Foliage phenols and nitrogen in relation to growth, insect damage, and ability to recover after defoliation, in the mountain birch *Betula pubescens* ssp *tortuosa*

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Abstract. We studied growth of the mountain birch, and the role of foliage phenols, nitrogen, and variance in the timing of bud burst, as potential defensive characters, in Finnish Lapland in 1975–1979. Annual and local variation both in phenol and nitrogen concentration of foliage were significant. Individual trees retained their position in the foliage and nitrogen distribution of the population in successive years, as well as in the order of leaf flush in spring. Growth of twigs, mature leaf size, and ability of trees to recover in the year following artificial defoliation correlated positively with the sum of degree days in the previous growing season. Foliage nitrogen correlated negatively with foliage phenols in within-site comparisons. Twig growth correlated negatively with foliage phenols, particularly in growing seasons following cool summers, but did not correlate with foliage nitrogen. Birches flushing early did not grow more than birches flushing late. Between-site differences in foliage phenol content were mainly determined by abiotic conditions, like temperature and nutrient availability. In a between-site comparison insect chewing marks in leaves correlated positively with foliage phenols as well as with nitrogen; intensity of invertebrate predation presumably explained variable herbivory between the sites. In a within-site comparison trees with the highest foliage phenol content had few herbivores only at the site with the highest average phenol level.

Introduction

High concentrations of noxious compounds, like phenols and resins, and low concentrations of positive nutritional factors like nutrients may protect plants from grazing and act as potential defences against herbivores (e.g. Feeny 1976, Rhoades and Cates 1976, but see Moran and Hamilton 1980 and Neuvonen and Haukioja 1984). Nitrogen and phosphorus are commonly considered to be important nutrients to herbivores. Among harmful compounds tannins and phenols, claimed to function as quantitative defences, are frequently used as general indicators of the level of plant defence. When importance of plant chemistry to herbivores is studied the basic problem with concentrations of nutrients and all defensive compounds is that the role of herbivory in moulding their concentrations is seldom, if ever, known. Nutrients are equally important for plants

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and animals alike. Secondary compounds in plants, besides being defensive compounds, may also be by-products of metabolic pathways or be produced because environmental conditions other than herbivores regulate their synthesis (e.g. Mattson 1980; Bryant et al. 1983). In addition, although phenolic substances have been shown to be harmful to certain herbivores (e.g. Lincoln et al. 1982), some phenolic compounds may also be beneficial (Bernays 1981). Consequently, relevance of phenols etc as general indices of plant's defensive commitments may be doubtful.

We have previously reported seasonal trends in certain, potentially defensive foliage characteristics in the subarctic mountain birch, *Betula pubescens* ssp *tortuosa*, and the results were generally similar to those characterizing temperate zone trees: nitrogen and water content of foliage decreased in the course of the season, while phenolic content rose. In addition, there were differences in these parameters between local birch populations (Haukioja et al. 1978). We have also shown a negative correlation between leaf phenolic content and performance of some early season (Haukioja et al. 1981, Haukioja et al. MS) and late season (Haukioja et al. 1978) herbivorous insects.

Our aim in this paper is to report chemical and ecological properties of the mountain birch which might have at least potential defensive functions. Especially we concentrate on annual and local variation in these measures, and on processes behind the variance. We feel that such data is urgently needed in attempts to try to find out to what extent variance in those parameters relates to herbivore pressure and to what extent to other characteristics of the sites. We report correlations between certain widely used defensive indices (nitrogen and phenol content of foliage, within population variance in bud break of birches) and also correlations between them and certain environmental characteristics, including herbivory. Because defensive commitments and other demands are claimed to compete for resources in the plant (e.g. Feeny 1976), we also studied how growth of the mountain birch correlated with the above indices.

Study area, materials and methods

The study was conducted at the Kevo Subarctic Research Station (69°45′N, 27°E) in northern Finland, in 1975–1979. Three study sites situated on the mountain Jesnalvaara (one at the lower part of the mountain, of which an abbreviation FJ, foot of Jesnalvaara, is used in tables and figures in

Table 1. Height (m) of birches at Jesnalvaara study sites. Data are mean and SD ($n=40$)

Site	Altitude (m a.s.l.)	Height	
TJ	330	1.3	0.51
MJ	240	2.8	1.01
MJud	210	4.8	0.89
FJ	80	5.2	1.20
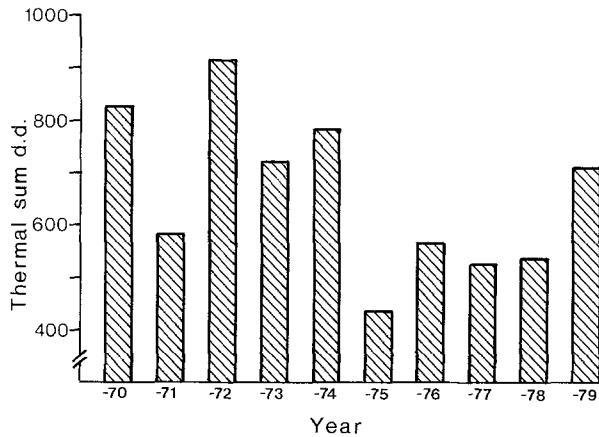
Fig. 1. Cumulative degree days (base + 5° C) at Kevo in 1970–1979

accordance with Haukioja et al. (1978), one at the middle slope of the mountain, MJ, and one at the summit of the mountain, TJ, top of Jesnalvaara). The birch forest on the slope of the mountain is characterized by tree-like birches up to the middle slope and by a scattered birch shrubbery up to the altitudinal tree line at the summit. In 1977–1979 another study site at the middle slope was used, belonging to a zone where birches were not damaged by the geometrid *Epirrita autumnata* during a massive outbreak in the mid-sixties (Kallio and Lehtonen 1973). The abbreviation MJud was assigned to the new site to indicate the undamaged state of that forest. Table 1 gives some characteristics of the sites.

