

Article



Decomposition of Herbivore-Damaged Leaves of Understory Species Growing in Oak and Pine Stands

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Abstract: Leaves are the largest component of forest litter. Their decomposition rate depends mainly on plant species, leaf chemical composition, microorganism biodiversity, and habitat conditions. It is known that herbivory by insects can modify the chemical composition of leaves, such as through induction. The aim of this study was to determine whether the rate of leaf decomposition is related to the susceptibility of the plant species to insect feeding and how leaf damage affects this rate. For our research, we chose six species differing in leaf resistance to insect damage: Cornus sanguinea, Frangula alnus, and Sambucus nigra (herbivore resistant), and Corylus avellana, P. padus, and Prunus serotina (herbivore susceptible). The decomposition of these plant leaves was examined in two monoculture forest stands, deciduous (Quercus robur) and coniferous (Pinus sylvestris). Litter decay rate k and change of litter mass, content of defensive metabolites (total phenols (TPh) and condensed tannins), and substances beneficial for organisms decomposing litter (nitrogen (N) and nonstructural carbohydrates (TNC)) were determined. Contrary to our expectations, leaf litter of herbivore-resistant species decomposed faster than that of herbivore-susceptible species, and damaged leaves decayed faster than undamaged leaves. We found that faster decaying leaf litter had a lower content of defensive compounds and a higher content of TNC and N, regardless of the plant species or leaf damage. Leaf litter decomposition caused a large and rapid decrease in the content of defensive compounds and TNC, and an increase in N. In all species, the tannin content was lower in damaged than in undamaged leaves. This pattern was also observed for TPh, except in S. nigra. We interpret this as the main reason for faster decay of damaged leaves. Moreover, the loss of leaf mass was greater under oak than pine stands, indicating that the microorganisms in deciduous stands are more effective at decomposing litter, regardless of leaf damage.

Keywords: decay rate; decomposition; insect damage; litter; nitrogen; nonstructural carbohydrates; phenolics; starch; tannins

1. Introduction

The understory is a very important forest layer for each biome, and is mainly composed of shrub species. In European countries, such species include common dogwood (*Cornus sanguinea* L.), glossy buckthorn (*Frangula alnus* Mill.), black elder (*Sambucus nigra* L.), common hazel (*Corylus avellana* L.), bird cherry (*Prunus padus* L.), and black cherry (*P. serotina* Ehrh.). There are also trees that grow tall under normal conditions, but under unfavorable conditions, such as under the canopy of fast-growing trees, they experience inhibited growth and development. The understory significantly affects the functioning of the entire forest ecosystem because it protects the soil from erosion, reduces evaporation from the soil surface, and improves the climate relations of the interior of the stand, strongly



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Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). inhibiting wind penetration into the forest. In addition, understory shrubs shed leaves that vary in terms of structure and chemical composition [1,2], and thus, contribute to faster degradation of dead organic matter accumulated on the soil surface [3,4].

The introduction of understory shrubs into a monoculture forest is a form of forest protection against outbreaks of insect pests, mainly of coniferous species, deprived of the natural regulatory mechanisms of pest populations. However, the understory plants themselves suffer severely due to the large number of associated herbivorous species [5]. This is most easily observed in the case of bird cherry, whose leaves begin to develop very early [6] and are severely damaged by leaf-eating insects of many species [7–9]. The leaves of this shrub are eaten by both polyphagous insects, mainly in the genus *Gonioctena* Kirby [10], and monophagous insects such as *Yponomeuta evonymella* L. [6,11].

The main reason for the differences in the degree of leaf damage by leaf-eating insects is variation in food quality, which can be analyzed mainly in two ways. The first is the physical barriers associated with the morphological and anatomical structure of the leaves, depending on the plant species and light conditions [12–14]. The second is leaf chemistry, affecting the digestibility and palatability of leaves as a food for herbivorous insects. This applies both to compounds that benefit herbivores in terms of growth and development of herbivores, i.e., attractants (nonstructural carbohydrates (TNC), nitrogen (N) compounds, proteins, and fats) [15,16], and to defensive compounds that the plant has to deter and discourage its consumption, i.e., repellents (phenolic compounds, terpenoids, and alkaloids) [17–19]. The chemical composition of the leaves affects not only the amount of damage they receive from insects, but also the rate of their decomposition [20,21].

Our research is an attempt to answer the question of whether the rate of leaf decomposition is related to the susceptibility of the plant species to insect feeding and how leaf damage affects this rate. To explain the reason for the differences in the rate of litter leaf decomposition between the chosen understory plant species and between undamaged and insect-damaged leaves, we conducted a number of chemical analyses. We hypothesized that (1) the rate of litter leaf decomposition would be slower in species resistant to feeding by herbivorous insects due to higher amounts of defensive metabolites and lower amounts of substances beneficial for the growth and development of herbivorous insects in the leaves. Some authors point to such a relationship [22,23]. In line with Burghardt et al. [24], we expected that the leaf litter microbial decomposition efficiency would correspond to herbivore resistance. Thus, we expected that the leaf litter of herbivore-resistant species would decompose more slowly than the leaf litter of herbivore-susceptible species. Additionally, we hypothesized that (2) the rate of decomposition of insect-damaged leaves would be slower compared to undamaged leaves. We supposed that damaged leaves would decompose more slowly because they would be devoid of soft tissues, and the tissues around the damage (necrosis) would be characterized by increased phenolic content. The protective function of phenolic compounds against microorganisms should inhibit the rate of litter decomposition, as stated by Gavinet et al. [25]. Similar to the previous hypothesis, we also assumed in this hypothesis that leaves that contain higher amounts of defensive metabolites and fewer beneficial substances for herbivorous insects would decompose more slowly. In our view, this should be a consequence of the following process: herbivore-induced defense reactions change the leaf palatability and these changes can cascade through to either inhibit or promote the decomposability of leaf litter [24]. In both hypotheses, the basis was the assumption that the above-mentioned substances would affect the microfauna and microorganisms that decompose the litter, just as they affect herbivorous insects [24,26].

We also studied the effect of overstory stand conditions on understory plant growth and the decomposition of leaf litter. There were two single-species overstory stands, English oak (*Quercus robur* L.) and Scots pine (*Pinus sylvestris* L.). We tested the hypothesis (3) that the leaves of understory plants would decompose faster in deciduous (oak) than in coniferous (pine) stands. We believe that the specific stand conditions, primarily the microfauna participating in the decay of leaves, are more favorable in oak stands than in pine stands, which is consistent with the "home-field advantage" hypothesis [27–29].

2. Materials and Methods

2.1. Plant Material

Research, including the collection of litter to determine their chemical composition and decomposition rates, was carried out at the Zwierzyniec Experimental Forest in Kórnik, Poland (52°14′ N, 17°05′ E). Six understory plant species (Sp) were included in the study, differing in susceptibility (Sus) to insect damage. Three species belonged to the resistant group, in which leaf perforation is less than 10%—common dogwood (*Cornus sanguinea* L.), glossy buckthorn (*Frangula alnus* Mill.), and black elder (*Sambucus nigra* L.)—and three belonged to the susceptible group, in which leaf perforation is more than 10%—common hazel (*Corylus avellana* L.), bird cherry (*Prunus padus* L.), and black cherry (*Prunus serotina* Ehrh.). This distinction was made based on results previously published by our research group on the percentage of leaf tissue loss in these species [9,30]. The plants selected for research, all in shrubby form, were from a dozen to several dozen years old. They grew in a mixed forest stand, under a canopy of oak, beech, hornbeam, birch, ash, alder, and pine.

