

Consequences of manipulations in carbon and nitrogen supply for concentration of anti-herbivore defence compounds in *Salix polaris*¹

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Abstract: The concentration of carbon-based anti-herbivore defence compounds is key to herbivore utilization of forage. Production of phenolics and condensed tannins in boreal woody plants is known to reduce grazing pressure. Their production depends, among other things, on the availability of nutrient resources, especially nitrogen, relative to the availability of assimilates. The carbon-nutrient balance (CNB) hypothesis (Bryant, Chapin & Klein, 1983) predicts a decrease in the concentration of carbon-based defence compounds with increased availability of nutrients. In a High Arctic heath, I manipulated the carbon-nitrogen balance of polar willow (*Salix polaris*) in a factorial, multi-level fertilizing and shading experiment. Other plots were subject to elevated temperature. After 2 years, shading and, to a lesser extent, fertilization had caused an increase in nitrogen concentrations in the leaves, which were highly and negatively correlated with lower total phenolic and condensed tannin concentrations. Elevated temperature caused no such effects, but increased growth significantly, while shading reduced shoot biomass, and fertilization had no detectable effect. These results are consistent with the CNB hypothesis. On the basis of this study it seems unlikely, however, that environmental modifications due to global climate change will have a major impact on defence chemistry, as very high shading (>70%) and fertilization levels (>1.5 g m⁻² years⁻¹) were needed to produce significant deviations from controls.

Keywords: Arctic, carbon-nutrient balance, fertilization, phenolics, secondary compounds, shading, condensed tannins.

Résumé : La consommation de plantes chez les herbivores dépend de la concentration des composés carbonés permettant aux plantes de se défendre. On sait que la production de phénols et de tannins concentrés chez les plantes ligneuses des régions boréales réduit la pression de broutement. Cette production dépend, entre autres, de la disponibilité des ressources nutritives, en particulier de l'azote, par rapport à la disponibilité des photo-assimilats. Selon l'hypothèse de l'équilibre carbone – éléments nutritifs (Bryant, Chapin & Klein, 1983), la concentration des composés carbonés de défense diminue lorsque la disponibilité des éléments nutritifs augmente. Dans une lande du Haut-Arctique, j'ai modifié le bilan carbone-azote d'une espèce de saule (*Salix polaris*) au cours d'une expérience factorielle à plusieurs niveaux de fertilisation et d'ombrage. D'autres parcelles étaient également soumises à des hausses de température. Après 2 années, l'ombre, et à un plus faible degré les fertilisants, ont entraîné un accroissement des concentrations en azote chez les feuilles. Ces concentrations étaient hautement et négativement corrélées avec de faibles concentrations de phénols totaux et de tannins concentrés. La hausse de température a pour sa part favorisé de façon significative la croissance des saules. L'ombrage a eu pour effet de réduire la biomasse des tiges alors que la fertilisation ne semble pas avoir eu d'effet sur la croissance ou la biomasse des saules. Ces résultats sont en accord avec l'hypothèse de l'équilibre carbone – éléments nutritifs. En conclusion, il semble peu probable que les changements environnementaux engendrés par le réchauffement climatique aient un impact majeur sur les défenses chimiques de ces plantes, car il a fallu appliquer des niveaux très élevés d'ombrage (>70 %) et de fertilisants (>1,5 g m⁻² année⁻¹) sur les parcelles expérimentales pour obtenir des résultats différents de ceux des parcelles témoins.

Mots-clés : Arctique, équilibre carbone – éléments nutritifs, fertilisation, phénols, composés secondaires, ombrage, tannins concentrés.

Nomenclature: Rønning, 1996.

