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Suitability of Turkey Oak, European Beech, and Hornbeam to Gypsy Moth Feeding

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Abstract: Pest resistance of trees should be taken into account in future forest strategy planning and predicting risks of defoliation. The gypsy moth (GM) (*Lymantria dispar* L.) is a serious forest pest with outbreaking population dynamics. To estimate defoliation risk of the most widely distributed tree species in Balkan Peninsula and Europe (Turkey oak *Quercus cerris* L., European beech *Fagus sylvatica* L. and hornbeam *Carpinus betulus* L.), we carried out laboratory feeding trials and investigated their acceptability and suitability for GM development. We determined morphological and chemical attributes of these hosts as well as larval host preference, growth and nutritional indices. Preference, growth, and efficiency of food conversion into biomass were ranked in the order: Turkey oak > European beech > hornbeam. Hornbeam was the most avoided and showed the lowest conversion efficiency although, comparing to optimal oak host, its leaves were less tough, contained more water and exhibited similar values of nitrogen (index of protein content) and C/N ratio (index of investment into carbon based plant defense). We suggest that hornbeam and beech leaf chemical profiles should be further studied to reveal specific compounds that impose high metabolic cost to GM larvae. Moreover, additional research are needed to understand how intermediate hosts in natural populations affect GM outbreaks.

Keywords: *Lymantria dispar* L.; insect–host plant relationship; intermediate hosts; feeding preference; larval growth; leaf consumption; metabolic cost; defoliation risk

1. Introduction

Understanding the relationship between tree species and their major pest insects is valuable for current forest practice and future management. In insects both short-term changes of plants during intra- and inter-specific host switching and long-term transgenerational use of a new host plant may modify insect behavior and/or physiological processes affecting plant acceptance for feeding and success of coping with its defense mechanisms [1–3]. Additionally, interaction of insects with plants is under the strong influence of abiotic factors [4–6]. Tree resistance to pests along with site (e.g., climatic conditions, soil type and moisture, altitude and latitude, slope of the land) and tree species characteristics (drought resistance, wood quality, biomass production or capacity for carbon sequestration) should be taken into consideration in the future forest strategy planning and predicting risks of defoliation by invasive pests [7,8]. Usually, forest practice put the priority on quality of wood production and neglects the tree resistance to pests. In this paper we

evaluated relationship between the gypsy moth (GM) (*Lymantria dispar* L., Lepidoptera: Erebidae), a major pest of forests, and three most widely distributed broad-leaved tree species in Balkan Peninsula and Europe: Turkey oak (*Quercus cerris* L.), European beech (*Fagus sylvatica* L.), and hornbeam (*Carpinus betulus* L.).

Turkey oak natural distribution ranges from Sicily in the south to Slovakia in the north and longitudinally from the northern part of Apennine to the Black See [9]. It grows in the see level, in Italy, up to the high mountains, where more than 1000 m altitude can be reached. European beech is the most abundant European broad-leaved tree species. Its natural range extends from Sicily in the south to southern Norway and longitudinally from the Cantabrian Mountains in the west to the Carpathians and Balkan Mountains in the east [10]. It can be found at the low altitude in the northern part of its range, whereas in the southern part of Europe beech reaches 1000 and in some regions 2000 m a.s.l [11–13]. The hornbeam distribution ranges from Balkan and Apennine peninsula, through the Central Europe, up to the south of England and Sweden. Longitudinally, it can be found from France to the Black Sea and Caucasian region, whereas altitudinal distribution ranges from the sea level up to 1000 m a.s.l. [14].

These three species differ in resistance to abiotic factors. For example, resistance to drought is the highest in Turkey oak [15,16], moderate in hornbeam [17], and the lowest in the beech [18,19]. Turkey oak could be found from lowland up to the hills on sites exposed to the sun, whereas beech occupy opposite slopes which are more humid. Turkey oak forms large forests with other oak species, but also with many other broad-leaved tree species including beech and hornbeam.

Quercus, *Fagus*, and *Carpinus* species are acceptable for GM feeding [20], but differ in preference and suitability for larval survival and growth [21–23]. Turkey oak is the most preferred and suitable among oak species in Balkan Peninsula [23] and thus its forests might be common sites where GM outbreaks begin and spread to other forests [24]. After defoliation of optimal oak hosts during outbreak, GM actively searches for available food and may accept less suitable hosts for feeding and oviposition [25–27]. For instance, during the last GM outbreak in Serbia, significant amount of beech forests were completely defoliated [28].

Switching of GM larvae among Turkey oak, beech, and hornbeam within the same and/or subsequent generations might be frequent if we take into account that these hosts co-exist in mixed forests or occupy spatially neighboring habitats. GM larvae can spread passively by wind during the 1st larval instar and by active movements among trees in late instars [29]. High mobility of larvae and adult males, as well as nutritionally heterogeneous and unpredictable environment promote exquisite plasticity in this generalist species [30].

