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Diversity of plant–animal interactions: Possibilities for a new plant defense indicator value?

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ABSTRACT

The interactions between herbivores and plants are of general interest in ecology. Even though the extensive research carried out during the last decades has culminated in many theories, additional studies are necessary to validate these findings. In particular, the hypotheses dealing with the complex interrelations of plant defense mechanisms and herbivores continue to be debated.

In this paper, we develop a new indicator value that quantifies the defense mechanisms of Central European woody plants against large mammalian herbivores. The indicator value is based on three plant-specific traits: chemical defense (toxic compounds, digestion inhibitors), mechanical defense and leaf size. Our validation of the newly established indicator shows that evergreen woody plants have a significantly higher indicator value than deciduous woody plants. Moreover, plant defense is correlated with growth height: woody plants growing in the browsing zone preferred by large mammalian herbivores have significantly higher levels of defense compared with woody plants capable of growth high above the reach of large herbivores.

We conclude that the new plant defense indicator value is a valuable tool for the validation of existing hypotheses and habitat calibration on a statistical basis. The quantification of plant mechanisms of defense against large herbivores produces a significantly better understanding of the multifaceted nature of plant–animal interactions and should contribute positively to future studies.

1. Introduction

The evolution of plant strategies of defense against natural enemies such as herbivores and pathogens has attracted considerable interest among scientists ever since the theory of coevolution was formulated (Ehrlich and Raven, 1964). Since then, many different disciplines, among them ecology, chemistry and agronomy, have focused their research on plant defense mechanisms and on their potential for reducing consumption by mammalian herbivores (Buchanan, 2000). These studies addressed three main aspects: first, the interactions between plants and herbivores mediated by secondary metabolites (Bryant and Kuropat, 1980; Bryant et al., 1991; Behmer et al., 2002; Bailey et al., 2007); second, the influences of nutrient availability and plant association as well as direct and indirect effects of enemies and mutualists on plant defenses (Goldberg et al., 1999; Morris et al., 2007); and third, the development of theories that are able to explain the specific adaptations of plants to their antagonistic herbivores (Mac Arthur and Pianka, 1996; Coley et al., 1985; Maschinski and Whitham, 1989; Mehrtens, 1999; Wise and Abrahamson, 2005; Karlovsky, 2008). Owing to a lack of empirical data, all these studies tried to tackle their complex subject from increasingly abstract points of view.

It is assumed that in the absence of humans and large herbivores, the landscape of Central Europe would be dominated by deciduous woodlands (cf. Firbas, 1949; Tüxen, 1956; Ellenberg, 1996). Large herbivores like aurochs (*Bos primigenius*), tarpan (*Equus ferus ferus*), bison (*Bison bonasus*), beaver (*Castor fiber*) or wild boar (*Sus scrofa*) influenced the development of the natural vegetation in prehistoric times. Large herbivores are found to have a significant impact on woodland ecosystems even today. Thus, the control of wild and domestic herbivores is an important factor in conservation management (Mitchell, 2005). The long-lasting coexistence of large herbivores and plants, including woody plants, in Central

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Europe implies their coevolution (cf. Howe and Westley, 1990). Large herbivores counteract the effects of plant defense mechanisms by selective foraging, fragmentation of intact plant tissues, microbial fermentation and expanded guts for microbial breakdown, whereas plants protect themselves through morphological, structural and chemical adaptations.

Several authors endorse the use of biological indicators for ecological studies because they offer basic predictions without requiring time-consuming physical and chemical measurements. Moreover, the application of biological indicators allows mathematical as well as statistical processing. Even though a few authors have warned against the use of indicators (Dürwen, 1982; Ellenberg et al., 2001), this approach has nevertheless proven to be a valuable and useful tool in ecology and bioindication (cf. Dierschke, 1994). In particular, Ellenberg's (1974) concept of bioindicators was a cornerstone of the quantification of ecological responses of plants to climatic and edaphic conditions. His indicator values have been intensively tested and adjusted (Grapow et al., 1993; Thompson et al., 1993), and their validity has been confirmed by field measurements (Schaffers and Sykora, 2000). Many other authors have developed biological indicator systems similar to those of Ellenberg, if only for parts of Central Europe (Switzerland: Landolt, 1977; eastern Germany: Frank and Klotz, 1990) or simply to quantify the mowing (Briemle and Ellenberg, 1994) and grazing compatibility (Briemle et al., 2002) of grasslands.