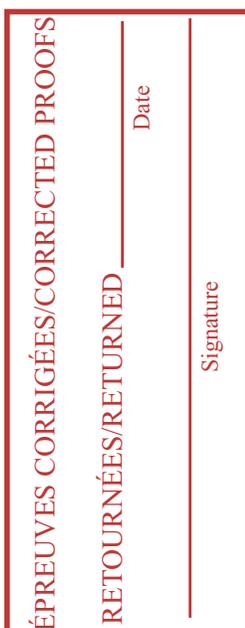
Introduction

The consequences of global climate change are predicted to be especially pronounced in the Arctic (Intergovernmental Panel on Climate Change, 1990; 1998); expected consequences include temperatures elevated by several degrees and increases in cloudiness and precipitation. In various field experiments it has been shown that warming, increased nutrient availability, and light attenuation will affect plant growth (reviewed in Dormann &

Woodin, 2002). Much less is known about the consequences of environmental changes on plant chemistry. In particular with respect to substances important to herbivores, such as nitrogen and grazing deterrents like phenolics and tannins, our ecological understanding is poor. Chapin, McKendrick and Johnson (1986) have been able to show how nitrogen and sugar fractions of tundra plants vary across the season, and Laine and Henttonen (1987) have tried to relate interannual differences in microtine density to weather-induced differences in phenolic and nitrogen content of blueberry (*Vaccinium vitis-idaea*). Data on the effects of environmental manipulations on defence chemistry are virtually absent for the High

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Arctic, however (for an exception, see Van der Wal *et al.*, 2000).

The anti-herbivore defence of woody arctic plants is generally carbon-based (Bryant & Kuropat, 1980; Bryant *et al.*, 1991), probably because nitrogen is the limiting nutrient in these systems (Shaver & Chapin, 1986) and nitrogen-based defence is thus too costly (Chapin, 1989). It has been proposed (Bryant, Chapin & Klein, 1983) that growth limitations due to low nutrient availability lead to a relative surplus of assimilates, which is then invested into carbon-based defence as a “carbon overflow” mechanism (for a review, see Hartley & Jones, 1997). Consequently, major changes in the balance of carbon and nutrient would lead to changes in the amount of carbon-based defence (Bryant, Chapin & Klein, 1983).

Global climate change will influence carbon assimilation (*e.g.*, shading due to increased cloud cover) and nutrient supply (*e.g.*, fertilization through increased mineralization in warmed soils, Nadelhoffer *et al.*, 1991). Consequently both shading and fertilization should increase the availability of the limiting nutrient nitrogen relative to carbon, but decrease carbon-based secondary compounds. However, elevated air temperature may lead to an increase in carbon assimilation, as photosynthesis of arctic plants is sensitive even to small increases in air temperature (Larcher, 1995), while it may also increase nutrient mineralization, therefore providing more nitrogen to the plant. The net effect on defence chemistry will depend on the relative magnitude of the environmental changes and the foliar chemistry responses to them.

This study investigates the consequences of the manipulation of light, nutrient availability, and temperature on the concentrations of nitrogen, phenolics, and condensed tannins in the leaves of *Salix polaris*. By varying shade and fertilization at four levels in a factorial design, a whole range of different carbon-nitrogen ratios is created, enabling an estimation of the sensitivity of anti-herbivore defence in *Salix polaris* to changes in the environmental factors manipulated. The experiment also allows me to discuss various defence allocation hypotheses differing in their predictions of the effects of carbon-nitrogen imbalances.

Methods

The study was carried out in Semmeldalen, Svalbard (77.90° N, 15.20° E), a valley *ca* 20 km south of Longyearbyen, Svalbard. All experimental plots were situated in a representative patch of *Salix polaris* heath (Rønning, 1996), over an area of *ca* 100 m × 50 m. The whole site was enclosed by an electric fence to prevent disturbance by reindeer.

THE STUDY SPECIES: *SALIX POLARIS*

Salix polaris (polar willow), Salicaceae, is common throughout Svalbard 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 (C. Skarpe, pers. comm.), when animals are cratering for food through the snow. Like most Salicaceae, *Salix polaris* is heavily defended against herbivory by a variety of phenolics, especially condensed tannins (Julkunen-Tiitto, 1985; 1989; Dormann & Skarpe, 2002).

