EFFECTS OF PEDUNCULATE OAK TREE VITALITY ON GYPSY MOTH PREFERENCE AND PERFORMANCE

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Abstract - Gypsy moths and powdery mildew play a significant role in oak decline processes. However, information is lacking on the effects on the gypsy moth of impaired tree vitality caused by defoliation or parasite infection. We assessed how pedunculate oak leaves collected from vigorous, declining, and infected trees influenced gypsy moth preference and performance (growth and nutritional indices). We found a negative effect of powdery mildew-infected leaves on gypsy moth performance, while declining trees had positive effects on gypsy moth performance and preference. All examined parameters of larvae fed declining oak leaves were higher than those of larvae fed vigorous oak leaves. Increased growth on declining oak leaves was caused by both higher consumption and more efficient food utilization. The results of this research could help us to better understand multitrophic interactions in complex communities such as oak forests.

Key words: Lymantria dispar L.; preference; performance; *Quercus robur* L.; tree vitality; *Microsphaera alphitoides* Griff. et Maubl.

INTRODUCTION

The gypsy moth *Lymantria dispar* L. is one of the most serious pests of hardwood forests in temperate regions (Montgomery and Wallner, 1988). This pest causes enormous damage from the defoliation of large areas that occurs after its frequent outbreaks (Muzika and Liebhold, 1999; 2001; Naiddoo and Lechowicz, 2001; Fajvan et al., 2008). It feeds on 500 plant species (Lance, 1983), but the species of the genus *Quercus* are the most suitable hosts (Janković, 1958; Barbosa and Krischik, 1987). Its native range stretches from Japan, China, and Si-

beria across Russia to Western Europe and as far south as the Atlas Mountains of North Africa. In North America, the gypsy moth has spread over most of the eastern United States (Tobin and Whitmire, 2005). However, the risk of defoliation by gypsy moths is not uniform across its range of distribution. In Central European countries, it rarely occurs and causes less damage then in the Balkan Peninsula, where climatic conditions for its development are the most favorable (Janković, 1960). In Serbia, the gypsy moth can be found in all areas, even up to 1600 m above sea level, although above 1000 m it is not considered to be a significant pest

(Janković, 1954). From 1862 to 1995, there were 16 gypsy moth outbreaks in Serbia (Marović et al., 1998), some of which had disastrous consequences. For example, in 1957 gypsy moths attacked 50% of all forests in Serbia, including all pure oak and most mixed oak forests (Milević, 1959), while outbreaks in 1997 and between 2004 and 2008 were less severe, with about 25% of all Serbian forests being attacked (Mihajlović et al., 1998; 2008). A new outbreak began in 2011 and is still in progress. Around 66 000 ha of oak and beech forests were completely defoliated and around 65 000 ha suffered from severe defoliation during 2013. After that, gypsy moths spread over more than 340 000 ha of forests, most of which were infested with more than 100 egg masses per ha (Mihajlović, personal communication). Frequent outbreaks damage forests, especially oak forests, which are the most suitable habitats for the caterpillars. For other tree species, the level of expected damage is correlated to the food quality. Plant characteristics such as chemical composition, physical properties, and phenology can strongly affect the insect's preference and performance (Larsson, 2002).

Carbon-based allelochemicals, which plants use to cope with folivorous insects, have a key role in the theory of plant/insect relationships (Tuomi et al., 1988). Compounds such as tannins, lignin, and phenols impede the digestion or consumption of leaves by herbivores (Mattson et al., 1983; Waring et al., 1985; Brayant et al., 1985; Larsson et al., 1986; Barbehenn et al., 2013; 2014). High carbon content in the leaves has been considered to indicate the increased content of defense compounds. The allocation of the carbon towards the synthesis of different compounds depends on the presence of nutrients. Among nutrients, proteins most strongly affect insect fitness and their content can be predicted from the content of nitrogen. Therefore, a high carbon to nitrogen ratio suggests a higher probability that the carbon was allocated towards defense compounds than towards carbon-based nutrients (Tuomi et al., 1988). Nitrogen is the most important nutrient for insect growth and survival (Mattson, 1980; Mattson and Scriber, 1987). Nitrogen levels vary from 0.03 to 7.0% of dry mass, with higher N content in young and expanding plant parts (Mattson, 1980) and decreasing levels during maturation later in the season (Bassett et al., 1970; Feeny, 1970; Thomas and Blank, 1996; Barbehenn et al., 2013; 2014).