Our aim is to establish a new plant defense indicator value for Central European woody plants. The indicator should provide a simple and objective measure for describing the complex patterns of plant defense mechanisms against large mammalian herbivores. We believe that the new indicator presents a useful tool for the statistical corroboration of the many theories and hypotheses about the defense strategies of plants against large herbivores developed over the past decades.

2. Materials and methods

2.1. Study area

The study area covers Central Europe, including Germany, Luxembourg, Poland, the Czech Republic, Austria, Switzerland, Liechtenstein and Slovakia (cf. Ellenberg, 1996). Roughly speaking, the area extends from 6° to 24°E and from 45° to 55°N. The study area is characterized by three major geographic regions: (i) the Central European lowland in the north, which passes southwards to (ii) the low mountain ranges that finally adjoin (iii) the Alps in the south. The altitude ranges from 50 m b.s.l. in the northern lowlands to 4600 m a.s.l. in the south (Swiss Alps, Dufour 4634 m a.s.l.) (Walter, 2007). The moderate, oceanic climate is primarily influenced by the warm Gulf Stream and the prevailing westerly winds. Summer temperatures seldom exceed 30 °C, and winter temperatures seldom drop below −20 °C (Ellenberg, 1996). The annual precipitation varies between 522 mm in Warsaw and 773 mm in Düsseldorf and 1169 mm in Salzburg (Deutscher Wetterdienst, personal communication). The climate of Central Europe generally favors deciduous trees with mesomorphic foliage. Only in the more continental northeastern part and at higher elevations does the tree flora change gradually to evergreen conifers (Ellenberg, 1996).

2.2. Plant defense indicator

We calculated defense indicator values for all Central European phanerophytes and nanophanerophytes listed in Ellenberg et al. (2001) unless they are cultivated, not indigenous (cf. Kowarik, 2003; Schütt, 2006) or belong to the genus *Rubus* (Table 1). *Rubus* species occur on heavily disturbed, nitrogen-rich sites that are produced as the result of human rather than herbivore activities. In accordance with the development of Ellenberg's indicator values, we believe that the establishment of adequate defense indicator values for *Rubus* species should be the object of future studies. The nomenclature follows Wisskirchen and Haeupler (1998).

Our analysis includes 131 plant species. Among them, deciduous species clearly dominate (89%) over evergreen ones (12%). More than half of all the species are shrubs (54%), trees account for one-third (33%), and the remaining species exhibit a growth form alternating between tree and shrub characteristics (13%) (referred to as the intermediate group). The intermediate group contains woody species that are able to adapt their morphological appearance to the given site conditions, in particular to the soil, climate, herbivores and competition present at the site. Among this group are plants like *Betula pubescens*, *Prunus padus* and *Sorbus aucuparia*. A more detailed analysis of the deciduous woody plants reveals that the majority (56%) consists of shrubs, whereas only one-third (29%) are trees and one-sixth (15%) belong to the intermediate group. In contrast, evergreen woody plants are characterized by a large percentage of trees (60%), whereas the rest (40%) are shrubs. Evergreen woody plants belonging to the intermediate group do not occur in the list of species analyzed.

The calculation of the defense indicator is based on data available from scientific literature and online databases (Table 2). The indicator values range from 1 to 6, where 1 represents no defense and 6 indicates a very high level of defense against large herbivores (Table 3). The calculation incorporates information about the two most important types of defense mechanisms of woody plants: chemical and mechanical (Crawley, 1983). In addition, we considered leaf size.

The chemical defense mechanisms are divided into two categories, namely, toxic substances and digestion inhibitors (Bryant et al., 1991). While toxic substances are highly poisonous, even in very low concentrations, digestion-inhibiting compounds have a deterrent effect that increases with concentration (dosage-dependent). Toxic substances that are used only for defense and have no further role in the plants' metabolism are called plant secondary metabolites (PSM) (Howe and Westley, 1990; Pallardy, 2008). The countless number of PSM (Buchanan, 2000) and the different types and amounts of toxicity that they might have for browsing herbivores are the most complex factors in the defense indicator value. The effects of plant chemicals vary inter and intraspecifically (Feeny, 1976; Rhoades, 1979), and in many cases, knowledge about certain plant substances is still lacking. According to Feeny (1976), overlap occurs between the categories of plant toxins and digestion inhibitors. Furthermore, the chemical defenses of woody plants vary by growth stage and by plant parts within growth stages (Bryant et al., 1991). In order to develop a high-quality categorization of chemical plant defenses, we considered a number of additional substance classes as toxic. Among these classes are cucurbitacins, alkaloids, cardenolides, cyanogenic glycosides and free amino acids (cf. Mehrtens, 1999). Because of great uncertainty about the toxic effects of sesquiterpenes (-lactones), diterpenes, triterpenes and polyacetylene (cf. Mehrtens, 1999), the final classification was submitted to expert judgement by two of the authors (HJB, MBD). All remaining secondary plant metabolites that could not be proven toxic were categorized as digestion inhibitors. These substances include hot- and bitter-tasting as well as fetid and antimicrobial plant compounds.