SHADING × FERTILIZATION EXPERIMENT

Plots of 0.5 m by 1m were established in early June 1999. Treatments consisted of a full-factorial combination of four levels of fertilizer (0, 0.5, 1.5 and 5 **kgN m⁻² year⁻¹**) and four levels of shading (0, 53, 72 and 83%). Each treatment was replicated three times, and replicates were arranged in a randomized block design. The fertilizer (ammonium nitrate, dissolved in 2 L of water per plot) was applied in rain on five occasions during the growing seasons of 1999 and 2000 (water only for the controls). Shading was attained by placing a wire-based shading frame with one, two, or three layers of optically neutral greenhouse shading cloth (B & Q, U.K.) over the plot, reducing both direct and diffuse radiation into the plot.

Light availability under the shading frames was measured with a deltaT microvolt integrator fitted with a PAR photosensor (deltaT, Cambridge, U.K.). Air temperature at soil level was recorded with an RS temperature data logger (Radio Supply, U.K.), recording hourly over the entire experimental period. Soil water content was measured with a soil conductivity insertion probe (SCIP, CEH Wallingford, U.K.) on 15 June, 28 June, 1 August, and 27 August 1999 and on 28 July 2000.

At the end of each season all shoots from a 25-cm × 25-cm square were counted and harvested from each treatment plot for determination of *Salix polaris* leaf biomass. Dead leaves were manually sorted and discarded, green leaves were counted, and shoots and leaves were dried at *ca* 45°C for 1 week, transported back into the lab, and re-dried before weighing. Leaves were then ground and analyzed for total carbon and nitrogen using a CNS autoanalyser (Fisons, U.K.). Total phenolic content of leaves was measured following the modified Prussian blue assay using tannic acid as standard, and condensed tannins were measured by the acid butanol method using purified quebracho tannin as standard (Hagerman, 1998).

ELEVATED AIR TEMPERATURE EXPERIMENT

Fifteen pairs of plots (60 cm in diameter) were carefully selected. The experiment consisted of warmed plots and controls, randomly assigned to the paired plots. Treatment plots were subjected to warming over most of the growing season in 1999, from 16 June 1999, *i.e.*, about 10 days after snowmelt, to 29 August 1999 and over the whole snow-free period in 2000, from 14 June 2000 until harvest (1 August 2000). Greenhouses of a modified “cloche” type (Strathdee & Bale, 1993) were used to raise air temperature. They consisted of an open cylinder (57 cm in diameter, 45 cm in height) made of a sheet of transparent plastic with a thin, optically neutral polyester gauze as a roof. For further details, see Dormann (2001). Leaf material was sampled only in 2000 and treated the same way as mentioned above.

OK?

Kg? Are you sure?

STATISTICAL ANALYSIS

All data were analyzed with the GLM procedure of SAS (SAS Institute, 1989), using block as random factor and treatments as fixed effects. To separate treatment from year effects, years were analyzed separately for the shading-fertilization experiment. The interaction of shading and fertilization was never significant at $P < 0.1$ and was thus removed from the statistical model. Shoot biomass was used as a covariate to correct for concentration or dilution effects of reduced or increased growth, respectively (Koricheva, 1999).

Results

ENVIRONMENTAL VARIABLES

Temperatures were altered by shading cloth (Table I). Both 73% and 82% shading plots were *ca* 1.3°C cooler than ambient, while the 53% shading treatment caused slight warming. This led to a cumulative temperature difference in degree-days compared to control of +5% for the 53% shading and -12% for the 72% and 83% shading treatments. Shading treatments differed little in soil water content on any of the four dates (Table I). An effect of shading on soil water content was detectable, but more pronounced on wet days (Table I). It was, however, lower than the variability over time.

Air temperature in the greenhouses was on average 2.3°C higher than in controls (11.8°C versus 9.5°C; $F_{1, 3288} = 103.2, P < 0.0001$). Soil water content at sampling date was significantly lower under elevated temperature ($18.7 \pm 2.00\%$ versus $22.6 \pm 1.78\%$; $F_{1, 28} = 8.64, P < 0.01$).

SHADING × FERTILIZATION EXPERIMENT

SHOOT BIOMASS

Above-ground shoot biomass was significantly reduced in shaded treatments in both years (Figure 1, Table II). However, this decrease became apparent only at the highest level of shading. Surprisingly, fertilization had a negative effect on shoot biomass in the first season (Figure 1a); however, this effect disappeared in the second season (Figure 1b, Table II).