Foliage was sampled for chemical analysis each year on 15 August. At that time the concentration of measured compounds in foliage changes slowly (Haukioja et al. 1978). Besides, the study sites are phenologically in comparable state in mid-August: growth of leaves has terminated but autumnal colour changes have not yet begun (Haukioja and Iso-Iivari 1976, P. Kallio, personal communication). In most cases the same, individually marked birches were used for foliage sampling each year. Foliage wounding is known to induce chemical, potentially defensive changes

in birch leaves (Niemelä et al. 1979) but foliage sampling was done in August when attempts to demonstrate inducible responses in the mountain birch foliage have failed (Haukioja & Niemelä 1979). Besides whole leaves were removed which may not have similar effects as leaf tearing (Mattson, personal communication, Valentine et al. 1983).

Nitrogen content of foliage was measured by the Kjeldahl method and total phenolics by the Folin-Dennis method (Niemelä et al. 1979). All values are expressed on a dry weight basis.

An index of the escape in time (sensu Feeny 1976) of birch foliage was obtained by measuring the scatter in bud break within the birch population at each site. Bud burst was interpreted to have taken place when tips of the leaves in bud were open enough to allow larvae to enter and start feeding.

Artificial defoliations were performed in July, at the period when natural consumption by *Epirrita* larvae is also highest. About 50% of foliage biomass was removed by tearing the distal part of all leaves. Natural densities of *Epirrita* larvae were very low during the whole study period.

An index of the annual growth of trees (below 4 m in height) was obtained by measuring annual length increments of 25 twigs per tree. Measurements were distributed around the tree, at breast height where possible.

A treatment to manipulate nutrient availability of trees was performed at the low altitude site in July 1975. Five trees were randomly assigned to each of the following treatments: unmanipulated controls, trees fertilized by an NPK fertilizer (27.5% N, 7% P, 17% K), and trees from which about 1/3 of the larger roots were cut. The latter was assumed to hinder nutrient uptake while fertilized trees had a better access. Growth of twigs (1976–1977) was measured later. Phenolic and nitrogen determinations of the same trees were given by Tuomi et al. (1984).

Birches were monitored for insect densities by the knocking method; by beating the trunk with a heavy wooden hammer, and by collecting dropping insects from a large plastic sheet beneath the three.

Weather data and thermal sums (base + 5° C) (Fig. 1) were obtained from the Kevo meteorological station situated ca. 1 km from the lower site at Jesnalvaara, at the same altitude. Temperature sums of the previous growth season sum values over the whole growth season; temperature sums of the current growth season are thermal sums accumulated up to mid August when leaves were sampled. Temperatures for the higher sites were interpolated by applying conversion factors in Kärenlampi (1972); he monitored microclimates at the same sites which we used: his *Oporinia* (= *Epirrita*) birch forest equals our middle site (MJ), and his low alpine heath is the same as the summit site that we used.

Table 2. Annual growth (mm) of twigs in birches at Jesnalvaara

Site	1976			1977			1978			1979		
	x	s.d.	n	x	s.d.	n	x	s.d.	n	x	s.d.	n
TJ	18.6	10.21	9	43.5	15.46	11	31.8	6.94	10	30.0	10.64	6
MJ	23.1	7.90	8	42.7	12.96	9	40.8	9.82	9	27.7	7.66	6
FJ	38.5	8.96	6	43.6	15.71	8	58.9	21.76	7	37.0	14.85	8

Differences among sites and years were significant (two-way ANOVA, $F=9.76$, $p<0.001$, and $F=10.83$, $p<0.0001$, respectively)
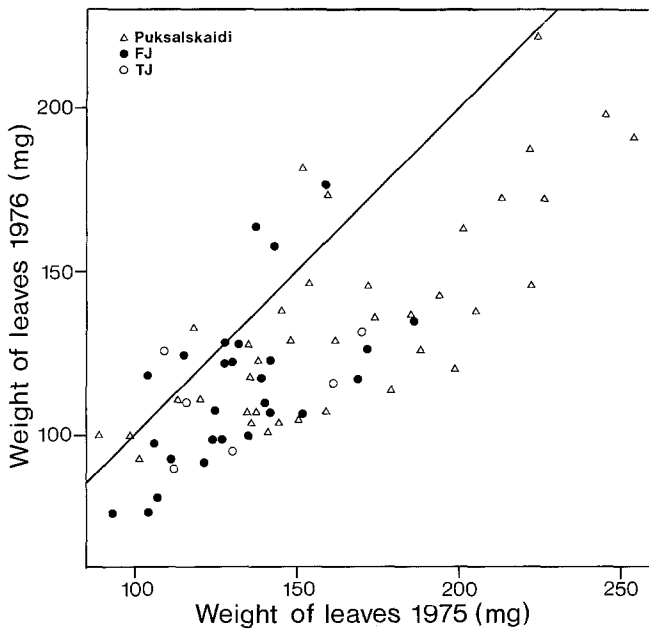
Fig. 2. Mean fresh weight of leaves in individual mountain birches at Jesnalvaara in August 1975 and 1976. Values differed between years (paired t-test, $t = 5.95$, $p < 0.001$). The line indicates identical values between years