The category of mechanical defenses includes all plant-surface structures that are designed to deter large mammalian herbivores from feeding. The most frequent structures in this category are thorns and spines that act by inhibiting the rate at which plant tissue can be ingested (Cooper and Owen-Smith, 1985; Milewski et al., 1991; Belovsky and Schmitz, 1994). Small structural defenses like hairs, glandular hairs and papillae are relatively less effective as defenses against large mammals (cf. Howe and Westley, 1990).

Table 1
Defense indicator values for Central European woody plants. The span of defense indicator values ranges from 1 to 6, with 1 denoting no defensive traits and 6 denoting very high defensive traits. The remaining defense indicator values are as follows: (2) very low, (3) low, (4) medium, (5) high. The binary nomenclature corresponds to Wisskirchen and Haeupler (1998).

Scientific name	Defense indicator value	Scientific name	Defense indicator value
Abies alba Mill.	3	*Ligustrum vulgare* L.	5
Acer campestre L.	1	*Lonicera alpigena* L.	5
Acer monspessulanum L.	1	*Lonicera caerulea* L.	6
Acer opalus agg. Mill.	1	*Lonicera caprifolium* L.	5
Acer platanoides L.	1	*Lonicera nigra* L.	6
Acer pseudoplatanus L.	1	*Lonicera periclymenum* L.	5
Alnus alnobetula (Ehrh.) K. Koch	2	*Lonicera xylosteum* L.	6
Alnus glutinosa (L.) P. Gaertn.	2	*Malus sylvestris* (L.) Mill.	5
Alnus incana (L.) Moench	2	*Mespilus germanica* L.	4
Amelanchier ovalis Medik.	1	*Picea abies* (L.) H. Karst,	3
Berberis vulgaris L.	6	*Pinus cembra* L.	2
Betula humilis Schrank	3	*Pinus mugo* Turra s. str.	3
Betula pendula Roth	2	*Pinus mugo* × *rotundata* Link	3
Betula pubescens Ehrh. s. l.	2	*Pinus nigra* J. F. Arnold	2
Betula pubescens subsp. carpatica Koch	3	*Pinus sylvestris* L.	2
Buxus sempervirens L.	6	*Populus alba* L.	1
Carpinus betulus L.	1	*Populus nigra* L.	1
Castanea sativa Mill.	2	*Populus tremula* L.	1
Clematis alpina (L.) Mill.	5	*Prunus avium* L.	2
Clematis vitalba L.	5	*Prunus fruticosa* Pall.	3
Colutea arborescens L.	5	*Prunus mahaleb* L.	2
Cornus mas L.	2	*Prunus padus* L.	5
Cornus sanguinea L.	2	*Prunus spinosa* L. s. str.	5
Corylus avellana L.	2	*Quercus petraea* Liebl.	2
Cotoneaster integerrimus Medik.	3	*Quercus pubescens* Willd.	2
Cotoneaster tomentosus Lindl.	2	*Quercus robur* L.	2
Crataegus laevigata (Poir.) DC. s. l.	5	*Rhamnus cathartica* L.	5
Crataegus monogyna Jacq. s. l.	5	*Rhamnus saxatilis* Jacq.	5
Cytisus scoparius (L.) Link	6	*Ribes alpinum* L.	3
Daphne laureola L.	5	*Ribes nigrum* L.	2
Euonymus europaea L.	5	*Ribes petraeum* Wulfen	2
Euonymus latifolia (L.) Mill.	2	*Ribes rubrum* L.	2
Euonymus verrucosa Scop.	5	*Ribes spicatum* Robson	2
Fagus sylvatica L.	1	*Ribes uva-crispa* L.	5
Frangula alnus Mill.	6	*Rosa abietina* Gren. ex H. Christ	4
Fraxinus excelsior L.	2	*Rosa agrestis* Savi	4
Hippophae rhamnoides L.	6	*Rosa caesia* Sm. s. l.	4
Ilex aquifolium L.	6	*Rosa canina* L. s. l.	4