In autumn (mid-November), both undamaged and insect-damaged leaves from the six species of shrubs were collected. The leaves were collected on sheets under the shrubs, after shaking the shrubs gently. Collected leaves were divided into two groups: including undamaged control leaves (C; 0% of the leaf surface damaged) and leaves damaged by herbivorous insects (D; damage > 0%). From the D group, random samples were chosen (20 leaves from each species) to determine the percentage of perforation using the WinFOLIA software (version 2003b, Regent Instruments Inc., Québec, QC, Canada).

After drying for a week at room temperature (approx. 25 °C), the leaves (5 g—except for *F. alnus*, 4 g) were placed in nylon bags (20 cm \times 20 cm) with a 0.3 mm mesh and placed on the ground in two single-species forest stands (St), oak (Quercus robur L.), and pine (Pinus sylvestris L.) A small mesh size was used because of the needle-leaved species stand in the experiment, and to limit organic matter ingress through the litterbag. The chosen stands were characterized by similarly aged trees, about 25 years old. Six bags representing each treatment of the experiment (plant species \times leaf damage) were placed on three randomly selected plots of each kind of stand species (n = 6 species \times 2 leaf damage \times 2 stands \times 3 plots within stand \times 6 bags = 432 samples). All bags were placed out on 30 November 2006 and were collected on 30 March, 30 June, and 30 September in 2007 and 2008 (always one bag out of six, i.e., three per treatment). An additional portion of leaves of each treatment was used to determine the initial levels of N and metabolites. The periodically collected bags of leaves in two consecutive years were used to determine the mass of remaining (undecomposed) litter and, after drying, to carry out the same analyses as mentioned above. The litterbags were cleaned with precision, and this type of work was done by one, and always the same, person.

The percentage of undecomposed litter was calculated for each time period relative to the initial mass (100%). In addition to determining the percentage of remaining litter mass, litter decay rate *k* was also calculated using a negative exponential distribution model, after Olson [31] and Hobbie et al. [32]. This calculation used the linear regression equations of the negative natural logarithm of the fraction of residue mass m_i in relation to the initial mass m_o from time *t* (year⁻¹), $k = -ln (m_i/m_o) t^{-1}$.

2.2. Chemical Analyses

Plant material was dried for 3 days at 40 °C using a Memmert ULE 400 dryer (Memmert GmbH & Co. KG, Schwabach, Germany) with forced air circulation, and ground into powder with a Mikro-Feinmühle-Culatti MFC mill (IKA[®]-Labortechnik Staufen, Janke & Kunkel GmbH & Co. KG, Staufen, Germany). Small amounts of the powder (0.1 g/sample) were separated for later determination of tannins, because these compounds decompose at temperatures above 40 °C. The remaining powdered material was dried at 65 °C and used for the remaining chemical analyses.

The determination of total soluble phenols (TPh), condensed tannins, TNC, and N content was described in by Karolewski et al. [9]. The content of total soluble phenols was measured colorimetrically using Folin and Ciocalteu's phenol reagent (Sigma F-9252) at $\lambda = 660$ nm. Condensed (catechol) tannins were measured using a color reaction with vanillin in an acid medium. Readings of absorption were taken at $\lambda = 500$ nm. Results of the phenol measurements were expressed as micromole of chlorogenic acid per gram of dry mass (μ M g⁻¹ d.m.), whereas condensed tannins were converted into micromole of catechin per gram (μ M g⁻¹ d.m.). N content (% d.m.) was determined using an ECS CHNS-O 4010 analyzer (Costech Instruments, Pioltello, Italy). TNC were assayed in methanol–chloroform–water extract and results were expressed as % d.m. The content of soluble carbohydrates was measured at $\lambda = 625$ nm, following a color reaction with anthrone, while content of starch was measured at $\lambda = 450$ nm, following the reaction with a spectrophotometer (UV-1700 Visible Spectrophotometer; PharmaSpec, Shimadzu, Japan).

2.3. Statistical Analyses

Analysis of variance (ANOVA) was performed to compare the effect of: susceptibility to insect damage (Sus), understory plant species (Sp), stand species (St), leaf damage (Ld), and time of decomposition (T) on the examined features: remaining mass calculated for the whole research period in relation to initial mass (%), TPh, condensed tannins, N, and TNC in the leaf litter. Understory plant species was nested within the susceptibility group. To assess the impact of the studied factors and associated variables, i.e., the initial content of metabolites (TPh, tannins, TNC) and N on the decay rate (k), ANCOVA was used. The Bliss (arcsin) formula was used for statistical analysis of the features, expressed as a percentage. Before all analyses, normal distributions were verified using the Shapiro-Wilk test. The assumption of homogeneity of variances was tested via Bartlett's test prior to analysis. For the ANOVA, the number of included data was smaller than the established n = 504 (i.e., the sum of bags (n = 432) and samples used immediately before laying in the leaf litter (n = 72)), because in some cases we were limited by the remaining (undecomposed) litter leaf mass to carry out chemical analyses. Moreover, five bags from different experiment treatments were damaged by animals, but since each experimental variable was represented by three replicates, it was still possible to perform statistical analyses. Statistical analyses were conducted using the JMP 14PRO program (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Differences in Rate of Litter Decomposition between Plant Species

Our classification of understory shrubs as either herbivore-resistant or herbivoresusceptible was supported by our leaf damage data. The average percentage of damaged leaf surface was as follows: in the resistant group: *C. sanguinea*, 3.4%; *S. nigra*, 4.7%; and *F. alnus*, 7.2%; and in the susceptible group: *C. avellana*, 16.8%; *P. serotina*, 19.6%; and *P. padus*, 24.3%.

Susceptibility and understory plant species had a significant impact on both the rate of litter decomposition, expressed by the decay rate *k* (Table 1), and the mass of undecomposed leaves, expressed as a percentage of the initial mass taken as 100% (Table 2). This indicates a clear trend of faster leaf decomposition in plant species characterized by low susceptibility to insect feeding (*C. sanguinea*, *F. alnus*, and *S. nigra*) and slower in other plant species (Figure 1). A similar relationship is also noticeable when comparing the mass of undecomposed leaf litter over time (Figure 2).

Table 1. Mean litter decay rate (*k*) with standard errors (SE) are presented in first part of table. In the second part are ANCOVA results for the influence of susceptibility to herbivores (Sus; resistant and susceptible), plant species (Sp) nested in Sus, stand species (St; oak and pine), leaf damage (Ld; C, control; D, damaged), and initial content of nitrogen (N), total phenolic compounds (TPh), tannins, and total nonstructural carbohydrates (TNC) on litter decay rate (*k*). *p*-values < 0.05 are indicated in bold.