Table 3. Survival of main trunks of mountain birches to the next growth season after artificial defoliation in the previous July

Site	Year of observation								
	1976			1977			1978		
	sur-vived	died	n	sur-vived	died	n	sur-vived	died	n
MJ	17	1	18	15	0	15	15	0	15
FJ	11	9	20	16	0	16	15	0	15

There was significant difference (Fisher's exact probability test, $p < 0.01$) between sites in 1976, and, at FJ, between the years 1976 and 1977, and 1976 and 1978

Results

Annual variation in resource state and growth of birches

In subarctic regions the thermal sum of the previous summer has been claimed to be important for tree growth (Sarvas 1970). We evaluated Sarvas' hypothesis by three tests, all of which corroborated it.

First, mean growth of birch twigs (Table 2) correlated positively with the temperature sum of the previous growth season (correlation between annual site means: $r = 0.763$, $p < 0.01$) but did not correlate ($r = -0.112$) with the temperature sum of the current summer. Secondly, leaves were smaller in 1976 (a warmer year after an exceptionally cold season, see Fig. 1) than in 1975 (Fig. 2). Thirdly, trees recovered successfully in 1977 and 1978 from artificial defoliations performed in the previous year, but not in 1976, i.e. after an exceptionally cold summer (Table 3).

Annual and local variation in potential defensive traits

There was significant variation both among years and among sites in foliage nitrogen and phenolics (Table 4). Nitrogen concentration of leaves in mid-August showed non-significant negative correlation (-0.49) with the temperature sum of the current year. In other words, nitrogen concentration of mid-August foliage was low in summers when the growth season was well advanced and leaves were relatively mature, and presumably had high content of structural carbohydrates. Correlation with nitrogen and the temperature sum of the previous year was -0.09. As regards foliage phenols, there was non-significant negative correlation with both the temperature sum of the previous (-0.42) and the current summer (-0.21) when all sites were pooled. This primarily reflects decrease in temperature with altitude, and high phenolic content of leaves at the upper slope of Jesnalvaara (Table 4).

Although there were significant annual differences in the phenolic and nitrogen content of foliage, the relative position of an individual tree within the tree population remained fairly constant in successive years (Fig. 3). Whether site-specific or genetic differences, or both, were involved is not known.

Variance in the bud break within a birch population may prevent *Epirrita* larvae from finding a host tree in
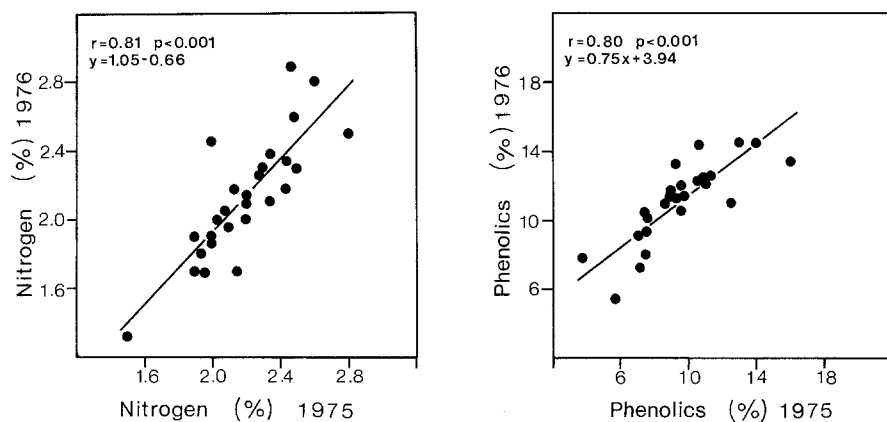
Table 4. Phenol and nitrogen content (per cent dry weight) of birch foliage at Jesnalvaara in mid-August

	1975			1976			1977			1978			1979		
	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n
Phenols															
TJ	9.7[a]	2.09	9	11.3[a]	2.52	10	9.8[a]	1.35	10	12.1[a]	0.99	6	11.0[a]	1.46	11
MJ	11.3[a]	2.20	9	12.1[a]	1.44	10	11.1[b]	1.65	10	11.7[a]	1.36	9	10.6[a]	1.78	10
FJ	7.5[b]	1.65	7	9.6[a]	2.28	7	8.9[a]	1.63	7	8.9[b]	0.95	6	8.2[b]	1.43	7
Nitrogen															
TJ	2.36[a]	0.23	10	2.23[a]	0.30	10	2.37[a]	0.36	10	2.03[a]	0.31	6	1.95[a]	0.27	11
MJ	2.11[a]	0.17	10	2.09[a]	0.21	10	2.01[b]	0.31	8	1.80[a]	0.29	8	1.77[a]	0.28	9
FJ	2.10[a]	0.36	7	2.09[a]	0.56	7	1.77[c]	0.32	7	2.08[a]	0.31	6	1.70[a]	0.31	7

Both phenolic and nitrogen contents differed significantly among years (ANOVA, $F = 2.82$, $p < 0.05$, and $F = 7.36$, $p < 0.0001$, respectively), and among sites (ANOVA, $F = 20.65$, $p < 0.001$, and $F = 8.30$, respectively). Different letters indicate different means among sites ($p < 0.05$, Student-Newman-Keuls test)