Juglans regia L.	2	*Rosa corymbifera* Borkh. s. l.	4
Juniperus communis L. s. l.	5	*Rosa dumalis* Bechst.	4
Juniperus sabina L.	6	*Rosa elliptica* Tausch	4
Larix decidua Mill.	3	*Rosa gallica* L.	4
Rosa glauca Pourr.	4	*Salix triandra* L.	2
Rosa jundzillii Besser	4	*Salix viminalis* L.	2
Rosa majalis Herrm.	4	*Salix* × *rubens* Schrank	2
Rosa micrantha Borrer ex Sm.	4	*Sambucus nigra* L.	4
Rosa rubiginosa L.	4	*Sambucus racemosa* L.	4
Rosa scabriuscula (R. Keller) Henker & G. Schulze	4	*Solanum dulcamara* L.	5
Rosa stylosa Desv.	4	*Sorbus aria* (L.) Crantz s. l.	2
Rosa subcanina (H. Christ) R. Keller	4	*Sorbus aucuparia* L.	2
Rosa subcollina (H. Christ) R. Keller	4	*Sorbus chamaemespilus* (L.) Crantz	2
Rosa tomentella Léman	4	*Sorbus danubialis* (Jáv.) Kárpáti	2
Rosa tomentosa Sm.	4	*Sorbus domestica* L.	2
Rosa villosa L.	4	*Sorbus intermedia* (Ehrh.) Pers.	2
Salix alba L.	2	*Sorbus mougeotii* Soy.-Will. & Godr.	2
Salix appendiculata Vill.	2	*Sorbus torminalis* (L.) Crantz	2
Salix aurita L.	2	*Staphylea pinnata* L.	2
Salix caprea L.	2	*Taxus baccata* L.	6
Salix cinerea L. s. l.	2	*Tilia cordata* Mill.	1
Salix daphnoides Vill.	2	*Tilia platyphyllos* Scop.	1
Salix eleagnos Scop.	2	*Ulmus glabra* Huds.	2
Salix foetida Sm.	2	*Ulmus laevis* Pall.	2
Salix fragilis L.	2	*Ulmus minor* Mill.	2
Salix myrsinifolia Salisb.	2	*Viburnum opulus* L.	5
Salix pentandra L.	2	*Vitis vinifera* subsp. sylvestris (C. C. Gmel.) Hegi	1
Salix purpurea L.	2		

Leaf size is considered to be another crucial factor for determining browsing intensity on woody plants. It is assumed that larger-sized leaves of plants face a higher risk of being browsed by herbivores. Small plant leaves are clearly seen as advantageous in the deterrence of large browsing herbivores. This assumption is based on the fact that an herbivore attempts to maximize its nutrient intake. Although foraging behavior varies with plant species composition, in general, deciduous species with large leaves allow

Table 2
Parameters and sources analyzed.

Parameter	Source
Leaf longevity, growth form	Ellenberg et al. (2001)
Leaf size[a]	Hegi (1981), Godet (1994), Schauer and Caspari (1996), Wisskirchen and Haeupler (1998), Aichele and Schwegler (2000), Kremer (2000), Aichele and Golte-Bechtle (2005), Roloff and Bärtels (2008)
Mechanical defense[a], ability to response[a,b]	Hegi (1981), Kiermeier (1990), Beutler (1996), Schauer and Caspari (1996), Wisskirchen and Haeupler (1998), Kremer (2000), Vera (2000), Horak and Horak (2001), Oberdorfer (2001), Weber (2003), Düll and Kutzelnigg (2005), Roloff and Bärtels (2008)
Chemical defense[a] (toxic substances and digestion inhibitors)	Hegi (1981), Habermehl (1990), Kiermeier (1990), Beutler (1996), Lampire et al. (1998), Wisskirchen and Haeupler (1998), Vera (2000), Kutschera (2002), Düll and Kutzelnigg (2005), Martín-Benito et al. (2005), Giertych et al. (2006), Roth (2006), Lacikova et al. (2007), Peev et al. (2007)