Host plant quality is a major determinant of GM preference, survival, and development of reproductively competent adults [31,32]. In addition, it significantly affects food consumption and utilization [33–36] and further population dynamics [37]. The present study is aimed to rank three wide-spread and economically important tree species (Turkey oak, beech and hornbeam) according to their acceptability and suitability for GM feeding. Therefore, we performed laboratory trials to compare the preference, growth, and nutritional indices in GM larvae fed these host plants and determined chemical and morphological leaf traits which may account for differences in larval preference and performance.

2. Materials and Methods

2.1. Insects

Egg masses used in the experiments were collected in the oak forest at Lipovica locality near Belgrade (44°38′15″ N, 20°24′00″ E). Initiation of larval hatching was done in a climate chamber (Sanyo model) at 23 ± 0.1°C, Rh = 65 ± 1% and photoperiod L:D 15:9. At the pick of hatching, larvae were randomly assigned to groups for conducting preference and performance bioassays. Until the beginning of bioassays larvae were reared on the artificial diet (MP Biomedicals, Inc., Irvine, CA, USA, cat. no. 296029304) at the same temperature, humidity, and photoperiod.

2.2. Host Plants

For testing the preference and performance of GM larvae, four trees of Turkey oak, beech and hornbeam, each aged approximately 40–50 years, were selected and marked in the forest of Košutnjak in Belgrade (44° 46′ 15″ N 20° 25′ 28″ E). The forest was not infested by GM or early defoliators (e.g., winter moths and tortrix moths). In order to standardize the effect of environmental factors on the bud burst and leaf chemistry, these trees were all located within a 100 × 100 m area, at the same altitude and with the same exposure. Collected leaves from four trees within each host plant species were mixed before insect bioassays and chemical analyses of leaves.

2.3. Leaf Characteristic

Leaves were analyzed for determining total carbon and nitrogen content. The leaves were taken from the mid-crown of selected trees in the middle of May. Carbon and nitrogen contents were determined in four samples (ten leaves per tree) within host species. Leaf samples were dried in oven at 40 °C for 48 h. Total carbon content was determined according to the method of Ansttet, as modified by Ponomarieva and Plotnikova [38], 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 sulfuric acid in the presence of a catalyst ($CuSO_4$ and K_2SO_4, 1:3) until all organic nitrogen had been transformed into ammonia. The distillation of ammonia was performed with a Kjeldahl apparatus, and the distillate was caught in orthoboric acid [39]. Prior to the determination of leaf water content and specific leaf mass (SLM), 40 leaves per host species were scanned, and their masses were measured before and after drying at 65 °C for 72 h. Water content was determined as a difference of fresh and dry mass of leaves and expressed in percentage, whereas specific leaf mass was determined as a quotient of dry leaf weight and scanned leaf area and expressed in mg cm^{-2}.

2.4. Preference Test

After the molting into the 2nd instar, larvae were starved for 24 h. An agar–water (2%) layer (2 mm thickness) was poured into Petri dishes (90 × 14 mm) and covered with moistened filter paper. Leaf disks (20 mm diameter) from different tree species were cut with the cork borer and put on opposite sides of the Petri dishes. Preference was analyzed by two-choice test for three pairs of tree species: Turkey oak vs. beech, Turkey oak vs. hornbeam, and beech vs. hornbeam. Leaf disks were fixed to the agar layer with pins. One larva was introduced into the center of each dish. For each pair of tree species, 40 larvae (replicates) were tested. After 48 h, the remains of the disks were scanned (200 dpi resolution, jpg format) and areas of discs before and after feeding were determined using the SigmaScanPro5.0 software (Systat Software, Inc., San Jose, CA, USA). The consumed area for each disc was calculated as the difference between the disk area before the feeding and the area that remains. Since hosts significantly differ in SLM, a regression of leaf mass on consumed area was applied to determine consumed leaf mass of each disc. A species was preferred if consumed leaf mass was greater than that of the other species in the pair. For the preference ranking of the tested tree species, we calculated the preference index (PI) by dividing the number of pairings in which one tree species was preferred (greater mass consumed) by the total number of pairings formed for that species, i.e., by 80 [40].

2.5. Performance Test

After molting into the 4th instar, larvae were grown individually in Petri dishes (120 × 15 mm) until the end of the experiment on Turkey oak, beech, or hornbeam leaves. Fresh leaves were provided every second day. To maintain leaf freshness, petioles were wrapped in wet cotton which was changed daily. Forty larvae were assigned to each host. However, due to experimental errors and death of 7 larvae on hornbeam (17.5% mortality) 36, 39, and 32 larvae were analyzed on Turkey oak, beech, and hornbeam, respectively.