Food quality can be modified due to changes in tree vitality and health. Some pathogens may affect plant defense responses, nutritional quality, vascular systems, rates of senescence, or the shape, color and form of host plant leaves (Barbosa, 1991). Vigorous trees are more resistant to primary diseases and pests (Jactel et al., 2012). On the other hand, stressed trees are more susceptible to the primary pests and diseases that attack leaves (Jactel et al., 2012), and declining trees are more susceptible to the parasites that cause tree weakness, secondary (Moraal and Hilszczanski, 2000, Muzika et al., 2000) and tertiary insects (Evans et al., 2007). Oaks are predisposed to opportunistic pests, such as insect borers; to pathogens, such as root rot; and to defoliation, primarily from insects, but also by fungi, late spring frosts, and drought (Wargo, 1996). To predict the risks of oak decline it is important to understand the relationships among oak trees, plant diseases, and herbivorous pests. It is well known that oak leaves after defoliation are much more suitable to powdery mildew (*Microsphaera alphitoides* Griff. et Maubl.) infections, which increase the severity of the plant stress. In addition, after several defoliations, stressed trees become suitable to *Armillaria* root rots (Marçais and Bréda, 2006) and *Phytophthora* (Jönsson et al., 2006) species. The positive interaction of both pathogens could be significant in oak decline syndrome (Marcais et al., 2011). Some diseases could improve and some could decrease leaf suitability for herbivorous insects (Rieske et al., 2003).

There are a many theories to explain oak decline in Europe (Fuhrer, 1998; Thomas et al., 2002). Some of them emphasize the role of vascular pathogens from the genus *Ophiostoma* and *Ceratocystis* (Josifović, 1926; Petrescu, 1974; Przybył and Morelet, 1993) and their vectors *Scolytus intricatus* or *Agrilus* sp. as casual agents of oak decline; however the highly pathogenic species that is the originator of

oak wilt in North America, the fungus *Ceratocystis fagacearum* (Bretz) Hunt. (anam, *Chalara quercina* Henry), has never been confirmed in Europe, where it is ranked as quarantine pest A1 (OEPP/EPPO, 1979, Gibbs, et al., 1984; IMI, 1993). Oszako (2000) stated that *Ophiostoma* species could not be recognized as primary agents in oak decline because their pathogenicity is not confirmed experimentally. According to other authors, oak decline is mainly related to tree ageing, inadequate stand conditions, or pollution (Schüt, 1984; Mueller-Dombois, 1992; Thomas et al., 2002). Oak decline in Europe results from the influence of several biotic and abiotic factors that follow each other across years (Thomas et al., 2002; Jönsson et al., 2006). For example, a succession of dry years and droughts combined with a heavy defoliation by *Lymantria dispar* and winter frosts without snow cover is recognized as the main cause of oak decline (Tomiczek, 1993; Thomas et al., 2004). Some authors emphasize abiotic instead of biotic factors as a trigger of oak decline processes, and other emphasize interactions among these stressors (Thomas et al., 2004). Drought affects the amount of damage from forest insects and pathogens (Chakraborty et al., 2000; Netherer and Schopf, 2010; Jactel et al., 2012). Prolonged droughts and sudden floods could increase oak sensitivity to *Phytophthora* species in the future (Balcì and Halmschlager, 2003; Jung et al., 2000; Jönsson et al., 2006). A causal relationship between *Phytophthora* species and climatic extremes with yellowing leaves, increased transparency, and crown dieback has been proven for many tree species (Jung, 2009; Corcobado et al., 2010). Generally, climate changes, defoliators, and pathogens contribute to oak decline processes (Oszako, 2000). In other words, expected global climatic changes will affect the severity of herbivore and pathogen attacks and their impact on the species composition, ecosystem function, and socioeconomic value of forests (Ayres and Lombardero, 2000).

It is known that the gypsy moth significantly contributes to oak decline processes, but we are lacking information about the effects of declining trees on gypsy moths.