[a] Indicates that parameters were obtained using additional information from the following online databases: Althaus (1998), BfN (2000), ISI Web of Science (2009; the database was searched for relevant literature by keywords combined with the scientific name, the genus and/or the family name of the plant species in question), Kleyer et al. (2008), Klotz et al. (2002), Poschlod et al. (2003).
[b] The ability of plants to respond to damage caused by large herbivores can result from fast regrowth of lost plant tissues like leaves or can result from growth from the stool. The responsiveness of plants is, however, not considered in the calculation of the defense indicator value.

a greater nutrient intake by the herbivores and thereby enable greater survival and reproduction (Belovsky and Schmitz, 1994). In order to rank the different leaf sizes of the plants analyzed, we defined four leaf-size classes: 1 – small = 2–4 cm; 2 – middle = 4.1–8 cm; 3 – big = 8.1–14 cm; 4 – very big > 14 cm. In our study, the leaf size is defined as the length from the leaf base to the tip. It represents the mean value of all length measures appearing in the references examined. Consequently, all possible leaf morphologies that can change within a single plant species (leaf heteroblasty) are considered. However, owing to a lack of applicable data, it was sometimes necessary to analyze the leaf width instead of the leaf length in the case of circular leaves. Wherever possible, we compensated for missing data by using information about allied species or related genera. Small leaves are seen as an advantageous feature of the plants' defensive structures, whereas big leaves are considered a disadvantage when exposed to browsing. Thus, the index values are negatively influenced (downgrading of the defense indicator value) by the occurrence of big leaves and positively affected (upgrading of the defense indicator value) by the occurrence of small leaf sizes (Table 3).

2.3. Statistical analyses

As our data did not satisfy the assumptions of the *t*-test (i.e., a normal distribution; Kolmogorov–Smirnov test), the Mann–Whitney *U* test (MWU) was used to compare two independent samples. Differences among more than two continuous variables were analyzed using the Kruskal–Wallis *H* test (incl. MWU with Bonferroni correction). The relationship between plant height and defense mechanisms of Central European woody plants was measured using the nonparametric Spearman's rank-correlation coefficient (r_s). The mean defense indicator values ± SE are given unless otherwise stated. Our statistical analyses always evaluate the plants according to the most efficient defense mechanism against large herbivores (toxic substances > structural defense > digestion inhibitors > no defense). Hence, the topmost group might include defense mechanisms belonging to lower-ranked groups. Categorical variables (defense mechanisms and the ability of the plant to respond to damage) were analyzed separately using a Fisher's exact test (Freeman–Halton). This test is an alternative to the Pearson's Chi-square test and is used for larger contingency tables and for cells with expected frequencies less than five. All statistical tests were performed using the SPSS 16.0 statistical package.

3. Results

3.1. Plant defense mechanisms

About half of all Central European woody plants (64 species, 49%) have digestion inhibitors (Table 4). Species with structural defenses (29 species, 22%) and species with toxic substances (24 species, 18%) occur less frequently. One in ten species (14 species, 11%) lacks any defense. Deciduous and evergreen woody plants differ significantly in their defense mechanisms. Deciduous species invest heavily in digestion inhibitors (57 species, 49%) and structural defenses (27 species, 23%), whereas evergreen species allocate their resources to the synthesis of digestion inhibitors (7 species, 47%) and of toxic compounds (6 species, 40%). Structural defenses (2 species, 13%) are far less widely distributed. Only *Ilex aquifolium* and *Juniperus communis* show structural defenses. However, all evergreen plants have defense characteristics, whereas more than one in ten (14 species, 12%) of the deciduous plants evaluated do not invest in protection against large browsing herbivores. Among these undefended plants are species like *Acer campestre*, *Carpinus betulus* and *Fagus sylvatica*, and the group of structurally

Table 3
Calculation of the defense indicator values of Central European woody plants. For explanations of the defense indicator values, see Table 1 for information about the calculation of the leaf-size classes, see Section 2.

Defense indicator value	Chemical defense		Mechanical defense	Leaf size
	Toxic compounds	Digestion inhibitors		
6	√	√	√	1–4
	√	√/–	–	1
5	√	√/–	–	2, 3
	–	√/–	√	1
4	√	√/–	–	4
	–	√/–	√	2, 3
3	–	√/–	√	4
	–	√	–	1
2	–	√	–	2–4
1	–	–	–	1–4

√ = feature present, √/– = feature mainly present, – = feature lacking.