	Species	k				
	opered	С	D			
	C. sanguinea	3.09 (0.29)	3.26 (0.29)			
Resistant	F. alnus	2.67 (0.20)	2.45 (0.17)			
	S. nigra	2.79 (0.25)	3.09 (0.19)			
	C. avellana	0.68 (0.07)	0.71 (0.09)			
Susceptible	P. padus	1.90 (0.15)	1.81 (0.09)			
	P. serotina	0.87 (0.15)	1.60 (0.27)			
Ct.	oak	2.06 (0.22)	2.25 (0.21)			
St	pine	1.94 (0.28)	2.06 (0.26)			
ANCOVA	d.f.	F	р			
Sus	1	11.7650	0.0011			
Sp (Sus)	4	9.3449	<0.0001			
St	1	0.9631	0.3306			
Ld	1	0.8274	0.3669			
$Ld \times Sus$	1	1.5219	0.2225			
$Ld \times St$	1	0.8464	0.3615			
Sus imes St	1	7.5202	0.0082			
$Ld \times Sus \times St$	1	0.2338	0.6306			
Ν	1	0.8636	0.3567			
TPh	1	3.4540	0.0684			
Tannins	1	0.0357	0.8509			
TNC	1	0.5931	0.4445			
df error	56					

Table 2. Influence of susceptibility (Sus; resistant and susceptible), understory plant species (Sp) nested in Sus, stand species (St; oak and pine), and leaf damage (Ld; C, control; D, damaged) and leaf decomposition time (T), on remaining mass calculated for the whole research period in relation to initial mass (%), content of total phenols (TPh; expressed as μ M of chlorogenic acid g^{-1} d.m.), condensed tannins (Tannins; expressed as μ M of catechin g^{-1} d.m.), nitrogen (N, % d.m.), and total nonstructural carbohydrates (TNC, % d.m.) in leaf litter. For the ANOVA, the results of all seven terms (¹) were used to assess the remaining mass, and for other parameters a maximum of six terms (²) (details in Materials and Methods). *p*-values < 0.05 are indicated in bold.

Factor			Mass		TPh		Tannins		Ν		TNC	
ANOVA	Df ¹	df. ²	F	p	F	р	F	р	F	р	F	р
Sus	1	1	662.03	<0.0001	0.18	0.6722	71.80	<0.0001	626.05	<0.0001	49.34	<0.0001
Sp(Sus)	4	4	63.16	< 0.0001	17.78	< 0.0001	12.18	< 0.0001	150.64	< 0.0001	38.65	< 0.0001
St	1	1	40.26	< 0.0001	2.10	0.1479	0.01	0.9078	25.27	< 0.0001	0.04	0.8390
Ld	1	1	6.03	0.0144	4.91	0.0273	12.51	0.0005	0.09	0.7617	0.01	0.9282
Time	6	5	1190.20	< 0.0001	224.30	< 0.0001	97.27	< 0.0001	75.89	< 0.0001	377.03	< 0.0001
$Ld \times Sus$	1	1	9.89	0.0018	3.63	0.0577	8.00	0.0049	12.51	0.0005	0.36	0.5478
$Ld \times St$	1	1	0.12	0.7285	0.01	0.9539	0.01	0.9560	0.77	0.3811	0.34	0.5572
$Ld \times T$	6	5	1.13	0.3428	5.83	< 0.0001	13.34	< 0.0001	1.22	0.2980	0.28	0.9249
Sus imes St	1	1	26.07	< 0.0001	0.63	0.4295	0.10	0.7522	0.90	0.3427	0.01	0.9931
T imes St	6	5	2.53	0.0205	0.21	0.9601	0.13	0.9865	1.92	0.0901	1.90	0.0943
T imes Sus	6	5	26.43	< 0.0001	7.74	< 0.0001	71.36	< 0.0001	11.96	< 0.0001	1.23	0.2937
$T \times St x Sus$	6	5	2.13	0.0487	0.36	0.8731	0.05	0.9988	0.97	0.4367	0.73	0.6049
$T \times St x Ld$	6	5	0.50	0.8102	0.04	0.9992	0.04	0.9990	1.49	0.1938	0.59	0.7087
$T \times Sus x Ld$	6	5	0.43	0.8594	3.61	0.0034	10.61	< 0.0001	2.01	0.0761	0.95	0.4518
$St \times Sus x Ld$	1	1	0.10	0.7536	0.03	0.8642	0.01	0.9630	0.01	0.9808	0.90	0.3448
$T \times Sus \times St \times Ld$	6	5	0.14	0.9911	0.10	0.9926	0.02	0.9998	0.41	0.8423	0.40	0.8464
df er	ror		3	31	2	.33	2	247	2	261	2	237



Figure 1. Coefficients of leaf litter decomposition (mean \pm SE) of six understory plant species (the three species on the left are resistant and the three on the right are susceptible to herbivory) in two stand species (*n* = 3; three bags/species in each stand/damage treatment): (**A**) oak and (**B**) pine monoculture. Significant differences between control and damaged and leaves within the same plant species are shown with asterisks (* *p* < 0.05 and ** *p* < 0.01).

The content of TPh and tannins in leaf litter was significantly affected by the understory plant species (Table 2). The differences in content of these metabolites for the entire leaf degradation period were mainly due to their initial level. Such high levels of TPh were first characterized for *C. sanguinea* leaves (Figure 3A), followed by *P. serotina* (Figure 3F), *C. avellana* (Figure 3D), and *P. padus* (Figure 3E). Initially, a higher content of tannins was found in the leaves of susceptible species: *P. serotina* (Figure 4F), *P. padus* (Figure 4E), and *C. avellana* (Figure 4D). An analysis of TPh and tannins indicated a very rapid decline in their content during the first half of the year. Low content was detected irrespective of the differentiated baseline and persisted for two consecutive years.

In the case of substances that may have a potentially beneficial effect on the microorganisms involved in the decomposition of litter, i.e., N and TNC, the impact of the species was significant (Table 2). N content significantly (p < 0.0001) increased with increased time for litter decomposition (Table 2). This increase is particularly evident in species less susceptible to insects (Figure 5). The content of TNC in leaves decreased especially in the



first period of decomposition (Figure 6). Differences between susceptible groups were also noted, where the TNC and N content were lower in susceptible species.

Figure 2. Dynamics of leaf litter decomposition of six understory plant species (herbivore resistant species: *Cornus sanguinea*—(**A**), *Frangula alnus*—(**B**), *Sambucus nigra*—(**C**), on the left and herbivore susceptible species: *Corylus avellana*—(**D**), *Prunus padus*—(**E**), *Prunus serotina*—(**F**), on the right), depending on leaf damage (Ld; control (C) and damaged (D)) in two stand species (St; oak and pine monocultures).

