) also argued in favour of this concept, but his model, depending on the assumption of this trade-off, yielded optimal defence allocation only for realised growth rates higher than those in this model. He finds a high investment into defence in slow growing species, which rapidly drops off as growth rate increases.

The model presented here is an extremely simplified version of the real world. Although on Svalbard only two vascular plant species, *Luzula confusa* and *Salix polaris* are present in the vegetation type under investigation by the author (see

General Introduction), there are mosses, absorbing atmospherically deposited nutrients, ground water percolation that leads to the import of nutrients and alters soil temperature and many other factors, which have an impact on the performance of a given species. Furthermore, model assumptions might not hold, e.g. grazing might be less selective (i.e. defence less efficient), trampling effects more prevalent, interannual variation in growing conditions more important and the shape of the logistic competition function unrepresentative. Unfortunately, data are not available for any of these factors. However, choosing a simple model produces very specific predictions which can be tested by field experiments: 1. Undefended plant types (e.g. grasses) should increase inside herbivore exclosures. 2. Competition between plants plays a major role in determining vegetation structure. 3. Along a gradient of reindeer grazing pressure, total plant population size should decrease, while the proportion of defended plants should increase. 4. This pattern should be detectable independent of variations in season length and air temperature differences between sites.

Some preliminary results and observations support these predictions: On Svalbard, a four year reindeer exclosure lead to an increase in the abundance of grasses and forbs, but also in the dominant (and defended) woody species (personal observation). Higher reindeer densities were accompanied by higher cover of grasses and a decrease in (highly palatable) lichens (Van der Wal & Brooker 2001; Van der Wal *et al.* 2001a). A field experiment detected strong competitive interactions between two plant species, incidentally a defended and an undefended (CHAPTER 5). Although these data are insufficient to validate the model, they underline the importance of herbivory in the High Arctic and the congruence with the model hints at a role for competition in the structuring forces of arctic vegetation.

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