Table 4
Defense mechanisms and the ability of plants to respond to damage, tabulated for deciduous and evergreen Central European woody plants. Deciduous vs. evergreen plants, defense mechanisms: Fisher's exact test (Freeman–Halton), $Chi^2 = 10.29$, $P \leq 0.05$; ability to respond to damage: Fisher's exact test (Freeman–Halton), $Chi^2 = 22.1$, $P \leq 0.001$.

Feature	Deciduous (*N* = 116)		Evergreen (*N* = 15)		Total (*N* = 131)	
	Share [%]	*N*	Share [%]	*N*	Share [%]	*N*
Defense mechanisms						
Toxic compounds	15.5	18	40.0	6	18.3	24
Structural defense	23.3	27	13.3	2	22.1	29
Digestion inhibitors	49.1	57	46.7	7	48.9	64
No defense	12.1	14	0.0	0	10.7	14
Ability to response						
Yes	66.4	77	26.7	4	61.8	81
No	14.6	17	60.0	9	19.9	26
No data	19.0	22	13.3	2	18.3	24

Table 5
Defense mechanisms and the ability of plants to respond to damage, tabulated for deciduous Central European woody plants according to their growth form. Comparison of all three groups, defense mechanisms: Fisher's exact test (Freeman–Halton), $Chi^2 = 40.50$, $P \leq 0.001$; ability to respond to damage: Fisher's exact test (Freeman–Halton), $Chi^2 = 7.56$, P = n.s.

Feature	Trees (*N* = 34)		Intermediate (*N* = 17)		Shrubs (*N* = 66)	
	Share [%]	*N*	Share [%]	*N*	Share [%]	*N*
Defense mechanisms						
Toxic compounds	2.9	1	5.9	1	24.2	16
Structural defense	5.9	2	11.8	2	36.4	24
Digestion inhibitors	55.9	19	76.5	13	37.9	25
No defense	32.4	11	11.2	13	1.5	1
No data	2.9	1	0.0	0	0.0	0
Ability to response						
Yes	73.5	25	82.4	14	59.1	39
No	17.6	6	0.0	0	16.7	11
No data	8.8	3	17.6	3	24.2	16

well-protected plants comprises *Crataegus* species and many *Rosa* species.

The ability to respond to damage differs significantly between deciduous and evergreen woody plants (Table 4). The majority of the deciduous species (77 species, 66%) are able to react to feeding damage. In contrast, evergreen species are much less capable of compensating for damaged plant parts and tissue loss (4 species, 27%).

In deciduous woody plants, strategies to avoid large-herbivore browsing differ significantly among the three growth forms (tree, intermediate, shrub) (Table 5). Almost all shrubs (65 species, 99%) invest in defense mechanisms, whereas only two-thirds (22 species, 65%) of the trees have defensive traits. The intermediate group, combining both growth forms, has an intermediate position among the groups of shrubs and trees (16 species, 89%). The ability to respond to feeding damage reveals no significant differences among the three growth forms.

3.2. Plant defense indicator

Evergreen woody plants (4.3 ± 2.9) have significantly higher plant defense indicator values than deciduous woody plants (3.0 ± 2.2) (Fig. 1). In deciduous woody plants, indicator values of shrubs (3.9 ± 2.0) differ significantly from those of trees (2.2 ± 1.6) and the intermediate group (2.5 ± 1.5), whereas those of trees and the intermediate group do not differ (Fig. 2). In general, plant defense differs significantly according to growth height (Fig. 3).

4. Discussion

Central European plants exhibit widespread chemical and structural protection against browsing by large herbivores. Categorization of the chemical defenses into toxic substances and digestion inhibitors reveals the high significance of the latter as mechanisms that deter herbivores from feeding. According to Howe and Westley (1990), digestion-inhibiting substances and structural defense mechanisms that belong to the group of quantitative defenses (Rosenthal and Janzen, 1979) are particularly important in defense against large mammalian herbivores. The synthesis of toxic compounds, also referred to as qualitative defense mechanisms (cf. Coley et al., 1985), is less pronounced because it is associated with a large investment of scarce nutrients that are also needed for vital functions in the plant's metabolism. However, evergreen plants in particular allocate a great amount of resources to the production of toxic compounds. Their long leaf lifespans permit the higher initial construction costs required to produce defense characteristics that are advantageous in the long term (Coley et al., 1985).

