

Feeding behaviour of red deer (*Cervus elaphus*) on Sitka spruce (*Picea sitchensis*): the role of carbon-nutrient balance

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Abstract

This study aimed to establish the relevance of the carbon:nutrient balance hypothesis (CNB) to the browsing behaviour of red deer on Sitka spruce. The responses of Sitka spruce saplings to the four factorial combinations of neutral shade/no shade and high/low fertilizer application were examined. The effects of the resultant chemical and growth responses of the trees on feeding behaviour by red deer hinds were then experimentally tested.

As predicted by CNB, high soil nutrient levels increased a range of growth characteristics and total nitrogen concentrations of shoots whilst the levels of condensed tannins, and fibre components were reduced. These growth effects were depressed by the simultaneous application of shade. In contrast, there were no treatment effects on leaf monoterpene content. In 36 trials, hinds were offered 16 saplings deriving from combinations of two of the four treatments. All six combinations of pairs of treatments were tested on each of six hinds. Larger trees or those with more lateral branches were more likely to be browsed by deer, were browsed for longer and suffered greater offtake than smaller or less bushy trees. Contrary to expectation, addition of the shade and fertilizer treatments into the regression model did not explain any additional variation in the probability of attack, offtake from trees or time spent at trees. In a further experiment to test the effects of the volatile monoterpenes on feeding behaviour, greater tree size was again associated with higher probability of attack while chemical parameters had no effect. However, those trees with greater leaf monoterpene concentrations suffered less offtake by deer when browsed, suggesting that these compounds only affect feeding behaviour *after* the tree was attacked. The hinds' prior assessment of trees as a food patch appeared to be limited to morphological assessment.

Although several chemical constituents of Sitka spruce responded to shade and fertilizer according to the CNB predictions, no effect of these treatments on deer feeding behaviour was detected. In contrast, monoterpenes did not obey CNB predictions but had a negative effect on foraging behaviour. Whilst CNB may be able to predict some aspects of trees' secondary chemistry, these responses may not necessarily influence herbivores' browsing behaviour.

Keywords: Red deer; Sitka spruce; Carbon-nutrient balance; Foraging

1. Introduction

Several hypotheses attempt to explain plant secondary metabolites in terms of available environmen-

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tal resources including the carbon-nutrient balance hypothesis (CNB), the resource limitation (Coley et al., 1985) and the growth differentiation balance hypotheses (Herms and Mattson, 1992). The CNB was proposed initially to explain the defences of boreal plants against vertebrate herbivores (Bryant et al., 1983). It states that under conditions of nutrient limitation, typical of boreal systems, plant growth is restricted more than photosynthesis, resulting in excess fixed carbon which is used for production of carbon-based secondary metabolites (Bryant et al., 1983). Where plants such as temperate tree species contain high levels of secondary metabolites, they are considered along with nutrient content, to be determinants of food selection and offtake by herbivores (Bryant and Kuropat, 1980; Tahvanainen et al., 1991). The CNB hypothesis explicitly links environmental resources, secondary metabolites and defence against herbivory in evolutionary and ecological terms, e.g. 'We conclude that the carbon:nutrient balance of plants strongly affects their palatability and response to herbivores over evolutionary and physiological time scales.' (Bryant et al., 1983).

There have been several tests of the CNB predictions regarding allocation of resources to secondary metabolites in boreal plants (Larsson et al., 1986; Bryant et al., 1992; Iason and Hester, 1993). However, relatively few studies have related the effects of plant responses to environmental manipulations to feeding by a vertebrate herbivore (Bryant, 1987; Rousi et al., 1993; Hartley et al., 1995). In this study we review the results of several experiments (Duncan et al., 1995; Hartley et al., 1995; unpublished), which taken together, permit an appraisal of CNB and its relevance to the browsing on Sitka spruce by red deer. Specifically, we tested the chemical and growth responses of Sitka spruce (*Picea sitchensis*) saplings to manipulations of light and nutrients designed to alter the plants' carbon:nutrient ratio. We then summarize the results of feeding choice trials using these manipulated saplings, in which we identified those plant factors which were determinants of red deer (*Cervus elaphus*) feeding behaviour and tree damage.

An effective defence against herbivory would be one which minimized the probability of attack of the plant and/or consumption from the plant (Augner, 1994). We used these as the main criteria to investi-

gate the functional significance as defences and modifiers of feeding behaviour, of the Sitka spruce responses to our environmental manipulations.

