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Heavy browsing by a mammalian herbivore does not affect fluctuating asymmetry of its food plants[1]

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Abstract: The only 3 published studies relating vertebrate herbivores to plant fluctuating asymmetry (FA) found significant correlations between grazing intensity and plant FA. The general value of these early findings is unclear, however, because FA studies are sensitive to selective reporting, the tendency to publish only a subset of studies that were undertaken. From 2000 to 2003 we quantified the correlations between past herbivory and plant FA in 3 plant–herbivore systems centred on a single mammal species, the North American porcupine (*Erethizon dorsatum*). We measured leaf FA in pairs of paper birch (*Betula papyriferae*; $n = 24$ pairs), quaking aspen (*Populus tremuloides*; $n = 25$ pairs), and jack pine (*Pinus banksiana*; $n = 15$ pairs) trees each containing a control (uneaten) and test (eaten) tree. Although damage incurred by trees from porcupine browsing was severe, we found no statistical association between plant FA and herbivory. We obtained this finding even though our study design did capture subtle variations in plant FA associated to plant genotype or year of sampling. Our study contrasts with earlier findings that plant FA is related to herbivory pressure. There may have been a publication bias as a result of selective reporting in this field of research. Therefore, replication (same hypothesis, same study system) and quasireplication (same hypothesis, different study system) are particularly important.
Keywords: aspen, birch, browsing, fluctuating asymmetry, herbivory, North American porcupine, pine.

Résumé : Les 3 seules études reliant le broutement d'herbivores vertébrés à l'asymétrie fluctuante (AF) des plantes rapportent des corrélations significatives entre degré de broutement et l'AF. La valeur générale de ces découvertes n'est cependant pas claire car les recherches sur l'AF sont sensibles à la publication sélective, c'est-à-dire à la tendance à ne publier qu'une fraction biaisée des recherches menées. Nous avons mesuré pendant 4 ans les corrélations entre le degré d'herbivorie et l'AF des plantes broutées par le porc-épic d'Amérique (*Erethizon dorsatum*). Nous avons mesuré l'AF de paires de bouleaux à papier (*Betula papyriferae*; $n = 24$ paires), peupliers faux-trembles (*Populus tremuloides*; $n = 25$ paires) et pins gris (*Pinus banksiana*; $n = 15$ paires) dont un arbre servait de témoin (non brouté) et l'autre de test (brouté). Les dommages causés aux arbres par les porcs-épics étaient sévères. Cependant nous n'avons pas trouvé de lien statistique entre l'AF des arbres et le degré d'herbivorie, même si notre stratégie d'échantillonnage nous a permis de révéler des liens subtils entre l'AF des arbres et leur génotype ou l'année d'échantillonnage. Nos résultats diffèrent donc de ceux des études précédentes. À cause des biais de publication possibles dans ce domaine de recherche, la réplication (même hypothèse, même système d'étude) et la quasi-réplication (même hypothèse, système d'étude différent) sont particulièrement importantes.
Mots-clés : asymétrie fluctuante, bouleau, broutement, herbivorie, pin, porc-épic d'Amérique, tremble.

Nomenclature: Marie-Victorin, 1995.

Introduction

Vertebrate herbivores play a key role in shaping the structure and functioning of ecosystems, and possibly in driving some aspects of plant evolution. Two major directions in research on the trophic relations between vertebrates and plants concern (1) how individuals choose which plants or plant parts to eat and (2) the consequences of herbivory on plant life history.

Many tools are used to explore these research directions, including chemical analyses of plants, behavioural observations of food choice, and experimental manipulation of herbivory pressure. Plant fluctuating asymmetry (FA) might represent an additional tool to study the relations between plants and vertebrate herbivores. FA refers to subtle deviations of symmetry thought to reflect the inability of organisms to control developmental processes during ontogeny (see Palmer, 1994; Palmer, 1996; and Møller & Swaddle, 1997 for extensive reviews of FA definitions and measurements). FA would be especially useful in studies of the relations between plants and vertebrate herbivores if plant FA were a predictor of food choice by individuals (an integrative measure of plant quality) or if plant FA indicated the level of stress imposed on plants by herbivores (an early warning signal regarding the impact of herbivores on ecosystems).