Fig. 3. Nitrogen and phenolic content of foliage in individual birches at Jesnalvaara in 1975 and 1976. The line represents the regression between values in the two years
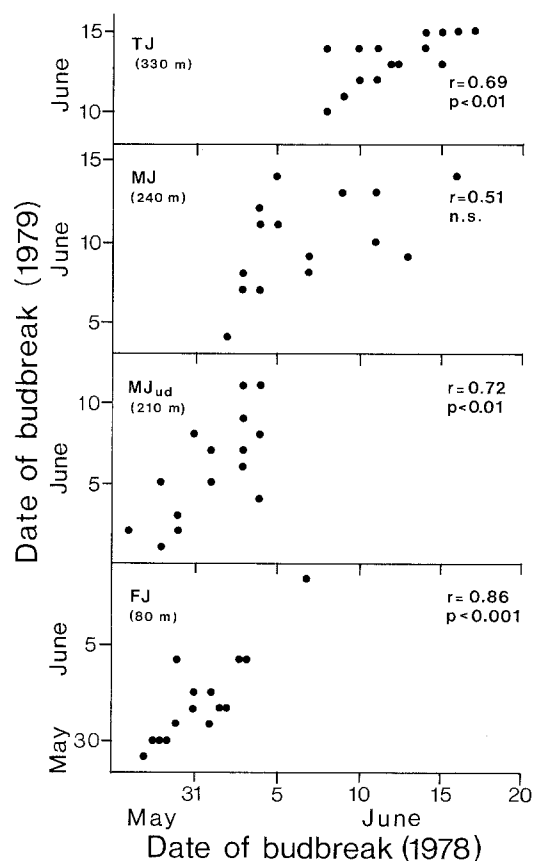

Fig. 4. Budbreak in individual birches at Jesnalvaara in 1975 and 1976

Fig. 5. Phenolic and nitrogen content of foliage in individual birches at Jesnalvaara

a suitable phase: larvae hatching too early may suffer because leaves have not yet flushed (e.g. Varley et al. 1973). Individuals hatching too late may suffer from reduced growth due to seasonal deterioration in foliage quality (e.g. Feeny 1970). Intrapopulation variance in the date of bud break was considerable, although the same trees tended to flush early and the same ones late in successive years (Fig. 4). Again, we do not know the role of site-specific and genetic factors behind this pattern.

Correlation between the nitrogen and phenolic content

At each site there was a significant negative correlation between foliage nitrogen and phenolics in individual trees (Fig. 5).
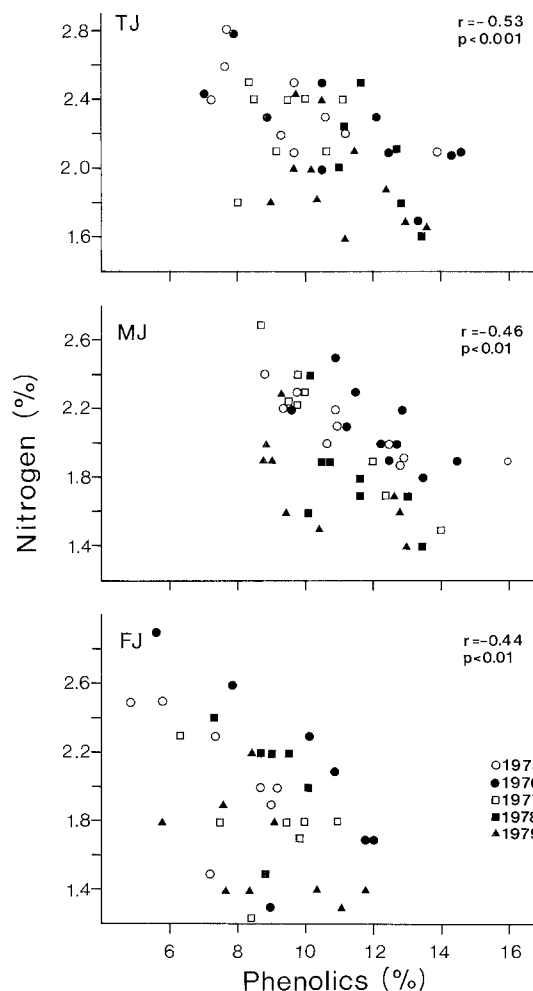
Correlation between growth of twigs and potential indices of foliage defence

Because growth of a tree cannot be meaningfully described by growth of leaves, we studied correlations between twig growth and foliage chemistry. There was a negative correlation between twig growth and the phenolic content of foliage when data from all sites were pooled ($r = -0.302$, $p < 0.01$). This, again, reflects the slow growth of birches at

Table 5. Correlation coefficients between birch growth and phenolic and nitrogen, respectively, content of foliage. n = number of trees. None of the values is significantly different from zero