Powdery mildew *Microsphaera alphitoides* Griffon & Maubl. also has a significant role in oak decline processes (e.g. Desprez-Loustau et al., 2011); it often infects oak leaves after gypsy moth or tortrix and winter moth defoliation. When it occurs after winter moth or tortrix moth defoliation, powdery mildew infection changes leaf quality and thus may affect gypsy performance. Sometimes, powdery mildew attacks old trees without previous defoliation. That is why we performed research on powdery mildew and tree vitality effects on gypsy moth performance. Preference was tested only between vigorous and declining trees using second instar gypsy moth larvae. Performance was tested on the leaves of all three groups of trees (vigorous, declining, and attacked by powdery mildew) using fourth instar larvae.

We assumed that differences in the disturbance of pedunculate oak trees such as decline or powdery mildew attack might result in changes in leaf chemical composition and, accordingly, affect gypsy moth performance. Results obtained in this research could help us better understand species interactions in complex communities such as oak forests.

MATERIALS AND METHODS

Insect material

Egg masses used in experiments were collected from Jabukovac near Negotin (44° 21′ 37″ N, 22° 23′ 38″ E) in the mixed Turkey oak (*Quercus cerris* L.) and Hungarian oak (*Q. frainetto* Ten.) forest during autumn 2011. Eggs were first mechanically cleaned of hairs, and then, the living eggs were surface disinfected by soaking in 0.1% sodium hypochlorite for 5 min. Eggs were then rinsed with distilled water for 10 min and finally dried. The eggs were then kept in a refrigerator at 4°C until the beginning of the experiments. Initiation of laboratory hatching was done in a climate chamber at 25°C.

Tree selection

We selected five trees per each group of healthy, declining, and powdery mildew-infected trees. Vig-

orous trees had large increments and dense crowns with undistorted primary and secondary branching (Longauer et al., 2004). Declining trees had sparse crowns, twig abscission, and water sprouts in the lower parts of the crown or on the main stem, and symptoms of attack by secondary insects were present (Tomiczek, 1993). The third group was the same as the first but with leaves infected by powdery mildew. All trees were selected from the same forest of Mala Moštanica near Belgrade (44° 39′ 26″ N, 20° 17′ 37″ E).

Visual assessment of crowns

For the visual assessment of crown conditions, we used the methods described in the manual for visual crown assessment from International Co-operative Program on Assessment and Monitoring of Air Pollution Effects on Forests (Anonymous, 2006). We used absolute reference trees from a photo guide (Innes, 1990) to assess the level of defoliation with an accuracy of 5%. Defoliation was assessed in the middle of August of the previous year.

Leaf characteristics

Leaves used as food for fourth instar gypsy moth larvae were the materials for chemical analysis. Those leaves were taken from the mid-crown of selected trees in the middle of May. Leaf samples were dried for 48 h at 40°C. Total carbon content was determined according to the method of Anstett, as modified by Ponomarieva and Plotnikova (1975), with wet combustion in CrO_3 and H_2SO_4. Total leaf nitrogen was determined according to the method of Kjeldahl. The destruction of the sample was done in sulphuric acid in the presence of a catalyst ($CuSO_4$ and K_2SO_4, 1:3) until all organic nitrogen had been transferred into ammonia. The distillation of ammonia was performed with a Kjeldahl apparatus, and the distillate was caught in orthoboric acid (Rhee, 2001). Prior to the determination of leaf water content and specific leaf weight, leaves were scanned, and their masses were measured before and after drying for 72 h at 65°C.

Preference (choice) test

Gypsy moth caterpillars were grown on an artificial medium (MP Biomedicals, Inc.) in Petri dishes (120 × 15 mm) at T = 23°C, Rh = 65%, Photoperiod 15:9 in a climate chamber (Sanyo) until molting into the second larval instar. After the molting, caterpillars were separated for 24 h of starvation. An agar-water (2%) layer (2 mm thickness) was poured into Petri dishes (90 × 14 mm), and covered with filter paper after turning solid. Then, we placed two disks (30 mm diameter) taken from healthy and declining trees into each Petri dish. Leaf disks were fixed to the layer with pins. Then one caterpillar was introduced into the centre of each dish. During the experiment, filter paper was watered occasionally to maintain the freshness of leaf disks. We tested the preference of gypsy moth caterpillars in the five combinations of disks made from leaves collected from five vigorous and declining trees. For each combination, 20 caterpillars were tested. At the end of the experiment (after 48 h), the remains of the disks were scanned (200 dpi resolution, jpg form) to determine the area consumed for each species in the pair using the ImageTool software package (UTHSCSA). The consumed area was calculated as the difference between the disk area before the feeding and the remaining area.