Recent studies have discussed the possibility that leaf FA could be linked to invertebrate (mostly insect) herbivory

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through 3 causal pathways. First, a change in leaf asymmetry could reflect a stress imposed on plants by insects (Zvereva, Kozlov & Haukioja, 1997; Zvereva, Kozlov & Niemelä, 1997). Second, insects could use leaf asymmetry as a visual cue to choose their food (Díaz, Pulido & Møller, 2004; Cornelissen & Stiling, 2005), since the ability to develop symmetrical traits could be related to the ability to produce defensive chemicals (Møller, 1995). Third, factors such as plant stress could affect both leaf asymmetry and leaf nutritional quality, the latter being the cue used by insects to select their food (Lempa *et al.*, 2000).

In contrast with the literature focusing on invertebrates, there are very few publications on the links between plant FA and vertebrate herbivory. To our knowledge, there have been only 3 published studies on this subject. These studies showed that intensity of reindeer grazing was positively correlated to FA of the willow *Salix lanata* (Olofsson & Strengbom, 2000) and that sheep and goat grazing modified FA of the Mediterranean shrubs *Periploca laevigata* and *Phillyrea latifolia* (Alados *et al.,* 2002 and Sirkou *et al.,* 2002; direction of effect depended on grazing pressure). In addition, FA of white birch (*Betula pubescens*) increased after winter browsing by moose (*Alces alces*) was experimentally simulated (Martel, Lempa & Haukioja, 1999). The small number of publications involving vertebrates and plant FA could reflect either a lack of research in this area or an under reporting of the results showing that vertebrate herbivory and plant FA are in general independent of each other. Research on FA is especially vulnerable to publication bias (Palmer, 2000) and non-significant results have a greater chance of ending up in the file drawer (Csada, James & Espie, 1996).

We studied 3 plant–herbivore systems centred on a single vertebrate herbivore, the North American porcupine (*Erethizon dorsatum*). Porcupines induce very severe stresses on plants, which can often lead to plant death (Roze, 1989). We chose 3 food plants preferred by porcupines: paper birch (*Betula papyriferae*), quaking aspen (*Populus tremuloides*), and jack pine (*Pinus banksiana*). Two of these species belong to genera already known to express their stress through increased levels of FA (birch: Kozlov *et al.,* 1996, Wilsey, Haukioja & Koricheva, 1998; Martel, Lempa & Haukioja, 1999; Lempa *et al.,* 2000; pine: Otronen & Rosenlund, 2001; Kozlov, Niemelä & Malkonen, 2002).

We tested, through a 4-y study, the specific hypothesis that FA of paper birch, quaking aspen, and jack pine leaves and needles varies according to past herbivory pressure by North American porcupines. To disentangle the different sources of variability in tree FA and to test the robustness of our sampling design, we also quantified the repeatability of FA at the individual tree level and the between-year differences in tree FA.

Methods

STUDY SITE AND PLANT–HERBIVORE SYSTEM

We worked in Parc national du Bic (48° 21' N, 68° 46' W), Québec, Canada, from June to October, 2000–2003. The study site was part of a mixed forest ecosystem located at the southern limit of the boreal forest. Berteaux, Klvana, and Trudeau (2005) and Klvana, Berteaux, and Cazelles (2004) provide a detailed description of the topography, local climate, vegetation composition, and plant phenology of the site.

The North American porcupine was probably the most abundant vertebrate herbivore at the study site. During winter, porcupines remove the outer bark and eat the phloem and cambium of selected birch and pine trees, leaving easy-to-identify scars on tree trunks (Figure 1). This damage is equivalent to bark stripping by squirrels (Snyder, 1992), deer (Putman & Moore, 1998), or voles (Danell *et al.,* 1987). The phloem acts as a conduit to transfer nutrients from the leaves to the roots. Porcupine herbivory disrupts this process, eventually leading to tree death when debarking is severe (Curtis, 1941; Storm & Halvorson, 1967; Sullivan, Jackson & Pojar, 1986). Quaking aspen is another plant species preferred by porcupines, but they feed on the leaves of the tree in summer, often cutting branches 1–2 cm in diameter in order to reach leaves located at the periphery of the canopy. Again, damage to selected trees can be severe and can result in considerable defoliation (Figure 1). Both bark stripping and branch cutting affect the fundamental