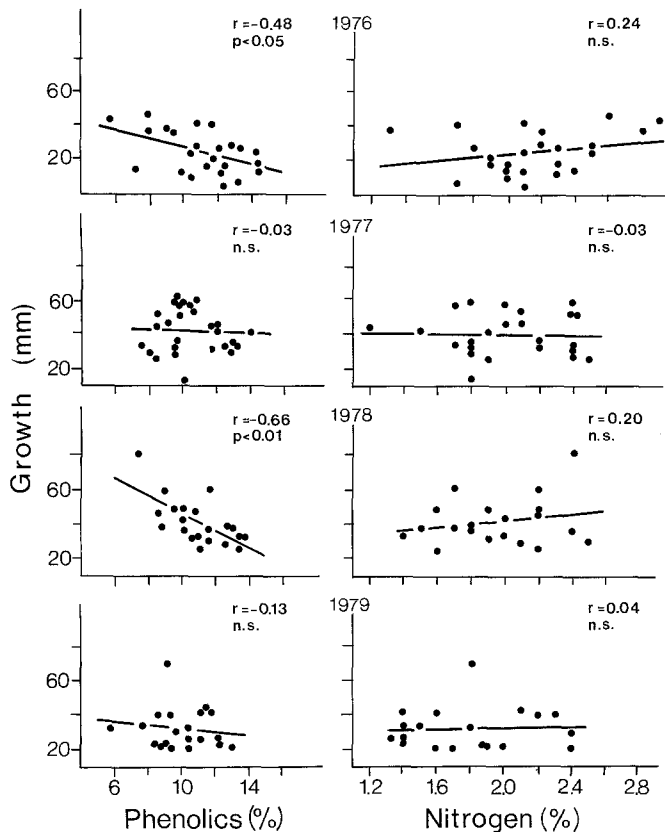| Site	1976	n	1977	n	1978	n	1979	n
Phenolic content vs. growth								
FJ	−0.54	6	−0.04	6	−0.75	6	−0.05	6
MJ	−0.50	8	−0.43	7	−0.70	7	−0.03	4
TJ	−0.82	5	−0.78	4	0.00	6	−0.23	6
Nitrogen content vs. growth								
FJ	0.54	6	−0.22	6	0.73	6	0.51	6
MJ	0.05	8	0.21	7	−0.16	7	0.36	7
TJ	0.83	5	0.81	4	−0.10	6	−0.21	6

Fig. 6. Foliage phenols and nitrogen in relation to mean growth of twigs in individual birches at Jesnalvaara

Fig. 7. Relation between budbreak and growth of twigs (solid dots 1976, open dots 1977) in individual birches at Jesnalvaara

higher elevations where foliage phenols also were high. However, the correlation coefficients were negative (or 0) when the sites were treated separately (Table 5). Twig growth did not correlate with foliage nitrogen (r = 0.009). When the data pooled over sites were treated year by year, the negative correlation between twig growth and foliage phenols was significant in the two years following the coldest summers (Fig. 6). Correlation between growth of twigs and foliage nitrogen was significant in none of the years (Fig. 6).

Early flushing trees did not grow more than late flushing ones although they had potentially longer growth season (Fig. 7).
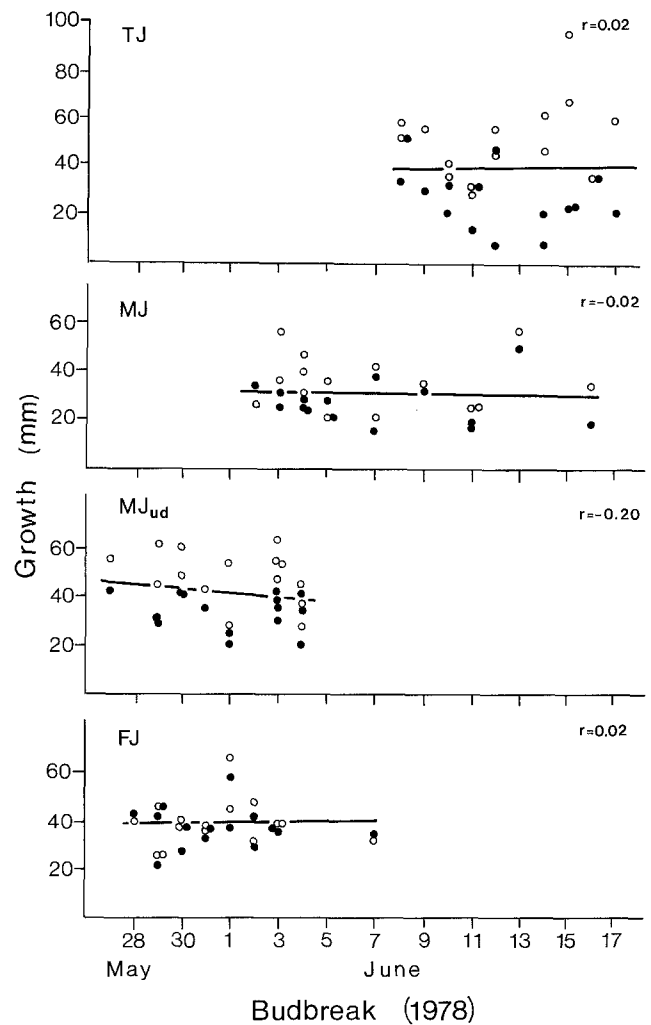
Dependence of twig growth on nutrient availability

In the year after the treatment, growth was high in all fertilization treatments, and was slightly lower than controls in trees whose roots were damaged (Table 6). In the ensuing year only trees with the highest levels of fertilization maintained high growth. Fertilized mountain birches had lower levels of foliage phenols than control trees, while trees from which part of their root system was mechanically damaged to disturb nutrient uptake, had higher pholiage phenols. Nitrogen levels did not vary significantly with fertilization (Tuomi et al. 1984). The reason why fertilizing did not increase foliage nitrogen may be that due to better growth, a larger amount of nitrogen was diluted over a larger biomass.