NITROGEN AND CARBON CONTENT OF LEAVES

Nitrogen content of leaves was significantly correlated with shoot biomass, both in 1999 and 2000 ($r = -0.305, P < 0.05$ and $r = -0.447, P < 0.001$, respectively; Pearson

correlation), indicating that some leaves had a lower N content simply because they were heavier (dilution by growth). To correct for this (Koricheva, 1999), shoot weight was used as covariate in the analysis (see Table II).

Salix polaris exhibited a significant increase in nitrogen content in response to shading in both years (Table II). However, in 1999 this increase can only be observed at the highest level of shading, while in 2000 it is a pervasive trend, leading to a 100% increase in leaf N in fertilized plus shaded plots (Figure 1). In 2000 the fertilization treatment also caused a significant increase in leaf nitrogen content (Figure 1b, Table II). Leaf nitrogen levels were higher in 2000 due to differences in phenological stage at the date of sampling. Sampling took place a week earlier in 2000 than in 1999 and the season began about 1 week later, resulting in a phenological difference between the 1999 and 2000 sampling of almost 2 weeks (data not shown).

Leaf carbon content was less responsive than leaf nitrogen: only in the second year was shading significant (Table II), while fertilization was never significant. The actual difference between shaded and control plots was very small, however (control: $47.1 \pm 0.36\%$; 85% shading: $46.1 \pm 0.32\%$). The grand means for 1999 and 2000 were $47.6 \pm 0.35\%$ and $46.3 \pm 0.19\%$, respectively (± 1 SE).

DEFENCE CHEMISTRY

Levels of anti-herbivore defence were generally high, with total phenolics at *ca* 14% dry weight tannic acid equivalents (TAE) and condensed tannins at *ca* 13% dry weight quebracho equivalents (QE). As for nitrogen, total phenolic and condensed tannin concentrations were significantly but positively correlated with shoot biomass in both years, and shoot biomass was used as covariate in the statistical analysis (Table II).

Phenolic concentrations showed too much treatment-independent variation to detect significant effects of shading in 1999. In 2000, however, shading caused a significant decrease in phenolic concentrations (Figure 1, Table II), indicating an over-proportional (non-linear) reduction of phenolics with increasing shading. It reduced levels of total phenolics to a minimum of 50% of controls. Fertilization had no detectable impact in either of the 2 years (Table II).

The concentration of condensed tannins followed much the same pattern as total phenolics (Figure 1).

Does this capture your intended meaning?

Why not the same?

TABLE I. Environmental variable responses to shading. Temperature measurements are not replicated, values in brackets are **standard deviation** over the experimental period, degree-days are number of days above 0°C. Soil water content (% water content) is given with **standard errors** in parentheses ($N = 12$, due to pooling of fertilization treatments, which were not significant: $F_{3, 218} = 0.46, P > 0.5$). There is a significant effect of shading on soil water content ($F_{3, 218} = 3.75, P < 0.05$), which is also dependent on the date of measurement (interaction: $F_{12, 218} = 12.18, P < 0.001$). *w* behind the date indicates wet days.

	shade	0%	53%	72%	83%
Temperature	mean	8.9 (5.9)	9.1 (5.0)	7.6 (4.5)	7.6 (4.6)
	degree-days	629	660	554	552
Soil water content	1999-06-15 <i>w</i>	23.3 (1.06)	24.4 (1.47)	26.8 (1.44)	26.6 (0.99)
	1999-06-28 <i>w</i>	27.7 (1.45)	27.5 (1.62)	28.5 (0.79)	27.8 (0.66)
	1999-08-01	18.6 (1.32)	18.0 (1.01)	18.7 (0.92)	18.8 (0.59)
	1999-08-27	19.6 (1.37)	19.5 (1.21)	20.3 (0.86)	20.0 (0.84)
	2000-08-27	20.2 (1.16)	23.1 (0.87)	23.7 (0.63)	25.1 (1.37)