Month

3.2. Differences in Rate of Litter Decomposition between Damaged and Undamaged Leaves

Month

There was no significant effect of leaf damage on the rate of litter decomposition, characterized by the decay rate k (Table 1). When analyzing each species separately, it was found that in *P. serotina*, damaged leaves decomposed significantly faster (higher k) than the controls (Figure 1). However, leaf damage significantly affected the mass of undecomposed leaf litter (Table 2). The mass of damaged leaves was 6.1% lower than that of control leaves. This faster reduction in the mass of damaged leaves was most evident in *P. serotina* (Figure 2F), and also noticeable in *P. padus* (Figure 2E) and *C. avellana* (Figure 2D). There was a significant Sp × Ld interaction, indicating that the impact of damage on the mass of the remaining litter was affected by understory plant species (Sp). The remaining litter mass data (average in both St) showed that, compared to control leaves, the mass loss of damaged leaves was the largest in *P. serotina* (27.1%), followed by *S. nigra* (6.1%), and *C. avellana* (1.7%). The opposite was true in *F. alnus* and *P. padus*, where there was more decomposition in the control than damaged leaves by 7.1% and 4.3%, respectively. In *C. sanguinea*, there was no difference.



Figure 3. Changes in content of total phenols (TPh; expressed as μ M of chlorogenic acid g⁻¹ d.m.) in leaf litter of six understory plant species (herbivore resistant species: *Cornus sanguinea*—(**A**), *Frangula alnus*—(**B**), *Sambucus nigra*—(**C**), on the left and herbivore susceptible species: *Corylus avellana*—(**D**), *Prunus padus*—(**E**), *Prunus serotina*—(**F**), on the right), depending on leaf damage (Ld; control (C) and damaged (D)) in two stand species (St; oak and pine monocultures).

Leaf damage significantly differentiated the content of TPh (Table 2). The understory plant species differentiated the content of TPh; however, there were no differences between the herbivore susceptibility groups. The content of TPh throughout the entire decomposition period and for all Sp was lower in damaged than in undamaged leaves.

Leaf damage did not significantly affect average N content for all species, but there was a significant interaction of Ld \times Sus (Table 2). The susceptibility affects N and TNC, where resistant species had 62% and 34% higher content of N and TNC respectively, than susceptible species (Table 2). As the results show by the curve representing changes in TNC content with time of decomposition (Figure 6), one of the reasons for the lack of significant differences between control and damaged leaves may be that in all species, the carbohydrate content after the first measurement period (4 months) of leaf decay decreased to a very low level and at later stages remained practically unchanged.

3.3. Rate of Litter Leaf Decomposition and Its Chemical Composition Variation between Stand Species

The stand species did not significantly affect the decay rate *k*. However, the interaction between Sus and the St in the impact on *k* was significant. In the oak stand, decomposition was faster in *C. sanguinea* than in *S. nigra*, while in the pine stand, the opposite was true

(Figure 2A,C). Additionally, decomposition of *P. serotina* and *C. avellana* leaves in oak (Figure 1A) was faster than in pine (Figure 1B). The stand species had a significant impact on undecomposed mass. In the oak stand, the leaves decomposed faster. On average, for all plant species and both treatments of Ld, the mass of undamaged control leaves was 14.8% lower in oak than pine. There was no St × Ld interaction, so regardless of damage, the leaves decomposed faster in oak than pine.



Figure 4. Changes in content of tannins (expressed as μ M of catechin g⁻¹ d.m.) in leaf litter of six understory plant species (herbivore resistant species: *Cornus sanguinea*—(A), *Frangula alnus*—(B), *Sambucus nigra*—(C), on the left and herbivore susceptible species: *Corylus avellana*—(D), *Prunus padus*—(E), *Prunus serotina*—(F), on the right), depending on leaf damage (Ld; control (C) and damaged (D)) in two stand species (St; oak and pine monocultures).

The stand species did not significantly differentiate the content of tannin and TPh in the leaves (Table 2). In all plant species, the levels of these compounds were practically the same under both stand species. The initial content of tested metabolites or N did not affect the decay rate (k), which depended primarily on insect susceptibility and understory plant species, and to some extent on the stand species; a significant interaction was noted between susceptibility and stand species (Table 1). The stand species did not affect the differences in average TPh and tannin content between damaged and undamaged leaves determined throughout their decomposition period (Table 2).





Figure 5. Changes in content of nitrogen (% d.m.) in leaf litter of six understory plant species (herbivore resistant species: *Cornus sanguinea*—(**A**), *Frangula alnus*—(**B**), *Sambucus nigra*—(**C**), on the left and herbivore susceptible species: *Corylus avellana*—(**D**), *Prunus padus*—(**E**), *Prunus serotina*—(**F**), on the right), depending on leaf damage (Ld; control (C) and damaged (D)) in two stand species (St; oak and pine monocultures).

Herbivore susceptible Corylus avellana



Figure 6. Changes in content of total non-structural carbohydrates (TNC, % d.m.) in leaf litter of six understory plant species (herbivore resistant species: *Cornus sanguinea*—(A), *Frangula alnus*—(B), *Sambucus nigra*—(C), on the left and herbivore susceptible species: *Corylus avellana*—(D), *Prunus padus*—(E), *Prunus serotina*—(F), on the right), depending on leaf damage (Ld; control (C) and damaged (D)) in two stand species (St; oak and pine monocultures).

4. Discussion

4.1. Differences in Rate of Litter Decomposition between Plant Species

Our prediction was that differences in the rate of litter decomposition would reflect differences in susceptibility to insect damage. We based this assumption on the influence of defensive compounds, soluble phenols, and condensed tannins on herbivorous insects. At the same time, we assumed that these compounds would similarly inhibit the decay of leaf litter by microorganisms, as they impede the feeding of insects on growing leaves [24,26]. However, we found the reverse: herbivore resistant species had a higher decay rate, which

means they decomposed faster. Thus, our first hypothesis, regarding faster leaf litter decomposition in plant species more susceptible to herbivorous insects, was not confirmed. This indicates that there is no direct effect of the resistance of growing leaves to insect feeding on the decomposition of fallen leaf litter by microorganisms.

Results different from ours were obtained by Chapman et al. [23], who examined the relationship between resistant and sensitive tree populations of *Pinus edulis* Engelm. The fallen needles of the resistant population decomposed slower than those of the sensitive trees. Additionally, Cornelissen et al. [22] obtained results that were opposite of ours. Conducting research in two countries (Argentina and Great Britain), Cornelissen et al. [22] concluded that there was a highly significant positive correlation between leaf palatability and litter mass loss and also a negative correlation between leaf thickness/strength and litter mass loss across all tested species. In contrast, research conducted on 14 temperate woody species by Simon et al. [33] indicated that metabolic profiles in the leaves or litter, including phenol content, does not allow simple grouping according to the decomposition of *P. serotina* leaves than *P. padus* leaves, with much greater resistance to feeding of insects in the former [9].

We assumed that the decomposition of leaf litter would be slower for plant species in which the leaves contain more defensive metabolites because these substances would adversely affect microorganisms decomposing litter, just as they adversely affect herbivorous insects [24]. The feeding of insects induces the synthesis of defensive compounds [19,34–37]. The TPh and tannin content also determines constitutive defense, but it can change during the growing season [9]. Gavinet et al. [25] found higher levels of phenolic compounds in aging leaves of *Cotinus coggygria* Scop. than in growing leaves. In contrast, our results in both the current and previous studies [9] show that the levels of defense compounds at the end of the growing season decrease rapidly, and the differences in TPh content in autumn leaves are smaller than at the beginning or the peak of the growing season.