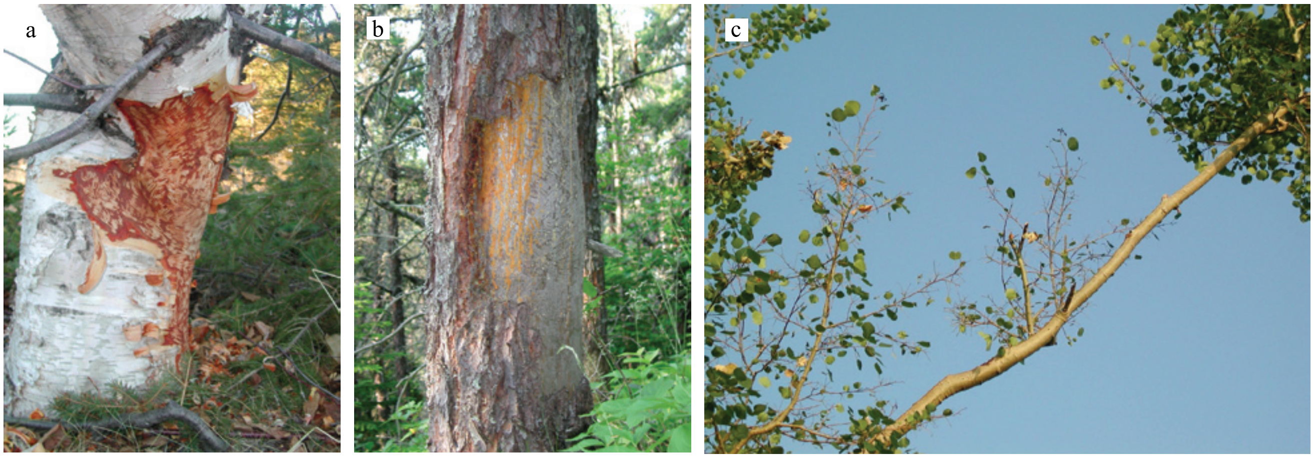

FIGURE 1. North American porcupines eat the phloem of paper birch (a) and jack pine (b) in winter, thereby inflicting severe damage on selected trees. Porcupines feed extensively on leaves of quaking aspen in summer, which results in partially defoliated trees with numerous branches being cut (c).

structure of trees and can thus generate long-lasting stresses potentially leading to tree death.

SAMPLING STRATEGY, LEAF HARVESTING, AND MEASUREMENT OF FA

Each adult tree bearing obvious signs of porcupine feeding (referred to below as test tree) was paired with a control tree of similar size that had not been fed upon by porcupines. The timing of porcupine feeding relative to leaf sampling was assessed through visual inspection of tooth marks and always indicated that feeding had occurred within a few years of the study. The intensity of damage incurred by test trees from porcupine feeding was always severe. Birches and pines bore 2–5 oval scars 100–1000 cm^2 in size, whereas aspens had hundreds of leaves and between 20 and 50 secondary branches cut down by porcupines. Distance between paired trees was generally ≤ 10 m and always ≤ 20 m. Our pair-wise sampling design minimized the effects of all obvious confounding variables, *e.g.,* light availability or soil composition and humidity.

We used 24 pairs of birches, 25 pairs of aspens, and 15 pairs of pines that were randomly chosen. More pairs of trees were initially selected, but some test trees died and some control trees were browsed by porcupines during the study. Since trees grow new leaves every spring, we repeated the study over several years to assess the between-year consistency of FA measurements on individual trees and to evaluate year effects relative to herbivory effects. Birch leaves were sampled in June and July 2000, 2001, and 2002, and aspen leaves in July 2002 and June 2003. Jack pines retain their needles for 3 easily discernable years, so we obtained data for 2001, 2002, and 2003 through a single sampling in October–November 2003.

Using a leaf cutter attached to a collapsible pole, we collected 17 birch and 15 aspen leaves per tree per year, from all parts of each tree (sun *versus* shade, crown *versus* lower branches, inner *versus* outer). We randomly collected 3 needle-bearing twigs per jack pine. Branching order (but not twig location in the canopy) affects FA of needles in the closely related Scots pine (Kozlov & Niemelä, 1999), so sampling was homogeneous across treatments and years with respect to this variable. From each twig, 8 pairs of needles from each year were measured, representing a total of 24 needle pairs per tree per year.