To estimate the larval dry mass at the beginning of the 4th instar (m_0), thirty randomly sampled larvae from each experimental group were weighed and dried at 65 °C for 72 h. Initial larval mass was evaluated as a regression of dry on fresh mass. Similarly, to estimate dry leaf mass before consumption (l_0), a regression of dry on fresh mass in a random sample of 40 leaves per tree species was used. At the end of feeding trial (t—number of days when 2 mm head capsule slippage was achieved), final larval mass (m_t), mass of leaf remains (l_t) and mass of excrements (m_e) were measured after drying. Nutritional indices were calculated according to the formulae of Waldbauer [41], except for the relative growth and consumption rates (RGR and RCR), which were calculated using the formula of Farrar et al. [42] (Table 1).

Table 1. Formulae for growth and nutritional indices.

Indices	Formulae	Units
Mass gain	$m_t - m_0$	mg
Amount of consumed food	$l_0 - l_t$	mg
Amount of assimilated food	$l_0 - l_t - m_e$	mg
Relative growth rate (RGR)	$(m_t - m_0)/(t \times m_0)$	mg/mg/day
Relative consumption rate (RCR)	$(l_0 - l_t)/(t \times m_0)$	mg/mg/day
Efficiency of conversion of ingested food (ECI)	$(m_t - m_0)/(l_0 - l_t) \times 100$	%
Approximate digestibility (AD)	$(l_0 - l_t - m_e)/(l_0 - l_t) \times 100$	%
Efficiency of conversion of digested food (ECD)	$(m_t - m_0)/(l_0 - l_t - m_e) \times 100$	%

m_0—initial mass; m_t—final mass; l_0—leaf mass before consumption; l_t—mass of leaf remains; m_e—mass of excrements; t—duration of feeding trial.

2.6. Statistical Analysis

Statistical analysis was performed using the software package Statistica 13.0 (TIBCO Software Inc., Palo Alto, CA, USA). For all traits, mean values and standard errors ($\pm$ SE) were determined. Achievement of assumptions for parametric analyses was tested by Kolmogorov–Smirnov (normality) and Levene's test (homogeneity of variances). If assumptions were not satisfied, appropriate transformations were applied.

Arcus sinus square root transformation was used for leaf carbon and nitrogen content and C/N ratio, whereas water content and SLM were transformed by square root (x + 0.5). Differences in the chemical composition of leaves were determined based on one-way analysis of variance (ANOVA) and Tukey HSD post hoc test.

Consumed leaf mass in preference bioassay and duration of feeding trial in performance bioassay did not satisfy assumptions for parametric analyses. GM larval preference was analyzed on untransformed values of consumed leaf mass using a Wilcoxon matched pairs test. Untransformed values of the duration of feeding trial were analyzed by Kruskal–Wallis ANOVA and Dunn's post hoc test.

Data on initial and final larval mass, mass gain and amounts of consumed and assimilated food were transformed by square root (x + 0.5) and subjected to one-way ANOVA and Tukey HSD post hoc test. To evaluate differences in the performance growth and nutritional indices of larvae fed on leaves from different tree species, one-way analysis of covariance (ANCOVA) and Tukey HSD post hoc test were applied. Nutritional indices were analyzed by ANCOVA, where the numerator of the index was the dependent variable and the denominator was the covariate [43]. RGR and RCR were analyzed by comparisons of growth $[(m_t - m_0)/t]$ and consumption rates $[(l_0 - l_t)/t]$, respectively, with the initial mass of larvae as a covariate. For ECI and ECD, the mass gain was analyzed by using amounts of consumed and assimilated food as covariates, respectively. The food consumption was a covariate for the comparison of the amount of assimilated food (equivalent to AD). For appropriate comparisons of growth and nutritional indices by ANCOVA, covariate should evenly affect the dependent variable over hosts [43]. Thus, before ANCOVA we tested homogeneity of slopes and obtained insignificant Covariate × Host interaction for all

traits ("RGR": $p = 0.6379$; "RCR": $p = 0.2422$; "ECI": $p = 0.1224$; "AD": $p = 0.8812$; "ECD": $p = 0.1993$).

To disentangle pre- and post-ingestive as well as pre- and post-digestive effects of tree species on GM larval growth, results on one-way ANOVA and ANCOVA on mass gain should be compared [44,45]. If differences in GM mass gain among experimental groups revealed by ANOVA disappeared after ANCOVA with consumption as a covariate, it would indicate that leaf quality affected growth through pre-ingestive mechanisms. Otherwise, both pre- and post-ingestive processes would be involved. Significant differences revealed by ANCOVA with assimilation as the covariate would point to the variation in metabolic cost imposed by food digestion.