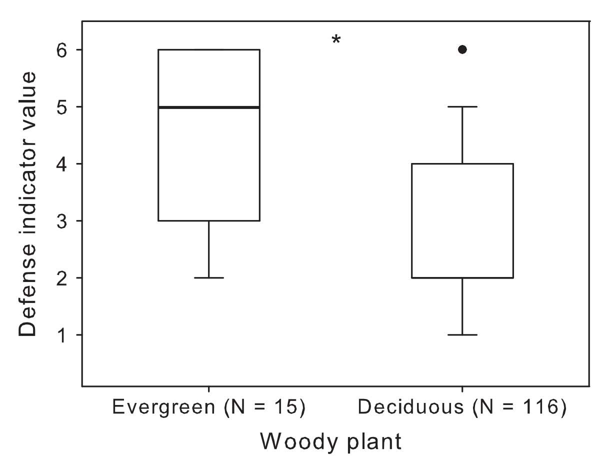

Fig. 1. Defense indicator values for deciduous and evergreen Central European woody plants. For explanations of the defense indicator values, see Table 1. Boxplots show the 10th and 90th percentiles (whiskers), 25th and 75th percentiles (boundary of the box), median (line) and outliers (dots). Mann–Whitney *U* test, $U = 476$, $^{*}P < 0.01$.

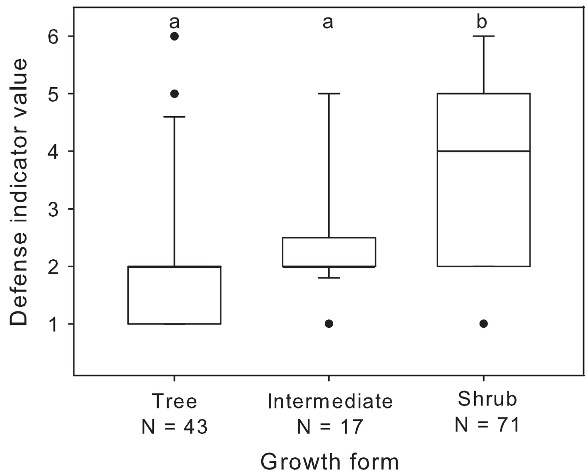

Fig. 2. Defense indicator values and growth forms of deciduous Central European woody plants. Boxplots show the 10th and 90th percentiles (whiskers), 25th and 75th percentiles (boundary of the box), median (line) and outliers (dots). Boxplots capped with different letters indicate significant differences at $P < 0.05$ (Mann–Whitney *U* test with Bonferroni correction, level for significance: $\alpha = 0.017$). The intermediate group contains plants with a growth form alternating between tree and shrub, depending on the site characteristics.

Our results on the different degrees of defense shown by evergreen and deciduous woody plants are consistent with information on the intensively studied interactions between woody plants and snowshoe hares in winter (Sinclair et al., 1988; Bryant et al., 1992). The high concentrations of secondary metabolites in evergreen plants serve to deter feeding by snowshoe hares. The hares therefore prefer deciduous plants to evergreen ones (Bryant et al., 1991). Large herbivores also seem to prefer the more palatable deciduous woody plants over evergreens (Bryant and Kuropat, 1980; Bryant et al., 1983; Coley et al., 1985). This preference in turn contributes to the abundance of unpalatable, usually heavily defended, evergreen species (Bryant et al., 1991) like juniper (*J. communis* ssp. *communis*, *Juniperus sabina*). The high fiber content, the low water content and the thick cuticle of many evergreen plant leaves are primarily adaptations to unfavorable conditions such as winter desiccation. Together with high concentrations of digestion inhibitors and toxic compounds, these attributes serve as effective browsing deterrents. Many Central European nature reserves inhabited by grazing and browsing animals furnish evidence of the general preference of these animals for deciduous over evergreen woody plants (cf. also McKey et al., 1978, cited in Coley et al., 1985). In evergreen plants, only young plants and buds, as long as they contain relatively low amounts of resins and secondary metabolites, are subject to feeding (cf. Bryant et al., 1991). Only in winter, when food is scarce, do they become a major forage source for browsing herbivores. Owing to this abruptly increasing feeding pressure (Grubb, 1992), a high level of defense is essential for the survival of evergreen woody plants.