We did not test gypsy moth preference between healthy and powdery mildew-affected leaves because of discrepancies in the appearance of second larval instars and the symptoms of powdery mildew, which occurs much later in the season.

Growth and nutritional indices

Gypsy moth caterpillars were grown on an artificial medium (MP Biomedicals, Inc.) in Petri dishes (120 × 15 mm) at T = 23°C, Rh = 65%, photoperiod 15:9 in a climate chamber (Sanyo) until molting into the fourth larval instar. After molting, caterpillars were separated and grown separately until the end of the experiment on leaves taken from healthy, declining, and powdery mildew-attacked pedunculate oaks. Up to ten caterpillars were grown separately in Petri

dishes (120 × 15 mm) for each pedunculate oak tree (total, 150).

Thirty caterpillars from the same experimental group were measured. Caterpillar mass was measured at the beginning and at the end of the experiment, i.e. after drying at 65°C for 3 days. A regression of dry on fresh mass in a random sample of 50 caterpillars per experimental group was used for calculating the dry mass of caterpillars at the beginning of the experiment. Caterpillar mass at the end of the experiment was measured after drying.

Excrement and leaf remains were collected during the experiment, dried, and used to calculate the nutritional indices according to the formulas of Waldbauer (1968), except for the relative growth rate (RGR and RCR), which were calculated using the mass at the beginning and at the end of experiment after three days, according to the formula of Farrar et al., (1989).

Growth rate $(GR) = (m_f - m_i)/d_e$ – [mg /day]

Relative growth rate $(RGR) = (m_f - m_i)/(d_e \times m_i)$ – [mg/[mg × day]]

Consumption rate $(CR) = w_c/d_e$ – [mg/day]

Relative consumption rate $(RCR) = w_c/(d_e \times m_i)$ – [mg/[mg × day]]

Efficiency of conversion of ingested food $(ECI) = (m_f - m_i)/w_c \times 100$ – [%]

Assimilation efficiency $(AD) = (w_c - w_f)/w_c \times 100$ – [%]

Efficiency of conversion of digested food $(ECD) = (m_f - m_i)/(w_c - w_f) \times 100$ – [%]

d_e – duration of experiment (days)

m_i – larval weight at the beginning of the fourth larval instar

m_f – larval weight at the end of the experiment (3 days)

w_c – weight of consumed food

w_f – weight of feces

Statistical analysis

Statistical analysis was performed using the software package Statistica 12.0 (StatSoft, Inc.).

Gypsy moth caterpillar preference was analyzed using a t-test for pairs of consumed areas for each pair of vigorous and declining trees. To normalize data before analysis we used the square root of (x + 0.5) transformation, where 'x' is the consumed area of disk.

Spearman coefficients of correlation between differences in defoliation and relative consumption of leaves in two-choice tests were determined to evaluate the relationship between defoliation and leaf acceptability.

Differences in the chemical composition of leaves used for the no-choice test were determined based on an analysis of variance and Duncan test of multiple ranks on square root (x + 0.5) transformed data.

To evaluate differences in the performance of caterpillars fed different types of pedunculate oak leaves, we used an analysis of variance (ANOVA) and analysis of covariance (ANCOVA). For each observed parameter, mean values and standard errors (± SE) were determined. Nutritional indices were analyzed by ANCOVA where the numerator of the index is the dependent variable and the denominator is the covariate (Raubenheimer and Simpson, 1992). The initial mass of caterpillars was used as a covariate for the analysis of the growth and consumption rate (equivalent to Waldbauer's relative growth rate [RGR] and relative consumption rate [RCR]). The mass of consumed food was a covariate for the comparison of growth (equivalent to the efficiency of the conversion of ingested food into biomass [ECI]) and

food assimilation (equivalent to approximate digestibility [AD]) while the difference between the mass of consumed food and mass of feces (food assimilation) was a covariate for the comparison of the growth rate that is equivalent to the efficiency of conversion of digested food into biomass (ECD). If differences in gypsy moth growth among experimental groups revealed by ANOVA disappear after ANCOVA with consumption as a covariate, it would indicate that leaf quality affects growth through pre-ingestive mechanisms. Otherwise, both pre- and post-ingestive processes are involved. Significant differences revealed by ANCOVA with assimilation as the covariate would point to the metabolic cost imposed by food digestion (Horton and Redak, 1993; Hägele and Rowell-Rahier, 1999).