3. Results

3.1. Leaf Characteristics

The results of the carbon, nitrogen, C/N ratio, water content, and specific mass of leaves are presented in Table 2. Beech leaves had the lowest nitrogen and water content, whereas C/N ratio was the highest. There were no differences in nitrogen content and C/N ratio between Turkey oak and hornbeam leaves. The highest specific leaf mass was recorded for Turkey oak and the lowest value was obtained for hornbeam leaves.

Table 2. Leaf traits (mean ± SE) of the different tree species (C—carbon content; N—nitrogen content; C/N ratio; W—water content; SLM—specific leaf mass) compared using one-way ANOVA (F and *p* values) and Tukey HSD tests. Means in the same row followed by different letters differ significantly ($p < 0.05$).

Leaf Traits	Turkey Oak	Beech	Hornbeam	F	p
C (%)	34.6 ± 0.56 a	33.8 ± 0.34 a	31.2 ± 0.13 b	22.4	0.0003
N (%)	2.4 ± 0.05 a	1.9 ± 0.04 b	2.3 ± 0.12 ab	8.96	0.0072
C/N	15.3 ± 0.98 ab	17.4 ± 0.45 a	14.0 ± 0.81 b	5.03	0.0342
W (%)	65.5 ± 0.53 b	63.6 ± 0.40 c	69.8 ± 0.55 a	38.68	<0.0001
SLM (mg cm^{-2})	4.5 ± 0.14 a	3.4 ± 0.11 b	2.3 ± 0.04 c	113.41	<0.0001

3.2. Larval Preference

Tree species were ranked on the basis of GM larval food choice in two-choice assays. The preference index (PI) was the highest for Turkey oak (0.89), moderate for beech (0.40), and the lowest for hornbeam (0.21). The 2nd instar larvae preferred Turkey oak leaves over those of the other two species, which was also indicated by the positive Z values in Wilcoxon matched pairs test (Figure 1). Beech leaves were preferred over those of hornbeam. Leaf mass consumed by the 2nd instar larvae was 96% and 190% higher in the group that was fed Turkey oak leaves than the groups fed beech and hornbeam leaves, respectively. Moreover, leaf mass consumed by larvae fed beech leaves was 57% higher than the group fed hornbeam leaves.

3.3. Larval Performance

Results of performance indices are given in Table 3 and estimated significance of host plant impact on these traits are given in Tables 4 and 5. There were no among host plant differences in initial larval mass, whereas all other traits were significantly affected by the host plant. The duration of feeding trial was significantly affected by host plant ($H_{2,108} = 13.46$, $p = 0.0012$) and lasted longer in larvae fed beech ($p = 0.0406$) and hornbeam leaves ($p = 0.0064$). Larval mass at the end of the 4th instar, larvae fed Turkey oak leaves had on average 23.6% and 30.95% higher values than larvae fed beech and hornbeam leaves, respectively. Mass gain during the 4th larval instar in larvae fed Turkey oak leaves was 31% and 45% higher than for those fed leaves of beech and hornbeam, respectively. Lower amounts of consumed and assimilated leaves of Turkey oak and beech than hornbeam

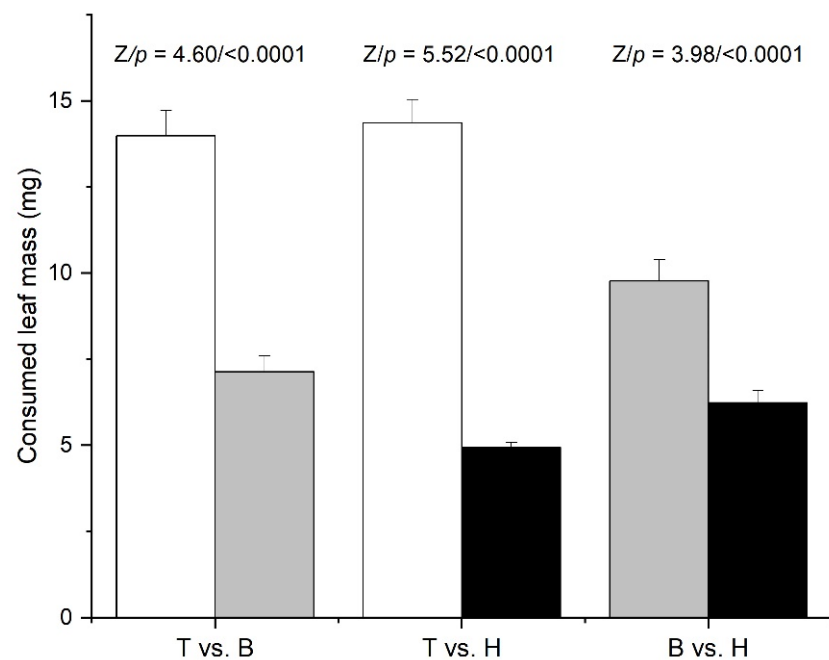were recorded (24 and 16%, respectively for consumption and 38.4 and 37.2%, respectively for assimilation).