Does foliage chemistry correlate with insect damage?

We tested one of the basic assumptions of the general plant defence theory (Feeny 1975, 1976, Rhoades and Cates 1976), ability of foliage phenols to precipitate proteins. This is a relevant test in the mountain birch because its phenolic compounds are responsible for the ability of leaf extracts to inhibit a digestive enzyme (bovine trypsin, Niemelä et al.

Table 6. Growth of twigs (mm) in 1976 and 1977 in birches at the lower site (FJ) in relation to treatment of trees in July 1975 (control, fertilization by an NPK fertilizer cutting 1/3 of roots). Standard deviations in parentheses, number of trees was five in each treatment

Treatment	Growth	
	1976	1977
Control	32.3 (6.83)	44.3 (11.74)
Fertilization		
1 dl/tree	40.0 (14.61)	37.7 (17.81)
3 dl/tree	46.9 (17.08)	51.8 (18.40)
6 dl/tree	51.4 (9.16)	54.1 (7.82)
Root damage	28.5 (5.16)	41.2 (13.63)

Growth was different between years ($F = 27.5$, $p < 0.001$) and treatments ($F = 50.3$, $p < 0.001$), and they had a significant ($F = 138.6$, $p < 0.001$) interaction
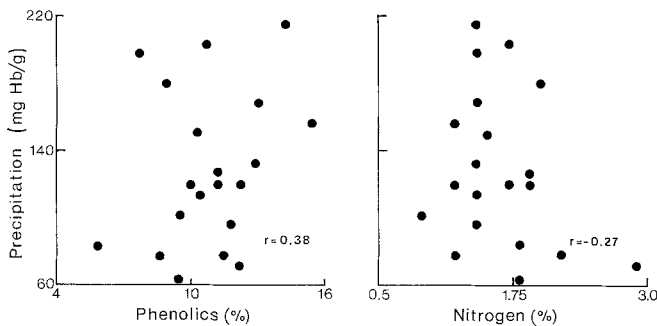

Fig. 8. Relation between the ability of leaf extracts to precipitate hemoglobin and foliage phenolics and nitrogen

1979). Phenol content of foliage did not correlate with the ability of leaf extracts to precipitate hemoglobin (Fig. 8 A). Neither was there any correlation between protein precipitation and foliage nitrogen content (Fig. 8 B).

We tried to determine the correlation between foliage chemistry and herbivore damage incurred by birches at Jesnalvaara from data showing indices of invertebrate herbivory (Table 7). Herbivore damage and foliage phenols correlated positively in a between-site comparison (see Table 4). Due to the strong negative correlation between nitrogen and phenolics, nitrogen, too, correlated positively with the degree of damage. Consequently, other site-specific factors than total leaf phenols seemed to determine the extent of foliage damage in between-site comparisons. Invertebrate predators, especially ants (Laine and Niemelä 1980), seem probable candidates (Table 7). Note that most herbivores at the two lower sites belonged to aphids which live in mutualistic relation with ants.

Although Table 7 shows the distribution of foliage damage in 1978 alone, it can be regarded as characteristic for the whole study period. Similar data for 1977 is given in Oksanen et al. (1981). It is worth noting that most damage experienced by trees at Jesnalvaara in the study period was caused by swafly larvae whose feeding peak distinctively falls to late summer (August - September) (see Haukioja and Koponen 1975). Therefore, their damage can be meaningfully correlated with mid-August foliage characters. This is not necessarily so with *Epirrita autumnata*, the most im-

Table 7. Proportion of chewed leaves and number of herbivores and predators at study sites in August 1978. 20 trees were sampled at each site

	FJ	MJud	MJ	TJ
Attacked leaves (%)	7.8	22.1	50.2	33.5
(n)	2,296	3,440	1,629	2,267
Number of herbivores				
chewers Symphyta	74	145	949	460
Lepidoptera	1	0	12	1
Coleoptera	10	8	89	119
suckers Aphids	253	217	48	41
Psyllids	14	27	2	4
Total	352	399	1,100	625
Number of predators				
Formicidae	1,144	1,011	8	1
Arachnida	37	12	22	11
Neuroptera	3	1	1	6
Total	1,184	1,024	32	18
Ratio of chewers to predators	0.07	0.15	32.81	32.22

Proportion of chewed leaves differed among sites (Kruskall-Wallis test, $p < 0.001$). Ratio of chewers to predators differed among sites (Kruskall-Wallis test, $p < 0.001$)

portant potential defoliator of birches at Jesnalvaara. Its main feeding period occurs a month earlier. However, the severe *Epirrita* damage in mid-sixties at Jesnalvaara had a similar spatial distribution as herbivory in 'normal' years (Table 7) (Haukioja et al. 1978, Niemelä 1980). No visible damage by *Epirrita* took place at Jesnalvaara in the seventies; in collections made during the larval period of this species (in 1975–1976), only 19 *Epirrita* larvae, mostly from the upper sites, were found from 180 trees sampled: 1 from the lower slope, 10 from the MJ and 8 from the summit. Consequently, early summer and late summer herbivory may be delimited by similar factors.