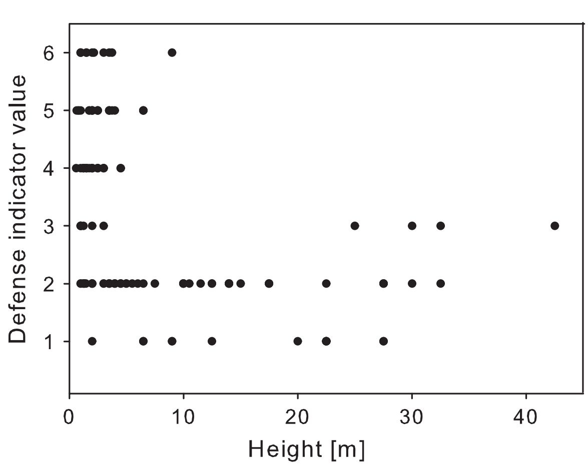

Fig. 3. Relationship between the defense indicator value and plant height of Central European woody plants ($N = 131$). $r_s = -0.53$, $P \leq 0.001$, $y = 2.76–0.8 \times x$.

To a certain extent, our findings support the theory of plant apparency (Feeny, 1976; Rhoades and Cates, 1976). This theory holds that plants easily found by herbivores (e.g., evergreen woody plants in winter) invest heavily in chemical defenses. Our considerations of the defense indicator presented in this paper reveal that evergreen and deciduous woody plants possess different levels of protection. Moreover, leaf susceptibility to browsing appears to depend on the time that a leaf is available.

An entirely new aspect in the overall picture of defensive traits is the ability to respond to damage. The high level of chemical defense in evergreen plants results in far fewer occasions in which damage occurs and in which response to damage would therefore be necessary. However, deciduous species are more frequently subject to browsing and are therefore characterized by multiple compensatory reactions (Ringler, 1995; Weber, 2003). Intensive browsing, even close to the base of a deciduous tree or shrub, often results in rapid growth from the stool.

In accordance with Herms and Mattson (1992), our study finds a link between the height of woody plants and intensity of defense. Trees and trees/shrubs (intermediate group) have a significantly lower defense indicator value than shrubs. Grime et al. (2007) argues that the vegetation found in any particular place in the world is the result of three interacting forces: competition, stress and disturbance (CSR model). These interacting factors vary from place to place and are altered by pathogens (Rosenberg et al., 2004), nectar robbers (Morris et al., 2007, reduction of plant performance), pollinators, seed dispersers, defenders, fungi, bacteria (Morris et al., 2007, exertion of positive effects on plant performance) and large herbivores that affect the vegetation by trampling, plowing and browsing. Consequently, the morphological characteristics of trees and shrubs reflect a diverse set of impacts, and growth height of woody plants is at least in part a consequence of browsing by large herbivores. Once a tree has reached a certain height, the risk of attack decreases gradually (Rooke et al., 2004). By contrast, shrubs continue to grow in the preferred browsing zone of large mammalian herbivores and thus remain target plants. Hence, shrubs have a higher level of defense than do trees. According to Augner (1995), defense mechanisms will generally be selected if the benefits of the traits exceed the costs and vice versa. The high defense indicator value for shrubs describes these risks and illustrates the consequences of natural selection for defensive traits.

5. Conclusion

Although chemically- and structurally-defended plants are usually browsed less heavily than undefended plants, no defense strategy offers complete protection. Thus, a high indicator value does not automatically mean that the plant is totally protected from use by all large herbivores. In fact, it is more likely, depending on the neighboring plants (Callaway et al., 2005) and the toxicity actually shown against a certain herbivore species, that even the best-adapted plant has at least one opponent. According to Laycock (1978), poisonous plants occur over a wide range of palatabilities, and palatability varies with the animal species. Hence, unpalatable as well as poisonous plant attributes do not offer total protection. Nevertheless, the evaluation of the defense indicator achieved in this study illustrates the coevolutionary adaptations occurring between Central European woody plants and large herbivores. The data set examined in this study supports the prevailing view that plants face a predicament: they must develop defense mechanisms as a response to herbivore damage, but they must also invest resources in morphological traits that are advantageous in the community where they grow. Even though the new indicator value might require further testing and adjustment, it appears to be an appropriate measure for the quantification of plant defense mechanisms.

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