Figure 1. The preference in terms of consumed leaf mass (mean ± SE) by 2nd instar GM larvae in two choice assays of three leaf pairs: Turkey oak versus. beech (T vs. B); Turkey oak versus hornbeam (T vs. H), beach versus hornbeam (B vs. H). Consumption of Turkey oak, beech and hornbeam leaves are presented in hollow, grey and black bars, respectively. The comparison of the area consumed in each host plant pair was done using Wilcoxon matched pairs test (Z and *p* values are presented above the bars).

Table 3. Performance indices (mean ± SE) for 4th instar GM larvae depending on host plant. After one-way ANOVA (see Table 4) or ANCOVA (see Table 5) data were compared by Tukey HSD post hoc test and significantly different values were marked by different letters within a row ($p < 0.05$).

Performance Indices	Turkey Oak	Beech	Hornbeam
Duration of feeding trial (days)	5.2 ± 0.09 b	5.7 ± 0.15 a	5.8 ± 0.14 a
Initial mass (mg)	7.9 ± 0.25 a	7.2 ± 0.12 a	7.6 ± 0.21 a
Final mass (mg)	23.3 ± 1.06 a	17.8 ± 0.82 b	16.1 ± 0.85 b
Mass gain (mg)	15.4 ± 0.94 a	10.6 ± 0.78 b	8.5 ± 0.73 b
Food consumed (mg)	108.0 ± 4.72 b	119.4 ± 6.22 b	142.1 ± 6.33 a
Food assimilated (mg)	38.9 ± 2.62 b	39.6 ± 3.63 b	63.1 ± 4.81 a
RGR (mg/mg/day)	0.38 ± 0.02 a	0.25 ± 0.02 b	0.19 ± 0.02 c
RCR (mg/mg/day)	2.7 ± 0.09 a	2.9 ± 0.15 a	3.4 ± 0.14 a
ECI (%)	14.2 ± 0.56 a	8.8 ± 0.39 b	5.7 ± 0.38 c
AD (%)	35.4 ± 1.53 b	32.2 ± 1.62 b	45.8 ± 2.20 a
ECD (%)	44.4 ± 3.35 a	31.3 ± 2.61 b	14.1 ± 1.41 b

RGR, ECI, and ECD gradually decreased in the order Turkey oak—beech—hornbeam (Table 3) and ANCOVA results confirmed significant influence of consumed host plant (Table 5). The RGR in the Turkey oak was 52% higher than in the beech and twice higher than in the hornbeam. In contrast, AD was the highest in larvae fed hornbeam leaves (29.4% comparing to Turkey oak and 42.2% comparing to beech). According to the ANCOVA analysis, there were no differences in RCR among the tested tree species (Tables 3 and 5).

Table 4. MS, F and *p* values from one-way ANOVA for performance indices. Host plant was fixed factor. Degrees of freedom: df = 2 for host plant effect, and df = 103 for error term. Significant effects are marked in bold.

Performance Indices	Source of Variation	MS	F	*p*
Initial mass	Host plant	0.108	2.70	0.0717
	Error	0.040		
Final mass	Host plant	6.253	16.60	**<0.0001**
	Error	0.377		
Mass gain	Host plant	9.634	18.30	**<0.0001**
	Error	0.527		
Food consumed	Host plant	23.490	9.74	**0.0001**
	Error	2.410		
Food assimilated	Host plant	40.394	19.14	**<0.0001**
	Error	2.110		

Table 5. MS, F and *p* values from ANCOVA for performance indices. Initial mass (a), consumption (b) and assimilation (c) were used as covariates. Each ANCOVA analysis represent equivalent to Waldbauer's indices (Waldbauer, 1968). Host plant was fixed factor. Degrees of freedom: df = 2 for host plant effect, df = 1 for covariate and df = 103 for error term. Significant effects are marked in bold.

Performance Indices	Source of Variation	MS	F	*p*
Growth rate~RGR	Host plant	1.949	30.10	**<0.0001**
	Covariate (a)	0.812	12.55	**0.0006**
	Error	0.065		
Consumption rate~RCR	Host plant	1.162	2.16	0.1204
	Covariate (a)	4.113	7.64	**0.0067**
	Error	0.538		
Mass gain~ECI	Host plant	16.585	54.86	**<0.0001**
	Covariate (b)	23.832	78.83	**<0.0001**
	Error	0.302		
Assimilation~AD	Host plant	9.377	10.74	**0.0001**
	Covariate (b)	129.535	148.43	**<0.0001**
	Error	0.873		
Mass gain ~ ECD	Host plant	12.590	26.63	**<0.0001**
	Covariate (c)	6.077	12.86	**0.0005**
	Error	0.473		