RESULTS

A two-choice test revealed that gypsy moths preferred leaves from declining trees to leaves from vigorous trees in all five pairs (Figure 1). Leaf area consumed by second instar larvae was 15% to 38% higher in the group that was fed declining leaves than the group fed vigorous leaves. The percentage of defoliation ranged from 50% to 70% in declining and from 10% to 20% in vigorous trees. The greatest differences in defoliation were recorded in the fourth and first pairs (60% and 50%, respectively) and the smallest (35%) in the second pair of trees in the two-choice test. Differences in defoliation between declining and vigorous trees in the fifth and third pairs were equal to 40%. Defoliation in oaks attacked by powdery mildew was less than 20% in each tree.

We found a significant positive correlation between differences in defoliation and differences in the consumed area of leaf discs in the test of choice between declining and vigorous trees (R = 0.97, P < 0.05).

The results of the analyses of the carbon and nitrogen content in leaves of all three types of tested oaks are presented in Table 1. Declining oak leaves had the highest and powdery mildew leaves had the lowest nitrogen and water content. The C/N ratio in declining oak leaves was the lowest while powdery mildew oak leaves had the highest ratio. Specific leaf weight, which indicates leaf toughness, was also the highest for powdery mildew oaks. Intermediate values of these traits were recorded for vigorous oaks.

Results of growth and feeding traits as well as growth and nutritional indices are given in Table 2. There were no differences in larval mass at the beginning of the experiment (Table 2). After three days of feeding, fourth instar larvae fed declining oak leaves had on average 5% and 35% higher body mass than larvae fed vigorous and powdery mildew oak leaves, respectively.

Mass gained (growth) after three days of feeding on declining oak leaves was 12% and 63% higher than for those fed leaves of vigorous and powdery mildew oak leaves, respectively. Lower consumption of powdery mildew than vigorous oak leaves was recorded. The dry mass of assimilated food was highest on declining oak leaves (Tables 2, 3).

The RGR of the declining oak was 12.5% and 64% higher than in vigorous and powdery mildew oak, respectively. According to an ANCOVA analysis, the RCR was lower in the powdery mildew group than in the two other groups (Tables 2, 4). Larvae kept on declining oak were better at the conversion of ingested food into biomass (ECI) and assimilated food more efficiently (AD) than larvae kept on powdery mildew oak. Larvae feed on vigorous oak had intermediate values for both parameters. The same trend was recorded in the conversion of assimilated food into body mass (ECD). We found significant host plant effects on growth in both ANOVA and ANCOVA where food consumption was used as the covariate (ECI). Accordingly, besides pre-ingestive mechanisms, post-ingestive mechanisms also contributed to growth variation. A comparison of AD and ECD by ANCOVA confirmed that, among post-ingestive mechanisms, both differential digestion and differential metabolic load imposed by ingestion of different oak leaves explained differences in growth among larvae.

Table 1. Foliar characteristics (mean ±SE) of the different type of pedunculate oak trees, compared using ANOVA (F and P values) and Duncan multiple range tests. Means in the same row followed by the same letter do not differ significantly (P < 0.05). d.f. – degrees of freedom.