2. Materials and methods

2.1. Sitka spruce responses to shade and fertilizer

In April 1990, one thousand 3-year-old Sitka spruce saplings (provenance QCI 711) were potted in seven parts *Sphagnum* peat and three parts composted bark, with 2 kg m⁻³ dolomitic lime, 350 g m⁻³ trace elements and 10% grit. They were potted in April 1990 and trees were allocated randomly to one of four treatments in factorial design of high fertilizer/low fertilizer and shade/no shade. The fertilizer treatments were either 1.1 or 6.6 kg m⁻³ of NPK fertilizer (Osmocote 18 month release) and the shade treatment consisted of green shade netting which reduced incident light by 30%, equally in all wavelengths (Lows, Dundee, UK). The resulting four treatments are labelled, control (F - S -), high fertilizer (F + S -), shaded (F - S +) and high fertilizer plus shade (F + S +).

In March 1991, 576 trees, 144 from each treatment were offered to red deer in feeding choice trials (see below). Immediately prior to the trials, the following morphological measurements (cm) were made on each tree: 1. Tree height (soil surface to leader-tip); 2. Leader length (from highest whorl to leader-tip); 3. Maximum span of laterals (widest diameter of tree); 4. Leader twig diameter (stem diameter at base of leader); 5. Leader maximum width (maximum width of leader from needle-tip to needle tip); 6. Top span (span of the top-most lateral branches); 7. Number of lateral branches; 8. Number of forks (number of bifurcations along all lateral branches on the tree).

In addition, 20 further trees were destructively harvested in March 1991 to provide samples for analyses of the effects of treatments on chemical composition. Ten lateral branches were sampled from each tree. Here we report the results of the analyses of lateral shoots for total nitrogen using a modified Berthelot reaction (Hinds and Lowe, 1980), acid detergent fibre (ADF) — a measure of structural carbohydrate and fibre (Van Soest, 1963) and condensed tannins compared with a purified Quebracho

standard (Waterman and Mole, 1994). Needles from lateral branches were analyzed for total monoterpenes by capillary gas chromatography following pentane extraction (see Duncan et al., 1995).

2.2. *Red deer feeding behaviour: Experiment 1 – The effect of shade and fertilizer treatments*

The aim of the first experiment was to ascertain the effects of the sapling responses to shade and fertilizer treatments on feeding behaviour by red deer.

The four treatments of the trees yielded six possible alternatives of pairs of treatments. In 36 choice trials conducted at the MLURI Glensaugh Research Station, six individual red deer hinds were offered the choice of trees from the six pairs of treatments. Trees were randomly selected from the pool and in each trial, 16 trees, eight from each of two treatments, were offered. Trials were conducted in a 7.5 × 7.5 m concrete-floored, outdoor arena to which all animals were accustomed and from which visual contact with other deer could be maintained. The 16 trees were assigned in a stratified random fashion to sites in a 4 × 4 array, in which the rows and columns were 1.5 m apart and contained equal numbers of trees from each treatment. The trees were presented intact in their pots which were anchored inside larger sand-filled pots to provide the necessary weight to permit normal foraging as on rooted trees.

During the trials in March 1991, the deer which were 17–20 years old and had complete dentition, were fed 1 kg day⁻¹ each of dried grass pellets and had access to grass pasture. All hinds had had prior access to a Sitka spruce plantation and this familiarity with the food type was reinforced by offering them cut branches for 3 weeks prior to and during the period of the trials.

Each trial lasted 10 min which avoided food depletion effects. Concealed observers counted bites from, and timed visits to, each individual tree. A visit was defined as the time from the first bite to leaving the tree. Detailed morphological measurements were made on each tree prior to the trials as described above. The trees were also weighed before and after each trial, and weight loss due to evapotranspiration was corrected for by weighing dummy trees not in the trials.