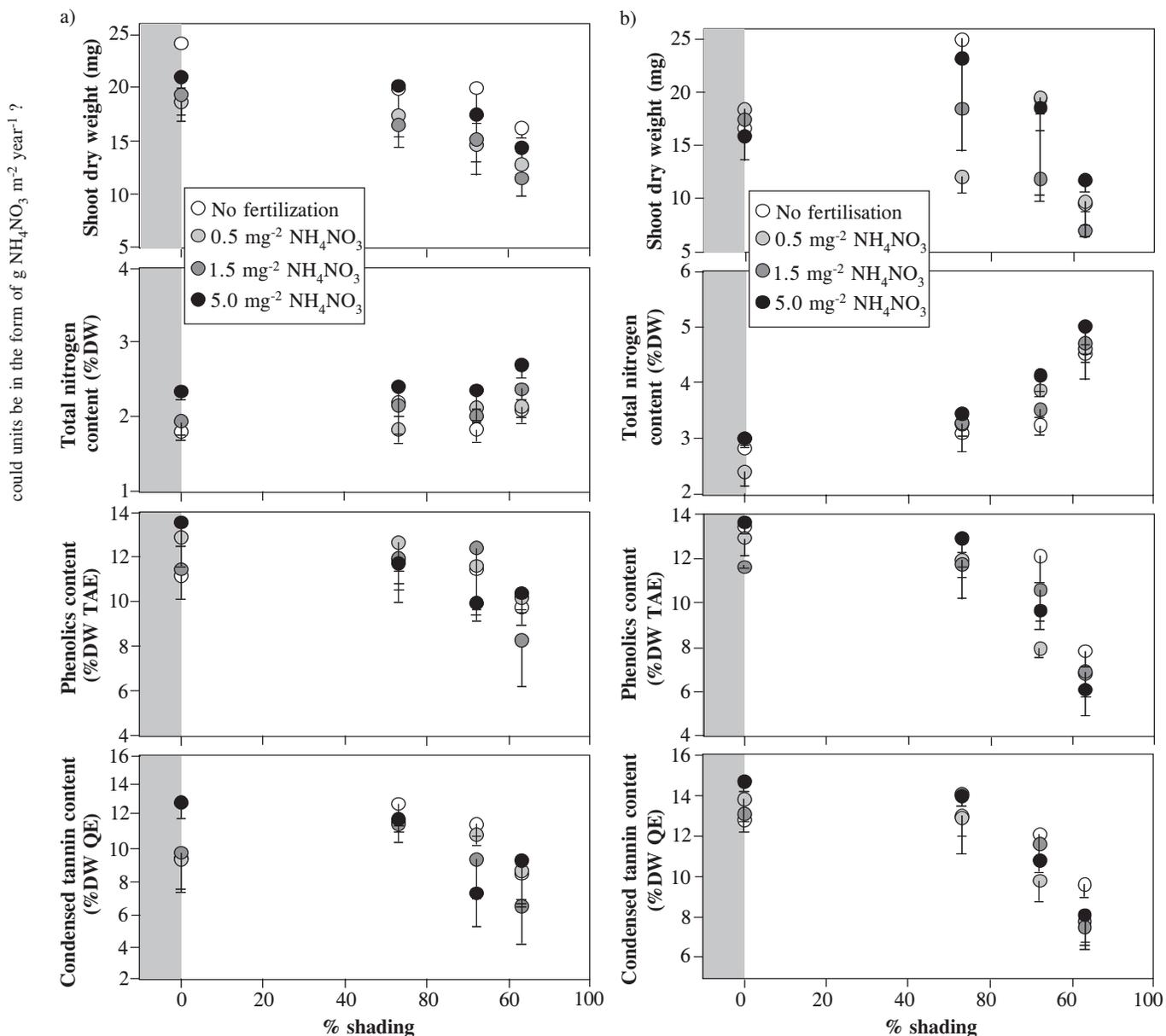


FIGURE 1. Shoot biomass, leaf nitrogen, phenolic and condensed tannin concentrations of *Salix polaris* in the four shading treatments in a) 1999 and b) 2000. Shading of points indicates level of fertilization. Error bars indicate -1 SE .

TABLE II. Statistical results of treatment effects on shoot biomass, nitrogen and carbon content, and total phenolic and condensed tannin content of *Salix polaris*.