The results of the influence of TPh (Figure 3) and tannins (Figure 4) on the litter decomposition rate are unclear. There were significant differences between species at the beginning of the experiment, before decomposition. However, in all species, the levels dropped rapidly after a short period of time. We see the greatest need for further research in this time period, possibly taking into account other groups of metabolites. In general, our results are not consistent with data in the literature, which show that leaves with a higher content of defense compounds decompose more slowly. The negative effect of phenols in fallen leaves on microorganisms decomposing litter, and thus, inhibition of the decomposition process, was indicated in a study by Silfver et al. [38] on individual Betula pendula Roth trees and by Jones et al. [39] on Rhododendron ponticum L. shrubs. In the case of tannins, this pattern is indicated in a review by Kraus et al. [40], and for both groups of defensive compounds (TPh and tannins) in other research [24,41,42]. The inhibitory effect of tannins on the decomposition process is also found in decaying roots [43,44]. In general, the content of the studied defensive compounds in leaf litter was lower in species resistant to insect damage. This trend could explain the reason for the faster leaf litter decomposition in plant species resistant to insect damage.

We found a higher content of TNC in the leaf litter of plant species characterized by faster decomposition (Table 2). Kiser et al. [45] reported on the positive effect of elevated TNC content of *Pinus taeda* L. needles on their decomposition. Additionally, according to Guo et al. [46], Fan and Guo [47], and Goebel et al. [44], a higher content of TNC in roots significantly contributes to their faster decomposition. Castells et al. [48] indicated a large role of carbohydrates in accelerating the decomposition of litter. Moreover, they suggested that TNC cause the release of N from litter, and their interaction can mask the negative effects of phenolic compounds. The effect of N compounds on reducing the content of defensive carbon compounds in living plants is well known [49]. Our results show that increased TNC content, but also N to some extent, affects litter decomposition. The positive effect of N content in fallen leaves on microorganisms decomposing the litter,

and thus, accelerating decomposition, was indicated by Silfver et al. [38], referring to reactions occurring in individual trees of *B. pendula*. A positive effect of N on leaf litter decomposition was also found by Osono et al. [50], but it concerned decomposition by fungi (*Xylaria* Hill ex Schrank). In some studies, however, the significance of the effect of N on leaf litter decomposition was negated or defined as negligible [51,52]. The increase of N that we observed was most likely related to the change in the proportion of this element in the decomposed litter. Thus, the proportional increase in N over time in dry matter was due to the relatively faster degradation of nitrogen-free compounds (e.g., carbohydrate).

4.2. Differences in Rate of Litter Decomposition between Damaged and Undamaged Leaves

The second tested hypothesis was also not confirmed. We hypothesized that the damaged leaves would decompose slowly because earlier insect damage would deprive them of soft tissues between the veins [23]. On average, in all species and in most of the leaves, damaged leaves decomposed faster than did undamaged leaves. Similar results, i.e., faster decomposition of damaged versus undamaged needles of Pinus edulis Engelm., were obtained by Chapman et al. [23], studying the feeding of *Matsucoccus acalyptus* Herbert and Dioryctria albovittella Hulst and by Piazza et al. [53], for Nothofagus pumilio Krasser leaves. The largest and most statistically significant differences in the rate of decomposition between damaged and undamaged leaves were for *P. serotina* (Figure 1). In *P. serotina*, shade leaves are eaten almost exclusively by herbivorous insects as opposed to sun leaves [9,10]. The two types of leaves differ greatly in their structure [13]. Shade leaves are very thin and soft, while sun leaves are thick, hard, and leathery. Sariyildiz and Anderson [54], who examined freshly fallen leaf litter from sweet chestnut (Castanea sativa Mill.), oak (Q. robur), and beech (Fagus sylvatica L.) trees classified sun, intermediate, and shade leaf types, and found that shade leaves decomposed faster than sun leaves. Shade leaves are characterized by a much higher specific leaf area (SLA) than sun leaves. The faster rate of decomposition for leaves with higher SLA is also indicated in the review by Cornwell et al. [55]. The likely reason for the faster decomposition of damaged leaves may be that they are generally shaded leaves (with a higher SLA, i.e., a larger area per unit of mass than undamaged leaves), and therefore, more accessible to the microorganisms that decay them. In addition to differences in chemical leaf quality, insects can affect physical quality by increasing tissue weakness and causing a pre-decomposition of damaged leaves, stimulating early fungal colonization [56]. These could be the reasons for the significantly faster decomposition of undamaged versus damaged leaves of P. serotina. Similar factors may have influenced differences (although not significant) between damaged and undamaged leaves for the other studied understory plant species.

We assumed that since leaves damaged by insects would have more defensive metabolites (because of phenolic compound induction) and less carbohydrate or N, they would be slower to decompose. Our results indicate that the content of these compounds does not predetermine the rate of the litter decay and does not cause decomposition differences between damaged and undamaged leaves. However, it was surprising to us that damaged leaves decomposed faster than undamaged leaves, although the difference in litter decay rate was not statistically significant. We knew from many of our previous studies that the damaged leaves [6,10,13,57], and especially the tissues around the necroses [58], are characterized by an increased phenol content. Above, we described the results showing that phenolic compounds inhibit the rate of litter decomposition. For the same reason, we thought that damaged leaves would have a higher content of defensive compounds than undamaged leaves. However, according to our current research, and contrary to our assumptions, the phenol content in fallen leaves just before decomposition turned out to be lower in all plant species in damaged leaves than in those undamaged by herbivorous insects.

The average tannin content in all plant species, and TPh in all species except *S. nigra*, was lower in damaged than undamaged leaves, not only immediately before decomposition but in the entire decomposition period. Thus, the results regarding defensive compounds

explain the faster decomposition of damaged versus undamaged leaves. The results of our research indicating the inhibitory effect of defensive compounds on the decomposition of litter are consistent with the results obtained by other authors [24,59]. However, our results clearly show that in a short time (after 4 months), there is a rapid decrease in the content of defensive compounds, both the TPh (Figure 3) and condensed tannins (Figure 4). A very large decrease in the level of phenolic compounds (by almost 75%) in the fallen needles of *C. coggygria*, after just over 3 months, was indicated by Santonja et al. [60]. Gavinet et al. [61] reported very rapid degradation of phenolic compounds in the leaf litter of six Mediterranean woody species, despite their very high levels immediately before decomposition. A similar scenario, i.e., a rapid decrease in the content in the first period of decomposition, was also observed in other compounds (terpenes).

Unlike defensive compounds, undamaged and damaged leaves did not differ in their N and TNC content (Table 2). However, when they were analyzed separately for each of the studied plant species, significant differences were noted for some species (Figures 5 and 6). Research carried out by Chapman et al. [23] showed that damage in *P. edulis* needles increased N content in litter and accelerated decomposition. Conrad et al. [62] explained higher levels of N in leaf litter by herbivory-induced desiccation and foliar mortality prior to the translocation of N back into plant reserves. Because high N content in leaves does not limit insect feeding [63], it is likely that litter-decomposing microorganisms are also unperturbed by high N levels, so differences in N levels do not contribute to differences in decomposition between damaged and undamaged leaves.