Before measurement, we dried birch and aspen leaves for 5 d, whereas we kept pine needles frozen in plastic bags. We performed all measurements to the nearest 0.01 mm using a vernier caliper ruler. We placed birch and aspen leaves on graph paper and measured on each side the greatest (widest) perpendicular distance between the mid-vein and the outer rim of the leaf. We straightened pine needles in a vise and measured the total length of each needle in the pair. We performed all measurements blind with respect to tree status (control *versus* test), and we repeated measurements once to separate FA from measurement error. We thus used a total of 24 432 measurements in this study (birch: 2 measurements × 2 sides × 17 leaves × 24 trees × 2 treatments × 3 y; aspen: 2 × 2 × 15 × 25 × 2 × 2; pine: 2 × 2 × 24 × 15 × 2 × 3).

The absolute difference between the left and right sides of leaves (or between the 2 needles) was independent of leaf size for all tree species/years (regression analyses), and the frequency distribution of this variable was always normally distributed around a mean of zero (Kolmogorov–Smirnov test for normality). Tree leaves thus showed FA rather than directional asymmetry or antisymmetry. We calculated FA for each tree/year using a two-way, mixed-model analysis of variance with repeated measurements of each side, as recommended by Palmer and Strobeck (1986). Sides were the fixed factor and individual leaves were the random factor on each tree. Using this approach, FA for each tree/year is calculated as $(MS_{sj} - MS_m)/M$, where MS_{sj} = the mean square interaction (side × genotype), MS_m = mean square measurement error, and M = the number of repeated measurements per side. This approach allows measurement error variance to be partitioned out of the total between-sides variance, is not biased by directional asymmetry, and lends itself to the most powerful test for differences between 2 samples (see index F10 in Palmer, 1994).

STATISTICAL ANALYSES

We used Levene tests of homogeneity of variance (O'Neill & Mathews, 2002) to analyse the effects of year, treatment, and paired tree blocs on FA. Prior to testing, the distribution of FA values was normalized using a log transformation. We assessed the year-to-year repeatability of FA by calculating intra-class correlation coefficients (r) of FA using a Model II 2-factor (year and tree) ANOVA (Lessels & Boag, 1987). This measure of repeatability describes the proportion of variance in FA that can be attributed to permanent differences between individuals. The proportion of variance that originates from intra-individual differences is represented by $1 - r$.

Results

Measurement error was always close to 0.5% of FA for birch and aspen, but 10 times higher (5% of FA) for pines (Table I), reflecting the difficulty of measuring small needles straightened in a vise. In all cases, measurement error was largely acceptable for comparing FA across treatments.

We did not detect any significant association between past herbivory by porcupines and FA of birch, aspen, and pine (results of Levene tests are presented in Table I; Figure 2 allows a visual inspection of the variability in FA within tree pairs). This absence of association was remarkably constant across all 8 tree species/year combinations investigated (Table I and Figure 2). Our lack of significant direct effects of treatment or year on FA was not due to low statistical power, since the proportion of browsed trees that had a higher FA than their paired control was 49.9% when averaged over all tree species/years (Table I). In other words, there was never any obvious trend in differences in FA between test and control trees, and high P-values were not due to small sample sizes. In pines, FA was significantly higher in 2002 than in 2001 or 2003, and this was the only significant effect detected across all our comparisons (Table I).

FA measurements were repeatable among years in birch, where 45% of the variability in FA measures could be attributed to permanent differences between individuals ($r = 0.451$, $F_{47, 96} = 3.42$, $P < 0.0001$). However, FA was not consistent within individuals among years in aspen

TABLE I. Fluctuating asymmetry (FA, mean ± SE) and measurement error expressed as a percentage of FA (ME, mean ± SE of control (uneaten) and test (eaten)) trees from 3 tree species preferred by North American porcupines in Parc national du Bic, Québec, Canada. Also displayed (FAe > FAc) is the absolute and relative (%, in parenthesis) number of tree pairs for which FA of the test tree was greater than FA of the control tree. Results of Levene tests indicate, for each tree species, the significance of effects of treatment, year, and the interaction between treatment and year.