2.3. *Red deer feeding behaviour: Experiment 2 – The effect of monoterpene levels*

This experiment was conducted to determine any possible effects of monoterpenes on red deer feeding behaviour. Such effects were unlikely to have been detected in Expt. 1 due to the large variability between individual trees in leaf monoterpene concentrations. Detailed procedures are reported in Duncan et al. (1995), but are briefly summarised here. Sixteen trees were offered in three replicate trials to each of six individual red deer hinds in the same experimental format as Expt. 1, but trials lasted for 15 min. Trees were previously unbrowsed and had not been used in Expt. 1. One month before the trials which took place in March 1992, two lateral branches were removed from each tree for chemical analysis. This permitted wound healing prior to the actual choice trials and measurement of monoterpenes at the level of the individual tree offered to red deer. In a sample of 20 non-trial trees, a further sample of branches was taken at the time of the trials to verify that there was no effect of this sampling procedure on monoterpene concentrations and that those one month before, were equivalent to those during the trials (Duncan et al., 1995). Trees were weighed before and after each trial and deer behavioural measurements were made as in Expt. 1, as were the tree morphological measurements with the exception of number of forks and top span of laterals (8 and 6 above).

2.4. *The relationship between chemical and morphological variables*

A further sample of 38 trees (10 trees from the F – S –, F – S +, F + S + and 8 from the F + S – treatment) which had been subject to the treatments for 2 years were measured prior to harvesting in March 1992 as previously described but with the omission of morphological variables 'top span' and 'number of forks'. The lateral branches were analysed for the chemical constituents as before, including monoterpenes in the needles.

2.5. *Statistical analyses*

The effects of shade and fertilizer treatments on morphological and chemical measurements were analyzed by a factorial analysis of variance.

In Expts. 1 and 2, the response variables biomass removed (normalized by $\log 1 + x$), and time spent at each tree were analyzed by a forward stepwise multiple regression approach which includes explanatory variables sequentially, choosing at each step, the one which minimized the residual sum of squares. Tree morphological variables were entered as continuous explanatory variables along with the categorical variables shade and fertilizer treatments, which represent variation additional to morphological variation. Individual deer, and row and column position in the experimental array were also entered as categorical variables. Row, column and any interactions between these and individual deer are represented in the results by 'spatial preference' of the deer for certain positions in the arena. In both experiments, whether or not a tree was attacked was compared with a calculated probability of attack using a binomial regression in which the standard logit link function was used to convert the sum of factors into a probability. Terms were entered by a forward stepwise regression approach as before, with terms

being selected on the basis of reduction in residual mean deviance. In Expt. 2, total monoterpene concentration was entered as an additional continuous variable. The extent to which variation in chemical parameters could be explained by morphological variables was similarly investigated using stepwise multiple regression.

3. Results

3.1. The effects of shading and fertilizer on sapling morphology and chemical composition

The results of the effects of treatments on the principal morphological and chemical composition is given in Fig. 1. The effect of the high fertilizer level was a strong increase in the growth and linear dimensions of the trees ($P < 0.001$), an effect which was lessened by the presence of shade (shade \times fertilizer interaction — Fig. 1). Shade resulted in significantly taller trees ($P < 0.05$) due to etiolation, but did not affect other linear measurements. Shade