It is likely that in the case of litter decomposition by microorganisms, the complex composition of secondary defensive metabolites and nutrients may be more decisive. Some of the results of our research showed a tendency toward such patterns, but their lack of significance diminished their use in inference. For example, there was no significant correlation of leaf damage with leaf decomposition rates of litter or with the level of some metabolites. One reason for this may be that the largest leaf damage in some of the understory plant species we studied was caused by insects classified as monophagous (C. avellana), others as polyphagous (C. sanguinea, S. nigra, F. alnus, P. serotina), and others as both (P. padus). The main pest of C. avellana leaves is the monophagous Altica brevicollis coryletorum Král, which is not harmed by a very high phenolic compound content, but prefers elevated levels of TNC [14]. However, leaf damage caused by this insect mainly affects sun leaves. This results not from the nutritional quality of the leaves, but from the insect's preference for high temperatures, which causes it to feed on the leaves of plants growing in direct sunlight. This example indicates that leaf damage is not always dependent on metabolite content. Other causes, such as the direct influence of external factors, may be more decisive. In contrast, P. padus leaves are severely damaged by polyphagous insects, mainly Gonioctena quinquepunctata F. [10], and the monophagous *Yponomeuta evonymella* L. [64,65], which tolerates high levels of phenolic compounds in leaves [6,66]. This may be another reason for the difficulties in obtaining an overall understanding of the relationship between leaf damage, metabolite levels, and the rate of leaf litter decomposition.

4.3. Rate of Litter Decomposition between Stand Species

Some authors point to the influence of the litter of one species on the leaf decomposition of other species [25,67]. According to Ristok et al. [67], this effect consists of accelerating the destruction of tannins, which inhibit the decomposition of litter. Others indicate that the fallen leaves of plant species with high levels of phenolic compounds negatively affect springtails (Collembola) decomposing the litter of other plant species. Soil organisms that decompose plant litter were thought to be mostly generalists [29]. Nevertheless, plant–decomposer interactions show a higher level of specificity than has been formerly thought [68]. Therefore, we formulated our third hypothesis regarding the possibility of differences in the decomposition of leaves depending on the stand, deciduous or coniferous. We assumed that leaves of understory plant species would decompose faster in deciduous versus coniferous stands, i.e., deciduous stands are more favorable for decaying organisms than are coniferous stands. Many leaf litter decay studies have suggested that decomposition occurs more rapidly when litter is placed beneath the plant species from which it has been derived (often referred to as a "home-field advantage") [28,32,69]. This hypothesis was partially confirmed, because the stand species did not alter the decay rate k; however, it had an influence on the remaining mass in relation to the initial mass (%), where the loss of leaf mass was larger under oak than under pine (Table 2). Horodecki and Jagodziński [70] came to a similar conclusion regarding several species of deciduous trees, noting that leaves decomposed significantly faster in home stands than in Scots pine stands. Furthermore, Ayres et al. [71,72] found that aspen litter degraded more rapidly than the pine litter and both litters decomposed more rapidly in the aspen stands than in pine stands. They speculated that "home-field advantage" may have been due to differences in bacterial and fungal community composition, and differences in the abundance of soil organisms such as rotifers, collembolans, nematodes, and mesostigmatid mites between soil communities in the pine and aspen stands [72].

5. Conclusions

Herbivore-resistant species had a higher decay rate, which means they decomposed faster. This indicates no direct effect of the herbivore resistance of growing leaves on the decomposition of leaf litter by microorganisms. We conclude that we cannot sufficiently confirm the negative impact of defensive compounds and the positive impact of TNC and N on the decomposition of leaf litter that is reported in the literature. Instead, we report that these compounds similarly affect the differences in the decomposition of leaf litter between understory plant species and between damaged and undamaged leaves. However, we cannot say that the tested metabolites play a key role in the rate of litter degradation, primarily because the majority of these substances are decomposed quickly (in the first few months). Moreover, when assessing the influence of these compounds on litter decomposition, we could not determine their content as growing leaves, but only as fallen leaves. Finally, it is worth emphasizing that the loss of litter mass was larger under oak than under pine stands, indicating that the microorganisms in deciduous stands are more effective at decomposing leaf litter from the six understory plant species we examined.