		Birch (n = 24 pairs)		Aspen (n = 25 pairs)		Pine (n = 15 pairs)	
		Control	Test	Control	Test	Control	Test
2000	FA	0.043 ± 0.007	0.059 ± 0.007				
	ME	0.54 ± 0.14	0.34 ± 0.06				
	FAe > FAc	17 (70.8 %)					
2001	FA	0.055 ± 0.007	0.055 ± 0.009			0.077 ± 0.006	0.115 ± 0.022
	ME	0.50 ± 0.06	0.65 ± 0.10			5.76 ± 0.56	4.66 ± 0.66
	FAe > FAc	12 (50.0%)				8 (53.3%)	
2002	FA	0.055 ± 0.009	0.057 ± 0.006	0.017 ± 0.003	0.014 ± 0.002	0.163 ± 0.024	0.166 ± 0.023
	ME	0.45 ± 0.07	0.39 ± 0.07	0.50 ± 0.08	0.59 ± 0.12	3.94 ± 0.56	3.86 ± 0.46
	FAe > FAc	13 (54.2%)		10 (40.0%)		8 (53.3%)	
2003	FA			0.016 ± 0.002	0.016 ± 0.005	0.067 ± 0.007	0.059 ± 0.008
	ME			**0.62 ± 0.06**	**0.81 ± 0.09**	**5.51 ± 0.63**	**6.34 ± 0.55**
	FAe > FAc	11 (44.0%)				5 (33.3%)	
Levene test	treatment	$F_{1,\,23}$ = 2.47, P = 0.1298		$F_{1,\,24}$ = 2.32, P = 0.1408		$F_{1,\,14}$ = 0.00, P = 0.9712	
	year	$F_{2,\,46}$ = 0.91, P = 0.4100		$F_{1,\,48}$ = 0.07, P = 0.7971		$F_{2,\,56}$ = 22.65, P < 0.0001	
	treatment * year	$F_{2,\,46}$ = 2.94, P = 0.0628		$F_{1,\,48}$ = 0.20, P = 0.6574		$F_{2,\,56}$ = 1.05, P = 0.3551	