Factor	df	Shoot biomass			Nitrogen			Carbon			Phenolics			Condensed tannins		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	F	P
1999																
Block	2	65.96	4.30	0.023	0.36	2.33	0.117	21.36	3.68	0.038	4.56	0.75	0.480	9.09	1.74	0.194
Biomass	1				1.58	10.19	0.003	1.76	0.30	0.586	43.44	7.17	0.012	31.72	6.08	0.020
Shading	3	106.46	6.93	0.001	1.16	7.44	0.001	2.35	0.40	0.751	3.63	1.06	0.621	15.31	2.94	0.051
Fertilization	3	53.27	3.47	0.028	0.24	1.51	0.232	1.10	0.19	0.903	6.40	0.60	0.383	3.84	0.74	0.540
Interaction	9	1.73	0.11	0.999	0.11	0.68	0.718	5.64	0.97	0.485	3.06	0.51	0.859	4.04	0.77	0.641
Error	29	15.35			0.16			5.81			6.06			5.22		
2000																
Block	2	133.08	6.05	0.006	0.52	3.82	0.034	3.85	2.52	0.098	0.67	0.31	0.737	4.28	2.47	0.102
Biomass	1				7.67	56.48	0.000	1.64	1.07	0.309	85.24	39.54	0.000	44.03	25.47	0.000
Shading	3	235.40	10.71	0.000	4.98	36.67	0.000	6.05	3.96	0.017	58.72	27.24	0.000	25.28	14.62	0.000
Fertilization	3	43.81	1.99	0.136	0.78	5.75	0.003	0.49	0.32	0.812	1.45	0.67	0.576	0.69	0.40	0.756
Interaction	9	37.45	1.70	0.013	0.15	1.07	0.412	0.84	0.55	0.827	3.67	1.70	0.134	1.36	0.79	0.630
Error	29	21.98			0.14			1.53			2.16			1.73		

However, here the shading effect was already marginally significant in 1999 (Table II). Again, fertilization was without consistent effect.

The similarity between the responses of phenolics and condensed tannins is reflected in a very high association for 2000 ($r=0.871$, $F_{1,46}=144.18$, $P<0.001$; Figure 2), while this association was not apparent in 1999 ($r=0.149$, $F_{1,44}=1.00$, $P=0.322$; Figure 2).

BLOCK EFFECTS

In some models in Table II, the random effect "block" is very strong. This is probably due to the location of the three blocks in places with slightly different soil moisture conditions. This led to differences in phenological stage at harvest and accordingly slight differences in leaf chemistry (C. F. Dormann, pers. observ.). After correction for the block effect, treatment effects were very comparable across blocks, however.

ELEVATED AIR TEMPERATURE EXPERIMENT (2000 ONLY)

Shoots in the warmed plots grew significantly heavier than in controls ($F_{1,14}=5.99$, $P<0.05$; Table III). However, nitrogen, carbon, phenolic, and tannin content of leaves (Table III) were not significantly altered by the manipulation of air temperature ($P>0.56$ for all compar-

isons). Here, no significant association between shoot weight and chemical properties could be detected ($P>0.42$ for all covariate regressions), indicating that growth was not causing a dilution of either nitrogen or defence compounds.

Discussion

As predicted by the CNB hypothesis (Bryant, Chapin & Klein, 1983), carbon-based defence compounds decreased as a function of nitrogen content (Figure 3). Manipulating shading and fertilization increased nitrogen concentrations in *Salix polaris* leaves. Shoot biomass explained some of the variation in defence concentrations (on average *ca* 20%), but nitrogen content was much more important (*ca* 60%). As both factors were correlated ($r=-0.447$, $P<0.001$, *i.e.*, lighter shoots have higher N content), nitrogen content as covariate reduced the importance of shoot weight to a non-significant level when both factors were included. These results do support the conclusion that "plants of extremely low nutrient environments tend to be unresponsive", compared to fast-growing species (Hartley & Jones, 1997, p. 307). However, this "unresponsiveness" is actually an ability to maintain the level of defence in the face of changes in the environment, *i.e.*, a buffering.