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References

- 1. Tuszyński, M.; Grzelak, A. An attempt of evaluating the impact of understory on soil, microclimate, and vegetation in pine stands on poor sandy forest soil. *Sylwan* **1998**, *142*, 15–26.
- 2. Horodecki, P.; Nowiński, M.; Jagodziński, A.M. Advantages of mixed tree stands in restoration of upper soil layers on postmining sites: A five-year leaf litter decomposition experiment. *Land Degrad. Dev.* **2019**, *30*, 3–13. [CrossRef]
- 3. Siles, G.; Rey, P.J.; Alcántara, J.M.; Bastida, J.M.; Herreros, J.L. Effects of soil enrichment, watering and seedling age on establishment of Mediterranean woody species. *Acta Oecologica* 2010, *36*, 357–364. [CrossRef]
- 4. Sardans, J.; Peñuelas, J. Plant-soil interactions in Mediterranean forest and shrublands: Impacts of climatic change. *Plant Soil* 2013, 365, 1–33. [CrossRef]
- Karolewski, P.; Łukowski, A.; Adamczyk, D.; Żmuda, M.; Giertych, M.J.; Mąderek, E. Species composition of arthropods on six understory plant species growing in high and low light conditions. *Dendrobiology* 2020, *84*, 58–80. [CrossRef]
- 6. Karolewski, P.; Jagodziński, A.M.; Giertych, M.J.; Łukowski, A.; Baraniak, E.; Oleksyn, J. Invasive Prunus serotina—A new host for *Yponomeuta evonymellus* (Lepidoptera: Yponomeutidae)? *Eur. J. Entomol.* **2014**, *111*, 227–236. [CrossRef]
- Leather, S.R. Feeding specialisation and host distribution of British and Finnish Prunus feeding macrolepidoptera. *Oikos* 1991, 60, 40. [CrossRef]
- 8. Uusitalo, M. *European Bird Cherry (Prunus padus L.)—A Biodiverse Wild Plant for Horticulture*; MTT Agrifood Research Finland: Jokioinen, Finland, 2004; Volume 61, ISBN 9517299192.
- 9. Karolewski, P.; Giertych, M.J.; Żmuda, M.; Jagodziński, A.M.; Oleksyn, J. Season and light affect constitutive defenses of understory shrub species against folivorous insects. *Acta Oecologica* **2013**, *53*, 19–32. [CrossRef]
- 10. Mąderek, E.; Łukowski, A.; Giertych, M.J.; Karolewski, P. Influence of native and alien *Prunus* species and light conditions on performance of the leaf beetle *Gonioctena quinquepunctata*. *Entomol. Exp. Appl.* **2015**, *155*, 193–205. [CrossRef]
- 11. Łukowski, A.; Mąderek, E.; Karolewski, P. Light conditions effect on bird cherry ermine moth—The main pest of bird cherry. *Sylwan* **2014**, *158*, 595–603.
- 12. Rodríguez-Calcerrada, J.; Reich, P.B.; Rosenqvist, E.; Pardos, J.A.; Cano, F.J.; Aranda, I. Leaf physiological versus morphological acclimation to high-light exposure at different stages of foliar development in oak. *Tree Physiol.* 2008, 28, 761–771. [CrossRef]
- 13. Mąderek, E.; Zadworny, M.; Mucha, J.; Karolewski, P. Light as a regulator of structural and chemical leaf defenses against insects in two Prunus species. *Acta Oecologica* 2017, *85*, 18–24. [CrossRef]
- 14. Łukowski, A.; Giertych, M.J.; Zadworny, M.; Mucha, J.; Karolewski, P. Preferential feeding and occupation of sunlit leaves favors defense response and development in the flea beetle, *Altica brevicollis coryletorum*—A pest of *Corylus avellana*. *PLoS ONE* **2015**, *10*, e0126072. [CrossRef]
- 15. Niinemets, Ü. Role of foliar nitrogen in light harvesting and shade tolerance of four temperate deciduous woody species. *Funct. Ecol.* **1997**, *11*, 518–531. [CrossRef]
- 16. Fortin, M.; Mauffette, Y. The suitability of leaves from different canopy layers for a generalist herbivore (Lepidoptera: Lasiocampidae) foraging on sugar maple. *Can. J. For. Res.* **2002**, *32*, 379–389. [CrossRef]
- 17. Haukioja, E. Induction of defenses in trees. Annu. Rev. Entomol. 1990, 36, 25-42. [CrossRef]
- 18. Bryant, J.P.; Reichardt, P.B.; Clausen, T.P.; Werner, R.A. Effects of mineral nutrition on delayed inducible resistance in Alaska paper birch. *Ecology* **1993**, *74*, 2072–2084. [CrossRef]
- 19. Eyles, A.; Bonello, P.; Ganley, R.; Mohammed, C. Induced resistance to pests and pathogens in trees. *New Phytol.* **2010**, *185*, 893–908. [CrossRef] [PubMed]
- Pavlović, P.; Kostić, O.; Jarić, S.; Gajić, G.; Pavlović, D.; Pavlović, M.; Mitrović, M. The effects of leaf litter chemistry and anatomical traits on the litter decomposition rate of *Quercus frainetto* Ten. and *Quercus cerris* L. in situ. *Arch. Biol. Sci.* 2020, 72, 543–553. [CrossRef]
- 21. Li, S.; Tong, Y.; Wang, Z. Species and genetic diversity affect leaf litter decomposition in subtropical broadleaved forest in southern China. *J. Plant Ecol.* 2017, *10*, 232–241. [CrossRef]
- 22. Cornelissen, J.H.C.; Pérez-Harguindeguy, N.; Díaz, S.; Grime, J.P.; Marzano, B.; Cabido, M.; Vendramini, F.; Cerabolini, B. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytol.* **1999**, *143*, 191–200. [CrossRef]
- 23. Chapman, S.K.; Hart, S.C.; Cobb, N.S.; Whitham, T.G.; Koch, G.W. Insect herbivory increases litter quality and decomposition: An extension of the acceleration hypothesis. *Ecology* **2003**, *84*, 2867–2876. [CrossRef]
- 24. Burghardt, K.T.; Bradford, M.A.; Schmitz, O.J. Acceleration or deceleration of litter decomposition by herbivory depends on nutrient availability through intraspecific differences in induced plant resistance traits. *J. Ecol.* **2018**, *106*, 2380–2394. [CrossRef]
- Gavinet, J.; Santonja, M.; Baldy, V.; Hashoum, H.; Peano, S.; Tchong, T.; Gros, R.; Greff, S.; Fernandez, C.; Bousquet-Mélou, A. Phenolics of the understory shrub *Cotinus coggygria* influence Mediterranean oak forests diversity and dynamics. *For. Ecol. Manag.* 2019, 441, 262–270. [CrossRef]
- 26. Santonja, M.; Foucault, Q.; Rancon, A.; Gauquelin, T.; Fernandez, C.; Baldy, V.; Mirleau, P. Contrasting responses of bacterial and fungal communities to plant litter diversity in a Mediterranean oak forest. *Soil Biol. Biochem.* **2018**, 125, 27–36. [CrossRef]
- 27. Wallenstein, M.D.; Haddix, M.L.; Ayres, E.; Steltzer, H.; Magrini-Bair, K.A.; Paul, E.A. Litter chemistry changes more rapidly when decomposed at home but converges during decomposition-transformation. *Soil Biol. Biochem.* 2013, 57, 311–319. [CrossRef]