Significant host plant effects on mass gain and assimilation were revealed by both ANOVA and ANCOVA where food consumption was used as a covariate (Tables 4 and 5; graphical presentation of ANCOVA in Figure 2a—equivalent to Waldbauer's ECI and Figure 2b—equivalent to AD). Therefore, besides pre-ingestive mechanisms (consumption), post-ingestive mechanisms also contributed to variation in mass gain. Such mechanisms were involved in significantly reduced mass gain on hornbeam despite the highest consumption of hornbeam leaves. A comparison of assimilation confirmed that, among post-ingestive mechanisms, differential digestion had a role in variation in amount of assimilated food and the highest value of AD on hornbeam. Moreover, comparisons of mass gain by ANCOVA with assimilation as a covariate confirmed that differential metabolic load imposed by ingestion of different host leaves explained differences in mass gain among experimental groups (equivalent to ECD, Figure 2c).
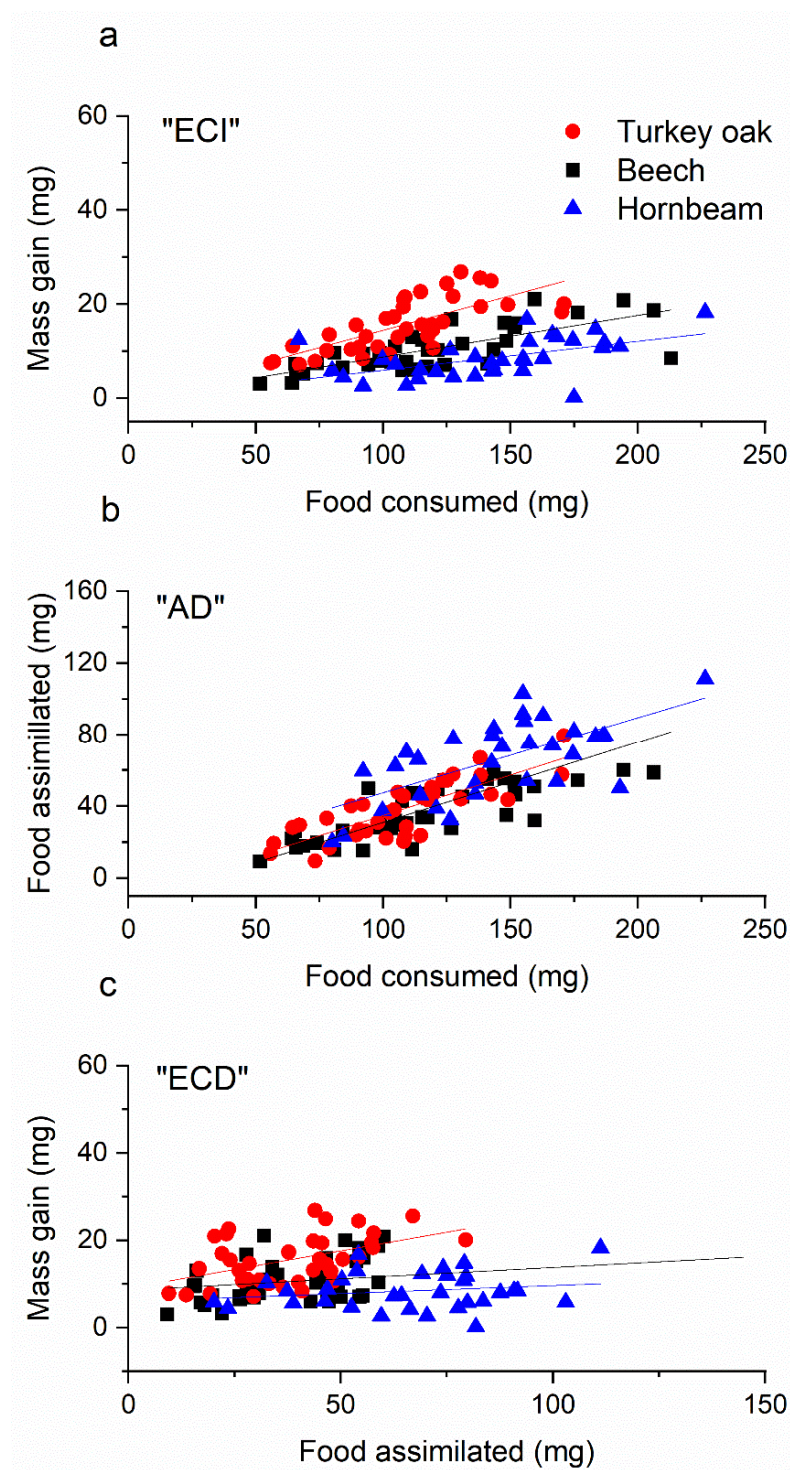
Figure 2. Bicoordinate plots of ANCOVA on mass gain against amount of consumed food (**a**), amount of assimilated food against amount of consumed food (**b**) and mass gain against amount of assimilated food (**c**).