Foliar characteristics	Declining	Vigorous	Powdery mildew	F	d.f.	P
C (%)	38.5±0.57a	38.6±0.70a	36.0±0.49b	6.00	2, 14	0.0155
N (%)	2.2±0.03a	1.8±0.04a	1.6±0.04c	95.00	2, 14	<0.0001
C/N	17.5±0.22c	21.0±0.44b	23.2±0.30a	78.50	2, 14	<0.0001
Specific leaf mass (mg/cm^2)	4.1±0.08a	4.2±0.07a	5.0±0.10b	32.00	2, 72	<0.0001
Water content (% in fresh mass)	64.7±0.32a	60.1±0.34b	56.5±0.47c	111.80	2, 72	<0.0001

Table 2. Growth and feeding data (Mean±SE) for 4th instar gypsy moth larvae depending on type of diet. After one-way ANOVA (see Table 3) data were compared by Duncan post hoc test and significantly different values were marked by different letters within a row (P 0.05). Duncan test which followed one-way ANCOVA (see Table 4) was used for comparison of growth and nutritional indices.

	Declining	Vigorous	Powdery mildew
Number of tested larvae	50	50	50
Initial mass (mg)	8.73±0.144a	8.81±0.183a	8.76±0.121a
Final mass (mg)	23.22±0.549a	21.58±0.771b	14.09±0.249c
Growth (mg)	14.49±0.475a	12.77±0.716b	5.32±0.220c
Consumption (mg)	88.78±4.083a	87.07±3.606a	65.74±2.038b
Food assimilated (mg)	47.71±3.232a	39.28±1.981b	25.20±1.570c
RGR (mg/mg day)	0.56±0.017a	0.49±0.026b	0.20±0.009c
RCR (mg/mg/day)	3.44±0.172a	3.35±0.151a	2.53±0.090b
ECI (%)	17.6±0.86a	14.7±0.62b	8.5±0.46c
AD (%)	54.3±2.41a	46.0±1.78b	37.8±1.69c
ECD (%)	35.1±1.78a	33.4±1.56b	25.9±1.96c

Table 3. F and P values from one-way ANOVA for growth and feeding data. Type of diet was a fixed factors. Degrees of freedom (df) for type of diet was equal to two, while df of error was 147.

Type of analysis	Source of variation	F	P
Initial mass	diet	0.07	0.9326
	error		
Final mass	diet	74.33	<0.0001
	error		
Growth	diet	90.54	<0.0001
	error		
Consumption	diet	14.62	<0.0001
	error		
Food assimilated	diet	23.04	<0.0001
	error		

The plots of growth against food consumption (Fig 2a) and assimilation (Fig. 2c) visualize how much of the ingested and digested food was allocated to the growth. These parameters of performance are highest in larvae fed leaves of declining oaks and worst on powdery mildew oak leaves. The same rank

Table 4. F and P values from ANCOVA for performance traits. Initial mass (a), consumption (b) and assimilation (c) were used as covariates. Each ANCOVA analysis represent equivalent to Waldbauer's indices (Waldbauer, 1968). Diet was fixed factor. Degrees of freedom (df) for type of diet was equal to two, for covariate was equal to one, while df of error was 146.

Performance traits	Source of variation	F	P
Growth rate ~RGR	diet	94.50	<0.0001
	covariate	7.27	0.0078
	error		
Consumption rate ~RCR	diet	14.52	<0.0001
	covariate	0.01	0.9334
	error		
Growth ~ECI	diet	63.56	<0.0001
	covariate	37.30	<0.0001
	error		
Consumption - Feces ~AD	diet	10.11	0.0001
	covariate	148.43	<0.0001
	error		
Growth ~ECD	diet	57.08	<0.0001
	covariate	9.69	0.0022
	error		

of oak suitability is shown in the plot representing the efficiency of nutrient extraction (Figure 2b).

DISCUSSION

A broad spectrum of defense mechanisms is used by plants against microbial pathogens or herbivorous insects (Berryman, 1988; De Vos et al., 2006). These mechanisms include physical and chemical traits (Baldwin and Preston, 1999) which could be constitutive or induced defense responses (Mattson et al., 1988; Slansky, 1990) that become activated upon pathogen infection or insect herbivory (De Vos et al., 2006). The nutritive value and allelochemical content significantly change during leaf maturation so that synchronization between leaf phenology and insect development exhibits a great impact on insect growth and underlying behavioral and physiological traits (Rossiter et al., 1988; Haukioja et al., 2002; Barbehenn et al., 2013).