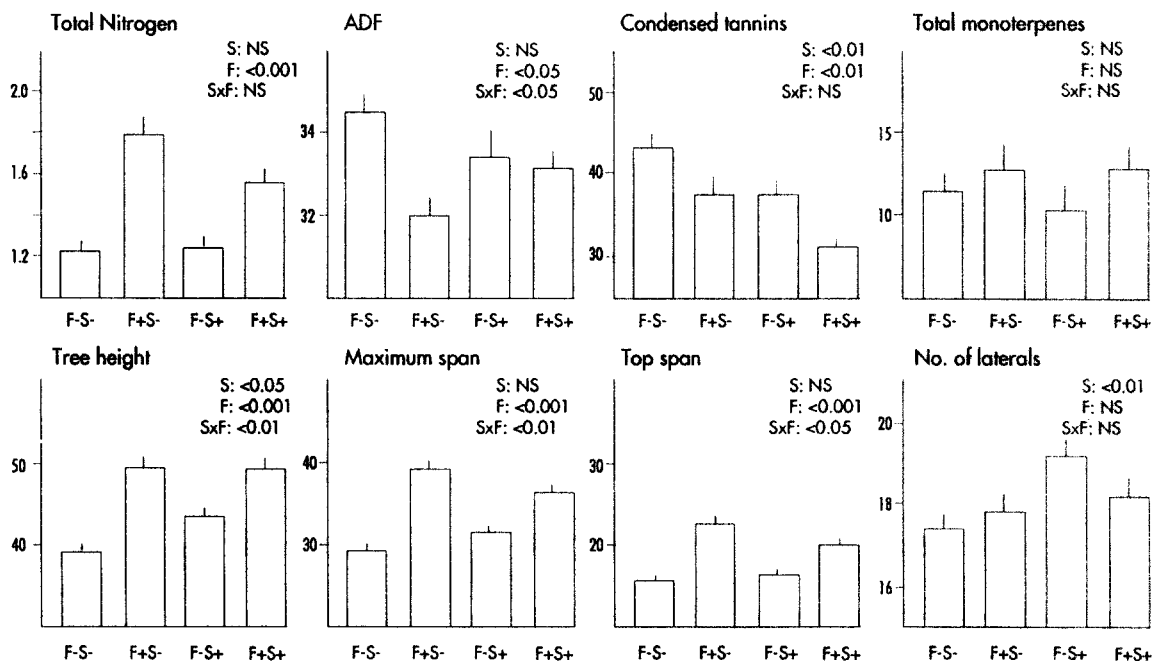


Fig. 1. The effect of fertilizer and shade treatments on total nitrogen, acid detergent fibre (ADF), condensed tannins and total leaf monoterpenes (all %DM) in lateral branches of 20 trees from each treatment; and tree height, maximum span, top span (all in cm) and number of lateral branches of 144 trees from each treatment. Means + SE are presented.

Table 1

Results of forward stepwise multiple regression for three response variables in Experiment 1. Probability of attack was analysed as the binomial logit link function and biomass removed was log transformed (see text). Units of explanatory variables are in centimetres, or whole numbers as appropriate

Response variable	Explanatory variables	Estimate	SE	$F_{(df)}$ ^a	Probability	Cumulative ^a r^2
Probability of attack	Constant	-1.184	0.836	–	–	–
	Deer	–	–	2.31 _{5,528}	< 0.05	
	Spatial preference	–	–	2.88 _{36,528}	< 0.001	
	No. forks	0.0528	0.0258	8.03 _{1,528}	< 0.01	
	No. laterals	0.0415	0.0243	2.94 _{1,528}	< 0.01	
Biomass removed (g)	Constant	1.741	0.150	–	–	–
	Deer	–	–	27.73 _{5,310}	< 0.001	26.5
	Max. span	0.0191	0.0044	47.01 _{1,310}	< 0.001	35.9
	Top span	0.0100	0.0045	4.90 _{1,310}	< 0.05	36.7
Time spent at each tree (s)	Constant	19.72	7.28	–	–	–
	Deer	–	–	11.18 _{5,313}	< 0.001	12.7
	Max. span	0.277	0.239	19.23 _{1,313}	< 0.001	17.4
	No. forks	1.002	0.405	4.37 _{1,313}	< 0.01	18.2
	Top span	0.493	0.225	4.80 _{1,313}	< 0.05	19.2

^a F values given for probability of attack are the deviance ratios, whose probability can be estimated but r^2 cannot.

stimulated growth of more lateral branches, whereas fertilizer had no effect.

Associated with the stimulation of growth under the high fertilizer level was a significant increase in total nitrogen ($P < 0.001$) and a reduction in ADF

concentrations ($P < 0.05$). Concentrations of condensed tannins were reduced by both fertilizer application and by shading ($P < 0.01$), whilst levels of total monoterpenes were not affected by any of the treatments (Fig. 1).

Table 2

Results of forward stepwise multiple regression for three response variables in Experiment 2. Probability of attack was analysed as the binomial logit link function and biomass removed was log transformed (see text). Units of explanatory variables are in centimetres, or whole numbers and % DM for monoterpenes

Response variable	Explanatory variables	Estimate	SE	$F_{(df)}$ ^a	Probability	Cumulative ^a r^2
Probability of attack	Constant	-0.291	0.921	–	–	–
	Spatial preference	–	–	3.54 _{1,98}	< 0.01	
Biomass removed (g)	Constant	1.086	0.570	–	–	–
	No. laterals	0.250	0.166	7.51 _{1,98}	< 0.01	5.0
	Deer	–	–	2.30 _{5,98}	< 0.1	9.7
	Monoterpenes	-0.473	0.167	4.95 _{1,98}	< 0.05	13.0
	Max. span	0.0245	0.0099	6.13 _{1,98}	< 0.05	17.2
Time spent at each tree (s)	Constant	-169.0	68.1	–	–	–
	Deer	–	–	8.20 _{5,90}	< 0.001	22.0
	No. laterals	4.64	2.03	13.88 _{1,90}	< 0.001	30.5
	Monoterpenes	-63.5	19.8	6.97 _{1,90}	< 0.01	34.4
	Max. span	2.97	1.19	6.18 _{1,90}	< 0.05	38.0

^a F values given for probability of attack are the deviance ratios, whose probability can be estimated but r^2 cannot.