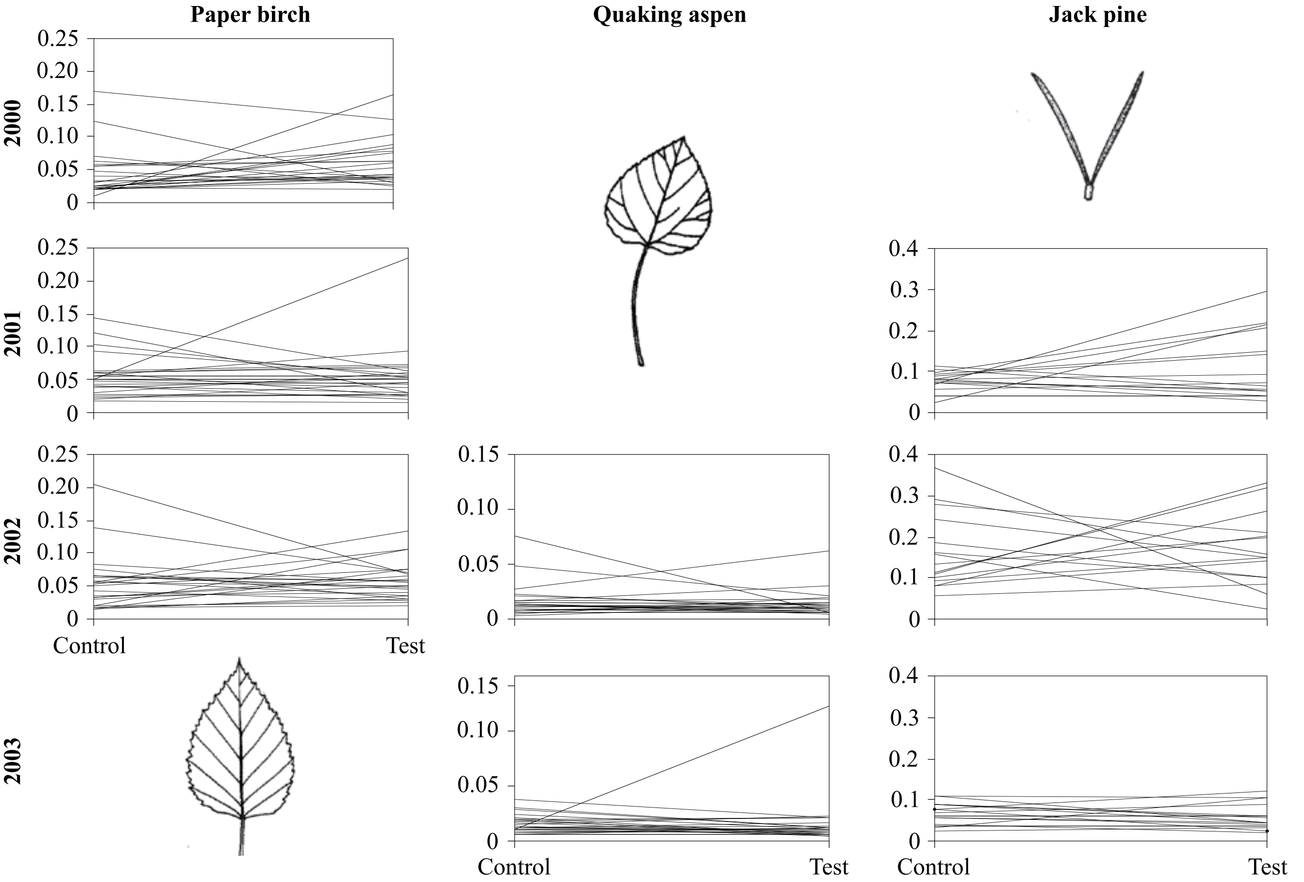

FIGURE 2. Differences in fluctuating asymmetry of control (uneaten by porcupines) and test (eaten by porcupines) trees of 3 species studied over 4 y in Parc national du Bic, Québec, Canada. Lines connect trees from the same pair.

(r = 0.082, $F_{49,\,50}$ = 1.16, P = 0.3067) or in pine (r = –0.068, $F_{29,\,60}$ = 1.35, P = 0.1660).

Discussion

Plant FA did not correlate to past herbivory in 3 plant species heavily browsed by a vertebrate herbivore, the North American porcupine. We obtained this result while simultaneously showing that plant FA was sensitive to some factors associated with individual genotype (birch) or year of sampling (pine). Our multi-year study thus captured some of the subtle variations present in plant FA, but failed to detect any trend regarding the potential association between vertebrate herbivory and plant FA. We reached this finding despite working with plants belonging to genera in which FA is apparently responsive to other stressors like pollution or insect herbivory. Our study was not experimental, so we cannot exclude the possibility that porcupines selected trees with lower FA, with damage subsequently increasing FA to the level of control plants. However, this is a far less parsimonious interpretation of the results than accepting the null hypothesis of no link between tree FA and porcupine browsing, especially given that a few control trees were also damaged by porcupines during the study (their associated pairs were accordingly removed from the sampling; see Methods).

Why do our results contrast with the current literature, which consistently shows that plant FA correlates with herbivory in invertebrates (Møller, 1995; Zvereva, Kozlov & Haukioja, 1997; Zvereva, Kozlov & Niemelä, 1997; Lempa *et al.,* 2000; Díaz, Pulido & Møller, 2004; Cornelissen & Stiling, 2005) and vertebrates (Olofsson & Strengbom, 2000; Alados *et al.,* 2002; Sirkou *et al.,* 2002)? There are 3 potential explanations that we will examine in turn. This examination will also lead us to more general conclusions regarding the potential of plant FA to be used as a routine tool to study the relationships between plants and herbivores: 1) Our study system differed from others in that none of the potential causal pathways linking plant FA to herbivory was present, *i.e.,* herbivory did not translate into a stress-related increase in plant FA, porcupines did not cue on plant FA to select feeding trees, and there was no factor correlated to both tree nutritional quality and FA (see Introduction for a description of these 3 causal pathways); 2) our FA measures were not sensitive enough to detect differences between control and test trees; and 3) earlier publications are a biased sample of studies linking plant FA to herbivory pressure, such that our results are not as unique as they appear to be and the relationship between plant FA and herbivory is actually far less consistent than suggested by the current literature.

With respect to the first explanation, porcupines can no doubt induce severe stresses to vegetation. It has long been known that porcupine bark stripping significantly reduces the diameter growth of trees (Storm & Halvorson, 1967), can result in severe distortion of tree trunks (Curtis & Wilson, 1953), and more generally reduces the fitness of trees (Spencer, 1964: Schubert, 1971). Browsing of leaves and cutting of branches in the canopy can also be highly detrimental to trees, as we witnessed in our study area, where some preferred aspen trees had been considerably defoliated by porcupines. Forest managers in North America all know that porcupine damage can considerably reduce the value of tree plantations (Roze, 1989). Therefore, it is reasonable to expect that porcupine herbivory is a severe stress to trees. However, we have no objective measure of this stress. More generally, the lack of objective measures of plant stress (Møller, 1995) is a major obstacle to testing the usefulness of FA measurements in detecting herbivory-related stresses on vegetation. Asymmetry–stress relationships differ between taxa, habitats, and sources of stress (Bjorksten, Fowler & Pomiankowski, 2000; Lens *et al.,* 2001), and there is yet no theoretical framework to predict when relationships between asymmetry and stress can be most expected.