Tests of the carbon/nutrient balance hypothesis (reviewed in Herms & Mattson, 1992; Hartley & Jones, 1997; Koricheva *et al.*, 1998) have shown the following pattern: different ways of manipulating CNB (fertiliza-

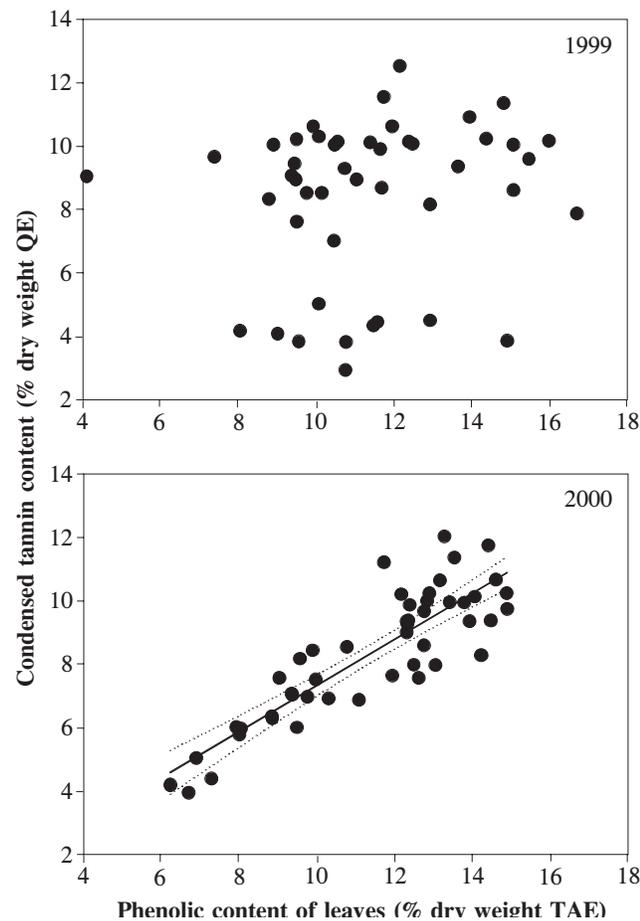


FIGURE 2. Correlation plot of total phenolic and condensed tannin concentrations in 1999 and 2000. Regression equation for 2000 (and 95% confidence limits) is $y=1.708 + 0.635x$, $R^2=0.758$.

TABLE III. Effect of elevated temperature after 2 years on plant characteristics.* Means \pm 1 SE are given.

	Ambient	Elevated
Shoot dry weight (mg)	15.9 \pm 1.46	19.8 \pm 1.53
Nitrogen content (%)	2.5 \pm 0.25	2.4 \pm 0.16
Phenolic content (%TAE)	12.7 \pm 0.58	14.7 \pm 0.94
Condensed tannin content (%QE)	13.8 \pm 0.85	14.2 \pm 0.59

*Temperature effect only significant on shoot dry weight ($P<0.05$).

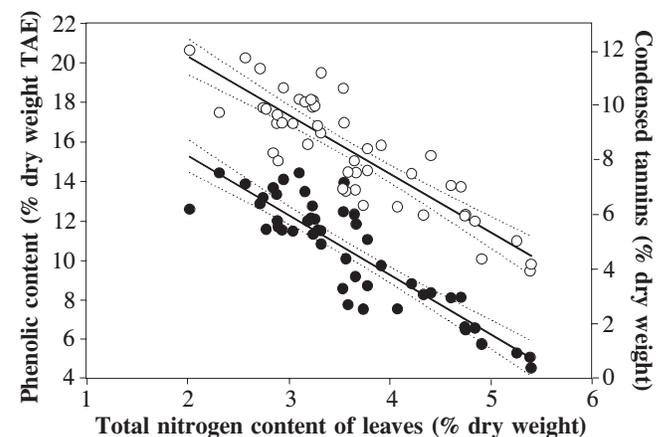


FIGURE 3. Bivariate plots of total phenolic (black circles) and condensed tannin (open circles) concentrations and nitrogen concentrations in 2000. Regression equation for the indicated line (and 95% confidence limits) is $y=21.41 - 3.03x$, $R^2=0.791$ for phenolic content and $y=16.12 - 2.15x$, $R^2=0.749$ for condensed tannin content.