The gypsy moth is a mobile species that uses passive windborne dispersal during the first and second instar to reach an acceptable host (Leonard, 1967). This passive movement can be repeated several times until larvae reach a suitable host (Mason and McManus, 1981). The acceptability of host plants is a complex process that depends on the physiological characteristics of the gypsy moth (Milanović et al., 2008), its genotype (Lazarević and Perić-Mataruga, 2003), and also on the physical and chemical properties of the host plant (Foss and Rieske, 2003). Various chemical and physical characteristics of plants are used by caterpillars for locating the hosts (Schoonhoven, 1973). For example, caterpillars can differentiate between light and dark leaves, between young and mature leaves, and between leaves exposed to different levels of shade or leaves collected from different layers of a crown (Feeny, 1970; Smitley et al., 1993; Hemming and Lindroth, 1999; Ruhnke et al., 2009). Well-developed chemical senses lead insects to their food source, helping monophagous insects to
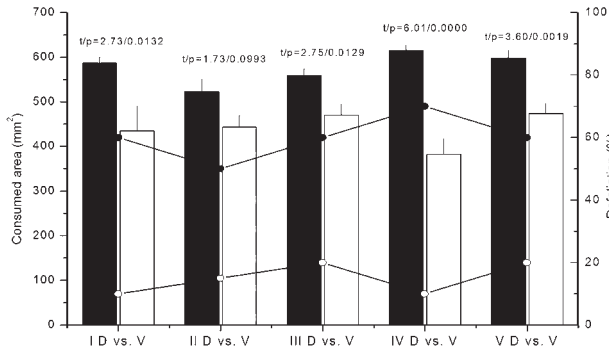
Fig. 1. The absolute preference in terms of area of leaf consumed (mean± SE) by 2nd instar gypsy moth larvae in two choice tests of five pairs (I-V) of pedunculate oak (D vs. V – declining vs. vigorous). Consumption of declining oak leaves is presented by filled columns while hollow columns are used for consumption of vigorous oak leaves. The comparison of the absolute area consumed in each choice test was done using t tests (t and p values are presented above the columns). Defoliation for each pair of declining and vigorous trees is presented as a percent of missing part of crown according to absolute referent tree (Declining – filled circles, Vigorous – hollow circles).

locate specific food and polyphagous insects to distinguish different plant species. Gypsy moth larvae can choose host plants depending on their nitrogen, carbohydrate, and tannin contents (Foss and Rieske, 2003). In our two-choice experiment with leaves from declining and vigorous trees, gypsy moth caterpillars preferred leaves from declining trees, which had higher nitrogen content and a lower C/N ratio. The differences in consumption were related to differences in the level of tree defoliation. If the difference in defoliation between trees in one pair was higher, then the difference in the amount of consumed food was also higher.

A no-choice experiment showed that gypsy moth larvae kept on declining tree leaves consumed the same amount of food as those on vigorous tree leaves. However, the amount of assimilated food and relative growth rate were higher. Faster growth was caused by improved digestibility (higher AD) and lower metabolic cost of processing high quality leaves (higher ECD). The high nitrogen and water content and low toughness of declining oak leaves may explain their post-ingestive effects on gypsy moth larval performance. Similar to our findings, nitrogen content in ar-
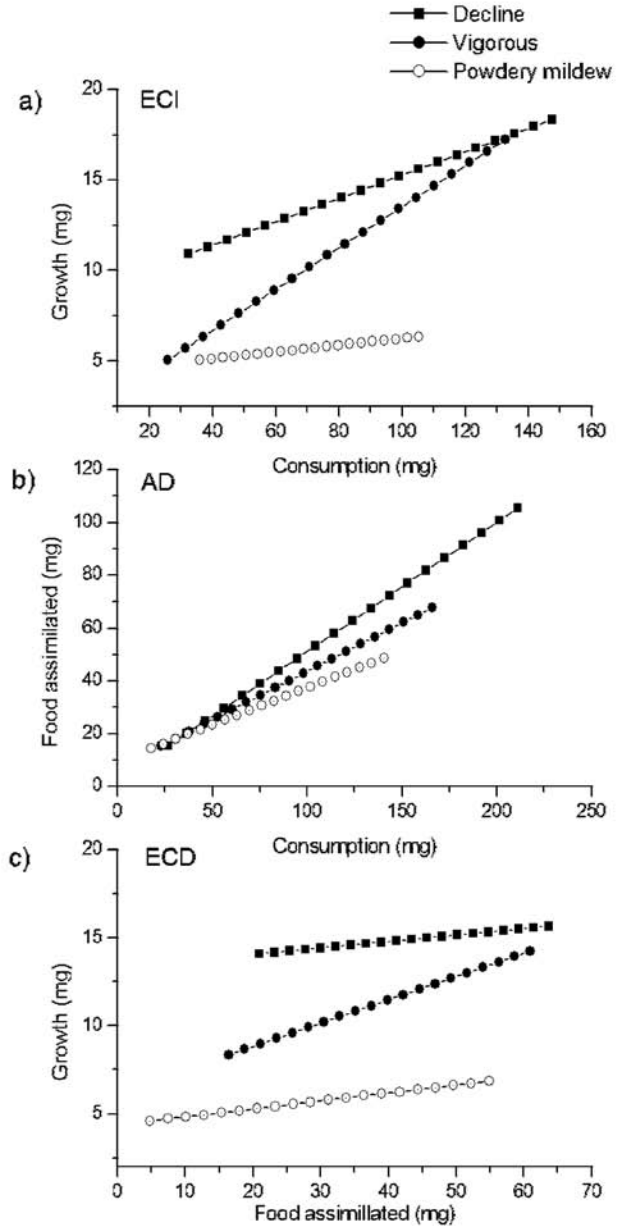