Accordingly, hornbeam appeared to be the worst host for GM larvae because the high costs of food processing could not be overcome by increased consumption and assimilation. On the other hand, Turkey oak was the most suitable host. Although consumption and assimilation did not differ between Turkey oak and beech leaves, lower metabolic load of processing Turkey oak leaves might contribute to the highest growth of GM larvae on the oak host.

4. Discussion

Preference and performance of folivorous insects vary depending on plant leaf quality [3,46]. Due to generalist feeding habit and high mobility, GM larvae encounter large inter- and intra-specific variation in nutritional, allelochemical, and morphological attributes of their hosts [22,33,35,47–50]. High quality plants that are nutritionally adequate and contain low level of toxic secondary metabolites are commonly preferred by GMs, improve their fitness, affect interaction with other environmental factors, and thus population dynamics and probability of outbreaks [8,51,52].

Results of our study point that Turkey oak is a superior host compared to beech and hornbeam. Namely, Turkey oak was preferred by 2nd instar larvae, 4th instar duration was the shortest, larvae achieved the highest mass, larval growth was the fastest and food processing cost was the lowest. Since body size is correlated with mating ability and fecundity [53] it is assumed that larger larvae fed oak leaves will develop into adults with higher reproduction performance comparing to beech and hornbeam fed larvae. Short development time is advantageous because, as stated by slow-growth-high-mortality hypothesis [54], it means short exposure to natural enemies and, thus, high survival of GMs in natural populations. These findings were expected since, in general, oaks are the most optimal hosts for GM development [55,56], and Turkey oak is among the most suitable oaks [23,57–59]. It is known that Turkey oak forests serve as natural reservoir for GM populations in Balkan Peninsula during latency period [28]. On the other hand, *Fagus* and *Carpinus* species are ranked as intermediate hosts [20].

Relative values of specific leaf mass (SLM), C/N ratio, nitrogen, and water content in oak, beech, and hornbeam leaves observed in our study are consistent with results of Schafellner and Schopf [60]. SLM, C/N and nitrogen contents indicate leaf toughness, resource allocation towards carbon-based plant defense, and protein content, respectively. Despite the highest SLM, high nitrogen and low C/N ratio in Turkey oak partly explain why it is an optimal host compared to beech and hornbeam. Barbehenn et al. [61] showed that decreased nitrogen during leaf maturation was related with decreased GM performance. Numerous literature data show that hornbeam and beech leaves contain secondary metabolites [22,62–64] which provoke avoidance behavior in GM larvae [32,65] and negatively affect GM larval growth and nutritional indices [22,33,34,37,66].

Host plant suitability indicated by larval growth in our study is in accordance with feeding preference, i.e., on the most preferred host Turkey oak and the least preferred host hornbeam, larvae achieved the highest and the lowest mass values, respectively. Positive preference—performance association is a characteristic of generalist insects [67,68]. Sugar to tannin ratio and the presence of alkaloids and sesquiterpenoids in leaves have been suggested as important for GM larval preference [26,32]. About 80% of rejected plant genera contain alkaloids and sesquiterpenoids [69]. Multiple choice tests recorded that European (*C. betulus*) and American hornbeam (*C. caroliniana*) are preferred hosts for GM relative to other *Carpinus* species [70], but our study is the first that recorded hornbeam preference relative to optimal oak species. Field and laboratory assays confirmed that American beech *F. grandifolia* was more avoided relative to oak hosts [26,71,72] due to presence of alkaloids and flavonoids in their leaves [65]. By using multiple choice test, Clavijo McCormic et al. [73] obtained that pedunculate oak (*Q. robur*) and European beech (*F. sylvatica*) were preferred relative to maple (*Acer campestre*) and pine (*Pinus sylvestris*) whose leaves contained sesquiterpenes. Higher sugar to tannin ratio has been recorded in Turkey oak than in beech and hornbeam leaves [22]. However, further and more detailed analyses of leaf chemistry are needed to evaluate which compounds contribute to higher oak consumption and feeding deterrent effects of intermediate hosts that we observed in a choice test.

Based on our results we expect that in mixed stands during latency and progradation phase of population dynamics, when larvae can chose among hosts, optimal oak leaves will be more consumed than leaves of beech and hornbeam. However, during outbreak and oak defoliation, larvae will be forced to consume less suitable hosts. Intermediate preference

of GM larvae to beech leaves on one side, and very large area covered by beech forest on the other side, point that young larvae might rapidly disperse during outbreak and, consequently, defoliate beech trees as confirmed in a study of Milanović et al., 2014 [28].