Table 3

The results of forward stepwise multiple regression relating chemical measurements to tree morphological measurements in 38 trees harvested in March 1992. Units of explanatory variables are in cm or whole numbers as appropriate

Response variable (% DM)	Explanatory variable	Constant	Regression coefficient	SE	$F_{(df)}$	Probability	r^2 (%)
Total nitrogen	Leader twig diameter	0.053	+1.617	0.258	39.40 _{1,36}	< 0.001	50.9
ADF	Leader max width	36.72	-0.938	0.390	5.80 _{1,29}	< 0.05	13.8
Condensed tannin	No. laterals	25.88	-0.139	0.067	3.96 _{1,36}	NS	7.4
Total monoterpenes	Leader length	2.88	+0.230	0.071	10.67 _{1,36}	< 0.01	20.7

3.2. The effects of shade and fertilizer treatments on red deer browsing

In almost all the response variables analyzed, particularly in Expt. 1, there was a significant effect of individual deer. Such effects are usual in studies of vertebrate behaviour but their inclusion in the linear regression analyses permits evaluation of treatment effects over and above this variation. The probability of attack of trees was related mainly to individual deer and their spatial preferences, in both Expts. 1 and 2, but number of forks and number of laterals had a significant effect in Expt. 1 (Table 1). Neither shade nor fertilizer treatment (Expt. 1), nor total monoterpene level (Expt. 2) explained a significant proportion of variation in the regression model.

In Expt. 1 the biomass removed from trees which were attacked was positively related to the initial size of the tree (maximum span of laterals). This was confirmed in Expt. 2, in which larger numbers of lateral branches also resulted in greater biomass removed. Although there were no shade or fertilizer treatment effects in addition to the morphological characteristics determining biomass removed in Expt. 1, in Expt. 2 trees with higher monoterpene levels had significantly less biomass removed (Table 2). Broadly similar results were obtained for the analysis of time spent at each tree, with higher levels of monoterpenes leading to a reduction of browsing time (Table 2). Deer generally spent longer browsing at larger trees and again there was no effect of shade and fertilizer treatments over and above this morphological effect.

3.3. The relationship between Sitka spruce chemical and morphological variables

The extent to which morphological measurements could be used to predict the chemical composition of

the 38 trees in which both were measured was very variable. It ranged from no significant relationship to 50.9% of the variation explained by a single morphological variable for condensed tannins and total nitrogen respectively (Table 3). The six morphological variables measured were highly correlated (Mean $r = 0.662$, range 0.390–0.897, all $n = 38$, $P < 0.05$). Hence in no case did the addition of more than a single morphological variable explain significantly more variation in a chemical parameter (Table 3).

4. Discussion

4.1. Sitka spruce sapling responses to shade and fertilizer

The high fertilizer treatment caused significant stimulation of growth in Sitka spruce saplings, associated with which were higher levels of total nitrogen and lower ADF concentration, all as predicted by the CNB hypothesis. The hypothesis also predicts that when the saplings' carbon:nutrient balance is decreased, both by high fertilizer treatment, and by application of shading, then the levels of carbon-based secondary metabolites should also decrease (Bryant et al., 1983). This prediction was borne out by the condensed tannins but not by total monoterpene levels, conforming to a general pattern identified by Bryant et al. (1992). It was suggested that the CNB predictions apply best to end product carbon-based secondary metabolites such as condensed tannins and not to rapidly turned over or intermediate compounds such as terpenes. However, this explanation for the different responses of tannins and terpenes is questioned by the suggestion that monoterpenes are in fact not rapidly turned over in plants (Gershenson, 1994). High variability between individual trees in monoterpene levels (Merk et al.,

1988) means that very large sample sizes, or clonal material, may be required to critically test the responses of monoterpenes to environmental manipulations.

4.2. *The effects of environmental manipulations of Sitka spruce saplings on herbivory by red deer*

In both experiments, the probability that a tree would be attacked was related mainly to spatial preferences of the deer for certain sites in the experimental array. Although the fertilizer and shade treatments altered morphology and chemistry of the trees, neither these variables in Expt. 1, nor total leaf monoterpenes in Expt. 2, significantly affected the probability of attack. In Expt. 1 there was a slight positive effect of the number of forks and the number of lateral branches of the tree on probability of attack.