A between-site comparison does not exclude the protective role of phenols within a birch population. We analysed from the data in Table 7 phenolic and nitrogen content of foliage in individual trees in relation to numbers of herbivores collected by the knocking method from their foliage. The only statistically significant result was arrived at on the middle slope (MJ) where trees with few herbivores had higher phenolic content than those with many herbivores (Mann-Whitney U-test, $p < 0.05$). Due to several (8) comparisons made (where significant differences might arise by chance alone), and because of sensitivity of the ranking of trees to sampling errors in (generally low) numbers of herbivores, the importance of this result remains somewhat open. We point out that birches at the MJ had the highest phenolic levels and therefore would be the most probable ones to show the protective role, if any, of total phenols.

Discussion

Control over growth

Growth of birches is proximately strongly affected by nutrient availability, as revealed by the fertilization experiment. Besides that, temperature had a strong effect.

Reduced growth of birches at high elevation sites may be due to direct effects of temperature on growth or to the effect of temperature on nutrient availability. The direct effect might be more important because sites differ more strongly in growth and trees actually have higher leaf nitrogen concentration at the upper elevations.

The positive correlation between temperature sum in the previous year and both twig growth and leaf weight indicates that growth depends primarily upon stored, and not upon current photosynthates. This is consistent with the strong correlation of photosynthesis with temperature in the mountain birch (Prudhomme, personal communication) and with physiological studies of control over growth of temperature trees (Kozlowski 1971). Correlation between leaf size and temperature of the previous year may depend on the fact that leaves are preformed in buds in the previous year. Thus number of cells in leaves obviously is determined at that time, although accumulation of carbon into structures must depend on current year conditions.

Ultimate factors determining growth of birches include importance of growth for survival and reproduction. As regards survival, growth obviously is important in a competitive situation. Because birch forest is the climax vegetation type on the area, established trees do not need extra growth to avoid shading to the same extent as in a successional stage. This is more obvious at the upper slope, where trees grow more widely spaced than at the lower slope. Another factor concerns importance of growth to herbivore resistance: because growth and phenols tend to compete for the same carbon reserves, it may be that selection for higher resistance at upper altitudes indirectly reduces growth. The negative correlation between growth and phenolics in years following cold summers suggests that in these years, plant carbon reserves are drawn down sufficiently that growth and production of phenolics compete for carbon.

Control over foliage nitrogen

The negative correlation of percent nitrogen with current year's temperature is characteristic of tundra plants (Chapin and Oechel 1983) and usually reflects dilution of a similar leaf nitrogen mass by added structural tissue in a warm year favourable for photosynthesis. Besides, phenological advancement of growth in warm years causes leaves to lose nitrogen from foliage earlier than in cold years.

The high phenolic and nitrogen concentrations at high elevation probably reflect temperature limitation of growth at these sites.

Control over phenols

Control over phenolics deserves a special treatment because of the argued importance of phenols as defensive compounds. Proximately, leaf phenols are affected by nutrient availability (Tuomi et al. 1984). Absolute carbon gain, as influenced by temperature, exerts another control over phenolic synthesis.

An evolutionary reason was proposed by Janzen (1974): defences should be high where nutrient availability is low and nutrients lost to herbivores are difficult to replace. This logic survived an empirical test (McKey et al. 1978), where phenols were used as an index of foliage defence.

However, it is hard to falsify a null hypothesis that proximate mechanisms (nutrient availability, and climatic control over growth) are sufficient to explain why phenolic levels are high in birches growing on nutrient poor-soils. Mattson (1980) and Bryant et al. (1983) emphasized that if plants have a shortage of nutrients, the use of carbon for growth may be blocked. In addition, poor soils select for stress-tolerant plants, that do not preferentially invest in growth (Grime 1977). Because low nutrient (nitrogen, phosphorus etc.) status does not necessarily affect carbon uptake, excess carbon can accumulate. This can be converted to storage compounds like sugars or to potentially defensive carbon-based compounds like phenols. At this point herbivory may select for higher proportion of defensive compounds among carbon-based substances, or to more effective individual compounds. In contrast, on nutrient-rich areas plants represent competive or ruderal types (sensu Grime 1977). Here growth has high priority and thus carbon, instead of mineral nutrients, may limit growth. This nutrient poverty hypothesis predicts negative correlation between plant growth and its carbon based defences. More importantly, it explains the negative correlation between phenols and nitrogen within sites. The near-zero correlation in these measures between sites may be explained by the fact that plants growing at low temperatures have high tissue nitrogen concentrations despite substantial nitrogen limitation and carbon accumulation. I.e. factors other than carbon-nutrient balance lead to differences in tissue nutrient concentrations in sites with different temperature regimes (Chapin 1980).

Foliage phenolic content as an index of defence against birch herbivores

The widely accepted theory of the chemical aspects of plant-herbivore interactions (Feeny 1975, 1976, Rhoades and Cates 1976, Rhoades 1979) assumes that phenolic compounds bind proteins and digestive enzymes. Their mode of action is assumed to be non-specific and dose-dependent, and therefore hard to circumvent even by specialist herbivores. Zucker (1983), especially, has argued that various tannins, assumed to be typical phenols in the above respect, actually may have very specific modes of action, and that their proposed mode of functioning has not been confirmed.

Our result that there was no correlation between foliage phenols and ability of the extracts to precipitate hemoglobin agrees with earlier studies by Schultz and Baldwin (1982) and Martin and Martin (1982). This result casts doubt on the relevance of total phenols in birch foliage as quantitative measures of the defensive commitments of trees as proposed by Feeny, and Rhoades and Cates. On the other hand, it may also show that hemoglobin is not a suitable protein in such a study: foliage phenols from birch precipitated bovine trypsin (Niemelä et al. 1979). It can be claimed that we measured total Folin-Dennis phenols, not tannins. However, concentration of tannins strongly correlates with total phenols in mountain birch foliage (Haukioja et al. 1978).