Our results showed that growth-reducing effects of feeding on beech and hornbeam mainly stem from influence of plant attributes on post-digestive processes. We did not record negative effects of these hosts on food consumption and assimilation. Moreover, in larvae fed intermediate hosts, consumption and assimilation either remained unchanged (beech) or exerted increased values (hornbeam). GM larvae fed high nitrogen and high water diet exhibited lower food consumption and higher assimilation [33,58,74], whereas leaf toughness reduced both traits and might prevent compensatory responses to nutritional inadequacy [23,61]. Increased AD in response to less optimal diet has also been recorded in other insect species [47,75,76]. Therefore, higher water content and lower toughness in hornbeam possibly account for observed higher larval consumption and assimilation comparing to oak fed larvae. However, although beech leaves were less tough comparing to Turkey oak, beech fed larvae did not show compensatory responses to low nitrogen content.

To fully understand GM—host plant relationship it is necessary to analyze the content of specific secondary metabolites and examine their potential to modify insect behavior and nutritional physiology, and limit adaptive responses to low nutritional quality [77]. It is reasonable to assume that different profiles of defense compounds in beech and hornbeam leaves [62,64] can provoke distinct responses of larvae at the level of interaction with gustatory receptors, gut structures, and physiological processes. Studies in GM and other insects showed that secondary metabolites affected AD by changing resources allocation to gut tissues, rate of food passage through the gut, composition of gut bacterial community, and activities of digestive enzymes [77–80].

In difference to our results, long-term (several weeks) feeding study of Schafellner and Schopf [60] revealed that both beech and hornbeam leaves lowered GM consumption and assimilation efficiency suggesting that capability for behavioral and physiological adjustments to intermediate hosts could be exhausted after prolonged exposure to their chemistry. However, our previous study detected significant variation in plasticity of GM pupal mass in response to oak—beech host switch during 4th instar which indicated potential for evolution of adaptations to intermediate hosts in mixed forests [81].

Adaptive responses to unbalanced nutrient ratios and presence of toxic and antinutritive compounds are costly, divert energy from biomass production, and lead to growth retardation. Growth was the most retarded in hornbeam fed larvae despite high consumption and assimilation. It appeared that host influences on post-digestive processes were the main determinant of reduced growth in both hornbeam and beech fed larvae. Lower ECD can result from damages to gut epithelium which impair nutrient absorption or metabolic changes in which energy resources are spent for induction of antioxidants, digestive, and detoxification enzymes. For example, reduced ECD [82], thin peritrophic membrane and partial loss of microvilli in columnar cells of midgut epithelium [83], and elevated activities of trypsin, leucine aminopeptidase, superoxide dismutase, and glutathione S-transferase [84,85] have been recorded in the 4th instar GM larvae fed locust tree, an unsuitable host whose leaves contained flavonoids and alkaloids.

In conclusion, present results along with studies of other authors [21,60,69,70] indicate that feeding on less preferred intermediate hosts may elevate metabolic load associated with defense mechanisms and thus provoke slower development of smaller individuals. Although it is known that forest stand composition influences fluctuations in GM abundance [8,52], the question arises: Do our results imply that increased share of intermediate hosts in forest stands would reduce severity of defoliation during outbreak? Such interpretation should be taken with great precaution due to limitations of our research. We carried out a laboratory study of host suitability under constant temperature and humidity; only one larval instar per bioassay was analyzed; larvae were originated from one locality with dominant oak hosts, and leaves were collected from a narrow forest area. Field research might provide different results for several reasons. First, variation in environmental factors

affects GM directly or indirectly through changes in host plant quality. Significant variation in leaf composition has been recorded depending on forest locality and season [64]. Second, in nature, GMs can forage for optimal hosts and recover larval growth during advanced instars. Moreover, different host-associated GM population scan diverge in resistance to intermediate host trees [81]. Finally, in difference to field research, laboratory experiments exclude natural enemies of GM (nuclear polyedrosis virus, *Entomophaga maimaiga*, mammal predators) that are highly important determinants of GM outbreak intensity and severity of defoliation [51,52]. All these issues can be considered as directions for future research aimed to elucidate mechanisms behind dynamics of GM populations.

Author Contributions: Conceptualization, S.M. and Č.M.; methodology, S.M., Z.M. and J.L.; software, Z.T.; validation, J.L., D.Š.J. and L.J.; formal analysis, S.M. and J.L.; investigation, S.M., Č.M. and Z.M.; resources, Z.T.; data curation, J.L. and Z.T.; writing—original draft preparation, S.M. and J.L.; writing—review and editing, L.J., D.Š.J., Z.M., Č.M. and Z.T.; visualization, Z.T.; supervision, L.J.; project administration, S.M. and J.L.; funding acquisition, J.L. and D.Š.J. All authors have read and agreed to the published version of the manuscript.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available on request from thecorresponding author.

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