The biomass removed from trees was positively related to aspects of tree size. Over and above this effect, again no further variation was attributable to fertilizer and shade treatments in Expt.1. This indicates that those variables such as total nitrogen and condensed tannins which were strongly influenced by these treatments, as predicted by CNB, had no effect on the biomass removed. These results are consistent with Danell et al. (1991a) who found that moose feeding behaviour was based on morphological rather than chemical characteristics of pine. In contrast in Expt. 2, there was a slight but significant negative effect of total monoterpenes on biomass removed from each tree. Further analysis of the deer behaviour showed that they spend less time at, and take fewer bites from those trees with higher monoterpene concentrations (Duncan et al., 1995).

Although monoterpenes are volatile and might be expected to influence food selection, they reside in resin canals in the stem and leaf of the trees, and their release would be accelerated *after* attack by a large mammalian herbivore. This may explain their failure to affect the probability of attack of a tree by red deer whilst still, albeit slightly, limiting the herbivore damage following attack. The distribution of defences between different plant tissues has strong implications for their perception by herbivores (McKey, 1979). We suggest that detailed analysis of the feeding behavioural responses to different anatomi-

cal distributions of secondary metabolites, may explain the apparent contradictory reports on their effects, including those of terpenes (Löyttyniemi, 1985; Elliott and Loudon, 1987). It is relevant to consider the extent to which a tree's morphology could be used by deer as a cue which reflects its chemical composition. The close association between the size variables meant that morphological variation was adequately represented by a single variable. Tree size was positively associated with its concentration of both total nitrogen and monoterpenes. Hence selection of larger trees by deer may have simultaneously led to high intakes of total nitrogen, but could not have resulted in ingestion of lower levels of monoterpenes. Although in the sample of trees analyzed here (Table 3), there was no significant decrease in condensed tannins with increasing tree size, the effect of fertilizer addition often results in stimulation of growth and reduction of condensed tannins and total phenolics (Bryant et al., 1992). It is thus possible that selection of larger trees also minimizes intake of a phenolic not specifically measured by us.

Predictions of optimal patch use by vertebrate herbivores including browsers (Åstrom et al., 1990; Lundberg and Danell, 1990), are often based on application of the marginal value theorem, which assumes that animals leave their foraging patch when its profitability drops below that of the environment as a whole (Charnov, 1976). Previous studies suggest that food selection by browsing cervids within a forest stand may be at the level of the individual tree, which thus equates to a foraging patch (Danell et al., 1991b). However, because deer respond negatively to monoterpene levels *after* attacking a tree, we conclude that their ability to assess the chemical quality of individual trees, and hence also the environment as a whole, is poor. Thus the predictions of the marginal value theorem are unlikely to be met with precision. Recent advances in foraging behaviour suggest that the rate of intake is asymptotically related to bite size in herbivores (Spalinger and Hobbs, 1992), and an examination of the effects of the environmental manipulation treatments of the saplings on these foraging parameters will be presented elsewhere (Hartley et al. unpublished).

Secondary metabolites in boreal trees may have evolved as defenses against mammalian herbivores (Bryant et al., 1989), but this study illustrates the

difficulty in ascribing a general anti-herbivore function to them. The failure of the CNB hypothesis to link environmental resources, Sitka spruce chemistry and red deer feeding behaviour, is somewhat surprising since both the deer and the tree species are native in North America and share some coevolutionary history. Furthermore, the red deer is primarily a forest grazer, which browses on woody plants when the circumstances require, notably when preferred food sources are scarce (Mitchell et al., 1977). The red deer would hence be expected to lack specific physiological adaptations to plant secondary metabolites (McArthur et al., 1991) and be behaviourally sensitive to them.

5. Conclusion

The CNB cannot adequately explain the feeding behaviour of red deer on Sitka spruce. Despite the overall responses of the trees to the environmental manipulations being in many respects in accordance with CNB, including growth and the total nitrogen, ADF and condensed tannin concentrations, the treatments had no significant influence on probability of attack or tree damage, over and above the effects of tree size. There was however, a small but significant effect of monoterpenes on deer feeding behaviour, a chemical measurement which did not obey the predictions of CNB in response to shade and fertilizer.

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