Fig. 2. Bicoordinate plots of ANCOVA on mass gain (growth) against consumption (a), food assimilated against consumption (b) and weight gain (growth) against food assimilation (c).

tificial food and plant leaves affects food utilization by the gypsy moth (Mattson, 1980; Stockhoff, 1992; Lindroth et al., 1997; Osier and Lindroth, 2001; Chen et al., 2004; Barbehenn et al., 2004; Barbehenn et al., 2013; 2014).

Lower consumption and food assimilation as well as retarded growth (RGR) in larvae kept on powdery mildew oak can be explained by a high C/N ratio, which according to the carbon nutrient balance hypothesis (Tuomi et al., 1988), indicates greater allocation of plant resources to carbon-based defense compounds. Besides, powdery mildew leaves had the highest specific leaf weight, which indicates higher leaf toughness and consequently lower RCR (pre-ingestive effects). Leaf toughness reduces nutrient intake and assimilation efficiency in locusts, and slows down the passage of food through the gut (Clissold et al., 2009). That the powdery mildew oak leaves had the lowest water and nitrogen content also contributed to the larvae feeding on them having worse growth than larvae fed vigorous or declining oak leaves. Experiments by Scriber (1979) have suggested that ECD is positively correlated with food water content and that lower leaf water content might be the major factor suppressing nitrogen assimilation and larval growth (however, see Barbehenn et al., 2014 and references therein). Powdery mildew leaves also exhibited post-ingestive effects, as can be seen from the lower ECI values. Less efficient food utilization was caused by both the lower digestibility and metabolic costs imposed by the ingestion of infected leaves. A recent report on the negative effect of experimentally changed leaf chemistry (with respect to lowered N and higher C/N ratio) on gypsy moth performance (Wang et al., 2009) supports our findings.

We recorded negative effects of powdery mildew-infected leaves on gypsy moth performance. However, declining tree leaves had a positive effect on gypsy moth performance and preference. All observed parameters were higher than those for vigorous oak leaves were. However, the highest defoliation in our experiment did not exceed 70%. In contrast to our results with declining trees, 90% artificial defoliation that induced defense responses in oaks led to decreased consumption in second instar gypsy moth larvae on leaves of both black and white oaks, while a slight but not statistically significant increase in RGR was recorded only in larvae fed black oak leaves (Rieske and Dillaway, 2008). Differences between the results of Rieske and Dillaway (2008) and ours point

to the importance of the host plant species, developmental stage of the gypsy moth, and level of defoliation and tree vitality for predicting host plant effects on gypsy moth performance and population dynamics.

In conclusion, declining trees could attract caterpillars in forests, and due to the caterpillars' better performance on those leaves the trees may serve as an incubator or small hot spot for future gypsy moth outbreaks. An implication for forest management could be the benefit of cutting declining trees, but the question of at which phase or level of defoliation it should be done is still open.

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