tion, shading, elevated CO₂) lead to different consequences (e.g., hardly any effects of drought, Koricheva *et al.*, 1998). With respect to the manipulation of light availability and fertilization, most recent studies lend support to the CNB hypothesis, despite its intellectually unsatisfactory lack of foundation in plant physiology (Hamilton *et al.*, 2001). The increase in phenolics and condensed tannins with light intensity led Mole, Ross and Waterman (1988) to suggest an overflow mechanism for the production of carbon-based defence. For arroyo willow (*Salix lasiolepis*), fertilization effects followed the predictions of the CNB hypothesis (Price *et al.*, 1989). Both fertilization and shading treatments caused an increase in nitrogen and decrease in phenolics and tannins in Sitka spruce (*Picea sitchensis*), but had no significant effect on nitrogen ($P=0.07$), phenolics, and lignin in heather (*Calluna vulgaris*) (Hartley, Nelson & Gorman, 1995; but see Iason & Hester, 1993). Gebauer, Strain and Reynolds (1998) report a significant decrease in phenolics and tannins with higher level of fertilization of loblolly pine (*Pinus taeda*), but provide no data on nitrogen content. Low light intensities significantly affected leaf concentrations of nitrogen, condensed tannins, and phenolics in quaking aspen (*Populus tremuloides*) (Hemming & Lindroth, 1999). Moreover, concentrations of condensed tannins correlated with nitrogen content, but not with that of phenolic glycosides.

GLOBAL CLIMATE CHANGE AND ANTI-HERBIVORE DEFENCE

These data provide a first and crude estimate for the impact of some environmental changes on plant anti-grazing chemistry. Although these experiments ran only for 2 years, cautious extrapolations can be attempted. In this context the resilience of *Salix polaris* growth and leaf chemistry to fertilization and, somewhat less, to shading are remarkable: growth and N content, phenolics, and condensed tannins only decreased noticeably in the extreme shade (Figure 2). No difference in leaf chemistry could be detected in the warming experiment, despite a significant growth response. This is in line with the findings of Ruohomäki *et al.* (1996), who, after 3 years of 50% shading, found a moderate decrease in phenolics and condensed tannins and a moderate increase in leaf nitrogen concentrations in *Betula pubescens*. For *Salix polaris* it is unlikely that the projected climate change will lead to any major change in anti-herbivore compounds or N concentration.

It is much less straightforward to extend the response of the shrubs to the effects on their herbivores. Under warmer conditions, food supply will be higher due to the increased growth caused by these conditions. Higher nitrogen concentrations will presumably lead to increased herbivore damage, as found by Richardson *et al.* (2002) for *Vaccinium* spp. They could not, however, detect any effect of reduced phenolic concentrations on consumption by insect herbivores. Ruohomäki *et al.* (1996) report that only fertilization of *Betula pubescens* ssp. *tortuosa* was transformed into higher pupal mass of the moth *Epirrita autumnata*, while shading remained without measurable effect (although phenolics and condensed tannins were significantly reduced under shading).

Vertebrate herbivores, with their completely different digestive system, may show deviant responses. Changes

in defence chemistry can also be translated into changes in preference by herbivores, as shown in the example of moose (*Alces alces*) grazing shaded and fertilized Scots pine more than controls (Edenius, 1993) or Orkney vole (*Microtus arvensis orcadensis*) preferably consuming treated Sitka spruce (Hartley *et al.*, 1995; see also Bryant & Kuropat, 1980; Bryant *et al.*, 1991). Treatment effects were generally low for shading and high for fertilization, and shading levels averaged 50% in these studies. This degree of reduced light availability is certainly much higher than can be expected due to climate change.

Moreover, the slow growth and high reliance on storage (Chapin, Schulze & Mooney, 1990; Grime & Campbell, 1991; Iwasa, 1997) of arctic plants probably will buffer minor climatic effects for some years. Consequently, I cannot anticipate major implications of altered defence chemistry due to climate change for herbivore population dynamics in the High Arctic.

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