Because phenols in birch foliage did not satisfy the assumptions of quantitative defences in all aspects they also did not test in a strict sense relevance of the theory proposed by Feeny and Rhoades and Cates. However, phenols and especially tannins have much served as general models of quantitative defences. For alternative explanations, see e.g. Fox 1980, Coley 1983, Zucker 1983.

Our data did not reveal any negative correlation between foliage phenols and insect damage in between-site

comparisons, on the contrary. But because trees with the highest foliage phenols contained fewer herbivores than trees with lower phenols at the middle slope (MJ), it still remains possible that very high total phenols deter herbivores. There are no data available showing whether phenols in these trees are qualitatively similar to those in trees with lower phenol content.

Consequently, total foliage phenols in Jesnalvaara birches may have some relevance in explaining levels of herbivory within sites but we cannot falsify the null hypothesis of between-site differences in phenolic levels basically being determined by abiotic conditions.

There are two general points to raise on the basis of the above treatment. First, if phenols function as defences, they do not need to be costly. If the carbon balance in foliage basically is determined by nutrient availability – i.e. by difficulties in allocating carbon to growth when nutrients are in a short supply – that part of the costs of phenol production which can be assigned to defence is the cost of converting sugars etc. (which might attract herbivores) to phenols, not the total cost of producing phenols. We cannot include any costs to the use of carbon for a certain purpose if there are no alternative ways to use it to enhance plant fitness. This logic implicitely assumes that under severe nutrient limitation extra carbon cannot be used e.g. in expansion of the root system. Secondly, high content of quantitative defences like phenols is claimed to be costly for the plant because sequestering them may be difficult (Rhoades 1979). However, Prudhomme (1983), when studying the photosynthetic activity of birches at Jesnalvaara, found that photosynthesis was most active where foliage phenols had the highest levels. This is not any paradox at all if we interpret high phenol content as a by-product of the photosynthetic activity. This does not cancel the possibility that (some) leaf phenols have a negative impact on herbivore performance.

Conclusions

Among the potential defensive systems studied, variance in bud burst does not seem to be important for birch herbivores in northern Finland (Haukioja 1980, Haukioja et al. 1983). Neither could we find strong correlations between the time of bud burst and other measured parameters.

The ability of birches to recover from artificial defoliation was generally good and was better at a more marginal site. We have two potential, non-exclusive explanations. Birches at a barren growth site may be good in recovery because stress tolerant plants (sensu Grime 1977) are characterized by large storages of nutrients and energy. Thus they are preadapted to recover well. Another explanation is that the birch population at the more barren middle slope experienced heavy defoliation by *Epirrita* in the mid-sixties. Trees which recovered form the present day population and obviously were better in recovery than trees which perished. At the lower slope such selection has not taken place, at least not in recent decades.

The nitrogen content of birch foliage correlated positively with feeding scars in leaves when sites were compared. However, this does not mean that low consumption at sites with low foliage nitrogen was causally affected. On the contrary, larvae of two species of sawflies, whose feeding season is in late season, grew better on leaves from the lower slope birches having low nitrogen content (Haukioja et al. 1978).

This indicates that in leaf quality something other than nitrogen was crucial.

We could not conclusively show that the two chemical measurements of leaf quality were important in determining levels of herbivory in mountain birches in the study years characterized by relatively low herbivore densities.

In evolutionary theorizing of plant defences the criterion of success of defence is the marginal increase in plant fitness caused by the lower consumption due to a certain investment to defence. As simple and straightforward as it is in theory, we have formidable empirical and theoretical difficulties in demonstrating success of a defensive commitment. When coevolutionary theories of plant defences are tested, these difficulties may actually be larger than the more technical problems involved e.g. in decisions which indices describe well plant defences. We finally deal with such complications because we feel that they may also contribute to results in the present paper.

First, we do not have any handy measure of fitness in long-lived trees. Neither do we know how low rates of consumption affect the trees, especially their fitness although years with low consumption are typical in most environments, also in that studied by us (Haukioja and Koponen 1975). Secondly, there are two different views how natural selection operates. It may have moulded solutions to give optimal or at least positive balance in benefits to costs ratio in commitments to defence. This might be observed under average conditions, good conditions or always. If this alternative is true, an analysis like ours is probable to reveal important correlations between foliage chemistry and herbivore damage. An alternative approach is that natural selection functions as a coarse filter and above all eliminates unfit phenotypes (Stearns 1982, Tuomi et al. 1983). In this case it is not the years with "normal" low consumption that are crucial but the years with peak consumption. If this alternative is true, there are selective deaths occurring in such years which should be studied and correlated with characters of foliage chemistry. Selective deaths of trees, caused by herbivores, may mould genetically settled limits for different types of defences in the birch population. These limits, together with environmentally determined possibilities of proper phenotypic responses, determine which trees can survive e.g. *Epirrita* outbreaks, which potentially lead to death of trees at vast areas (Kallio and Lehtonen 1973). The limits need not reflect themselves in factors like nitrogen or phenolic content as such, but e.g. in ability of trees promptly to respond to cues indicating an imminent threat of herbivory (Haukioja 1980, 1982).

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