Porcupines can be highly selective herbivores, even at the within-species level (Snyder & Linhart, 1997). However, we doubt that they could have selected feeding trees according to their FA. First, porcupines eat the bark of birch trees in winter when there are no leaves, and they often limit their browsing of pines to the lower parts of tree trunks, far from the canopy, where leaves develop. Second, although porcupines do enter into close contact with aspen leaves when deciding which aspen to browse, feeding generally occurs at night, when visual inspection of food is difficult. Contrary to what has been suggested for insects (Cornelissen & Stiling, 2005) it is thus highly unlikely that porcupines (and other mammalian herbivores) could select aspens (or other species) from subtle differences in FA levels.

Porcupines select the most nutritional trees within a given pine (Snyder & Linhart, 1997) or aspen (B. Diner *et al.,* unpubl. data) stand and thus have the potential to select individuals with especially low or high FA if FA is correlated to nutritional quality. Between-individual differences in the nutritional quality of trees generally have a genetic basis (*Pinus*: Snyder & Linhart, 1997; *Populus*: Lindroth & Hwang, 1996; *Betula*: Laitinen *et al.,* 2004). Therefore, nutritional characteristics are long-lasting features of individuals and are repeatable across years. The fact that FA was not repeatable at the individual level in pines or aspens indicates that FA was probably not a good indicator of nutritional quality in these species. FA was repeatable in birch trees, but we do not know if FA was correlated to nutritional quality. Unfortunately, little is known as to how developmental disorders are connected to plant metabolism and nutritional quality (Lempa *et al.,* 2000), so predictions as to when plant FA should correlate to herbivore food choice are still impossible.

With respect to the sensitivity explanation, our study design was not robust enough to detect differences in FA between control and test trees. Our sample sizes at the tree (n = 15–25) and leaf (n = 15–24) levels are in the same range as those of other studies, and the same is true for the measurement errors we obtained. To our knowledge, no published study replicated measures for more than 3 y, as we did here. Therefore, we have no reason to doubt the robustness of our sampling design relative to those of previous studies reporting effects of herbivory on FA. The power of our tests is further demonstrated by the fact that we managed to detect between-year and between-individual differences in FA for some of the tree species.

Finally, with respect to the possibility that earlier publications are a biased sample of attempts to link plant FA to herbivory pressure, FA studies are highly vulnerable to selective reporting (the tendency to publish only a subset of studies that were undertaken) and thus publication bias (deviations in average effect sizes caused by selective reporting; see Palmer, 2000 and references therein). Because FA studies can be quick and cheap, the research community can generate data at a high rate, but scientists may be more motivated to write articles reporting on significant results. Editorial processes may also contribute to selective reporting if "positive" results are favoured over "negative" ones

(Palmer, 2000). For example, the proportion of studies supporting a role of FA in sexual selection has declined from 100% in the early 1990s to 36% 10 y later (Simmons *et al.,* 1999), and studies on the relations between FA and individual fitness were also likely reported selectively (Palmer, 2000).

It is unknown if the biased reporting described above also applies to studies on the relations between plant FA and herbivory. The number of published studies is not large enough to allow a quantitative analysis of the literature in order to detect these biases. In the specific case of vertebrate herbivory, Olofsson and Strengbom (2000), Alados *et al.* (2002), and Sirkou *et al.* (2002) found that plant FA responded to mammalian herbivory, while Escós, Alados, and Emlen (1997) and Alados *et al.* (1998) showed that grazing by sheep and goat affected plant developmental stability, which in that case was measured through translatory symmetry with scale (a form of symmetry different from bilateral symmetry). We are aware of no study showing an absence of relations between plant FA and vertebrate herbivory. Our contrasting results should encourage replication (same species of plants and herbivores) and quasi-replication (other plant–herbivore systems) of published studies, since replication is the strongest test of a particular finding, while quasi-replication is the quickest route to biological generalization (Palmer, 2000).

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