- 28. Ayres, E.; Steltzer, H.; Simmons, B.L.; Simpson, R.T.; Steinweg, J.M.; Wallenstein, M.D.; Mellor, N.; Parton, W.J.; Moore, J.C.; Wall, D.H. Home-field advantage accelerates leaf litter decomposition in forests. *Soil Biol. Biochem.* **2009**, *41*, 606–610. [CrossRef]
- 29. Veen, G.F.C.; Freschet, G.T.; Ordonez, A.; Wardle, D.A. Litter quality and environmental controls of home-field advantage effects on litter decomposition. *Oikos* 2015, 124, 187–195. [CrossRef]
- 30. Żmuda, M.; Karolewski, P.; Giertych, M.J.; Żytkowiak, R.; Bąkowski, M.; Grzebyta, J.; Oleksyn, J. The effect of light conditions on leaf injury in underbrush shrubs caused by leaf-eating insects. *Acta Sci. Pol. Silv. Colendar. Rat. Ind. Lingar.* **2008**, *7*, 47–57.
- 31. Chen, Y.; Ruberson, J.R.; Olson, D.M. Nitrogen fertilization rate affects feeding, larval performance, and oviposition preference of the beet armyworm, *Spodoptera exigua*, on cotton. *Entomol. Exp. Appl.* **2008**, *126*, 244–255. [CrossRef]
- 32. Hobbie, S.E.; Reich, P.B.; Oleksyn, J.; Ogdahl, M.; Zytkowiak, R.; Hale, C.; Karolewski, P. Tree species effects on decomposition and forest floor dynamics in a common garden. *Ecology* **2006**, *87*, 2288–2297. [CrossRef]
- Simon, J.; Dörken, V.M.; L.-M.-Arnold, A.; Adamczyk, B. Environmental conditions and species identity drive metabolite levels in green leaves and leaf litter of 14 temperate woody species. *Forests* 2018, *9*, 775. [CrossRef]
- 34. Stevens, M.T.; Lindroth, R.L. Induced resistance in the indeterminate growth of aspen (*Populus tremuloides*). *Oecologia* **2005**, 145, 298–306. [CrossRef]
- 35. Poelman, E.H. From induced resistance to defence in plant-insect interactions. Entomol. Exp. Appl. 2015, 157, 11–17. [CrossRef]
- Mathur, V.; Ganta, S.; Raaijmakers, C.E.; Reddy, S.A.; Vet, L.E.M.; van Dam, N.M. Temporal dynamics of herbivore-induced responses in *Brassica juncea* and their effect on generalist and specialist herbivores. *Entomol. Exp. Appl.* 2011, 139, 215–225. [CrossRef]
- 37. Mooney, E.H.; Tiedeken, E.J.; Muth, N.Z.; Niesenbaum, R.A. Differential induced response to generalist and specialist herbivores by *Lindera benzoin* (Lauraceae) in sun and shade. *Oikos* **2009**, *118*, 1181–1189. [CrossRef]
- Silfver, T.; Kontro, M.; Paaso, U.; Karvinen, H.; Keski-Saari, S.; Keinänen, M.; Rousi, M.; Mikola, J. Intrapopulation genotypic variation in leaf litter chemistry does not control microbial abundance and litter mass loss in silver birch, *Betula pendula*. *Plant Soil* 2018, 426, 253–266. [CrossRef]
- 39. Jones, G.L.; Scullion, J.; Worgan, H.; Gwynn-Jones, D. Litter of the invasive shrub *Rhododendron ponticum* (Ericaceae) modifies the decomposition rate of native UK woodland litter. *Ecol. Indic.* 2019, 107, 105597. [CrossRef]
- 40. Kraus, T.E.C.; Zasoski, R.J.; Dahlgren, R.A. Fertility and pH effects on polyphenol and condensed tannin concentrations in foliage and roots. *Plant Soil* **2004**, *262*, 95–109. [CrossRef]
- 41. Schweitzer, J.A.; Bailey, J.K.; Hart, S.C.; Wimp, G.M.; Chapman, S.K.; Whitham, T.G. The interaction of plant genotype and herbivory decelerate leaf litter decomposition and alter nutrient dynamics. *Oikos* **2005**, *110*, 133–145. [CrossRef]
- 42. Kurokawa, H.; Nakashizuka, T. Leaf Herbivory and decomposability in a Malaysian tropical rain forest. *Ecology* **2008**, *89*, 2645–2656. [CrossRef] [PubMed]
- 43. Wells, C.E.; Eissenstat, D.M. Beyond the roots of young seedlings: The influence of age and order on fine root physiology. *J. Plant Growth Regul.* 2002, *21*, 324–334. [CrossRef]
- Goebel, M.; Hobbie, S.E.; Bulaj, B.; Zadworny, M.; Archibald, D.D.; Oleksyn, J.; Reich, P.B.; Eissenstat, D.M. Decomposition of the finest root branching orders: Linking belowground dynamics to fine-root function and structure. *Ecol. Monogr.* 2011, *81*, 89–102. [CrossRef]
- 45. Kiser, L.C.; Fox, T.R.; Carlson, C.A. Foliage and litter chemistry, decomposition, and nutrient release in *Pinus taeda*. *Forests* **2013**, *4*, 595–612. [CrossRef]
- 46. Guo, D.L.; Mitchell, R.J.; Hendricks, J.J. Fine root branch orders respond differentially to carbon source-sink manipulations in a longleaf pine forest. *Oecologia* 2004, 140, 450–457. [CrossRef]
- 47. Fan, P.; Guo, D. Slow decomposition of lower order roots: A key mechanism of root carbon and nutrient retention in the soil. *Oecologia* **2010**, *163*, 509–515. [CrossRef]
- 48. Castells, E.; Peñuelas, J.; Valentine, D.W. Are phenolic compounds released from the Mediterranean shrub *Cistus albidus* responsible for changes in N cycling in siliceous and calcareous soils? *New Phytol.* **2004**, *162*, 187–195. [CrossRef]
- 49. Björkman, C.; Kytö, M.; Larsson, S.; Niemelä, P. Different responses of two carbon-based defences in Scots pine needles to nitrogen fertilization. *Ecoscience* 1998, *5*, 502–507. [CrossRef]
- 50. Osono, T.; To-Anun, C.; Hagiwara, Y.; Hirose, D. Decomposition of wood, petiole and leaf litter by *Xylaria* species from northern Thailand. *Fungal Ecol.* **2011**, *4*, 210–218. [CrossRef]
- 51. Prescott, C.E. Does nitrogen availability control rates of litter decomposition in forests? *Nutr. Uptake Cycl. For. Ecosyst.* **1995**, 83–88. [CrossRef]
- 52. Sanchez, F.G. Loblolly pine needle decomposition and nutrient dynamics as affected by irrigation, fertilization, and substrate quality. *For. Ecol. Manag.* 2001, 152, 85–96. [CrossRef]
- 53. Piazza, M.V.; Mazía, N.; Kitzberger, T.; Chaneton, E.J. Chronic insect herbivores accelerate litter decomposition and nutrient recycling rates along an environmental/herbivory gradient in northern Patagonia. *For. Ecol. Manag.* **2021**, 479, 118534. [CrossRef]
- 54. Sariyildiz, T.; Anderson, J.M. Decomposition of sun and shade leaves from three deciduous tree species, as affected by their chemical composition. *Biol. Fertil. Soils* **2003**, *37*, 137–146. [CrossRef]
- Cornwell, W.K.; Cornelissen, J.H.C.; Amatangelo, K.; Dorrepaal, E.; Eviner, V.T.; Godoy, O.; Hobbie, S.E.; Hoorens, B.; Kurokawa, H.; Pérez-Harguindeguy, N.; et al. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol. Lett.* 2008, *11*, 1065–1071. [CrossRef]

- 56. Cárdenas, R.E.; Dangles, O. Do canopy herbivores mechanically facilitate subsequent litter decomposition in soil? A pilot study from a Neotropical cloud forest. *Ecol. Res.* **2012**, *27*, 975–981. [CrossRef]
- 57. Giertych, M.J.; Karolewski, P.; Grzebyta, J.; Oleksyn, J. Feeding behavior and performance of *Neodiprion sertifer* larvae reared on *Pinus sylvestris* needles. *For. Ecol. Manag.* **2007**, 242, 700–707. [CrossRef]
- 58. Karolewski, P. Visible and invisible injury to Scots pine (*Pinus sylvestris* L.) needles caused by sulphur dioxide. *Arbor. Kórnickie* **1990**, *35*, 127–136.
- 59. Kraus, T.E.C.; Dahlgren, R.A.; Zasoski, R.J. Tannins in nutrient dynamics of forest ecosystems—A review. *Plant Soil* 2003, 256, 41–66. [CrossRef]
- 60. Santonja, M.; Baldy, V.; Fernandez, C.; Balesdent, J.; Gauquelin, T. Potential shift in plant communities with climate change: Outcome on litter decomposition and nutrient release in a mediterranean oak forest. *Ecosystems* **2015**, *18*, 1253–1268. [CrossRef]
- 61. Gavinet, J.; Prévosto, B.; Bousquet-Melou, A.; Gros, R.; Quer, E.; Baldy, V.; Fernandez, C. Do litter-mediated plant-soil feedbacks influence Mediterranean oak regeneration? A two-year pot experiment. *Plant Soil* **2018**, *430*, 59–71. [CrossRef]
- 62. Conrad, B.; Acharya, K.; Dudley, T.L.; Bean, D.W. Impact of episodic herbivory by the tamarisk leaf beetle on leaf litter nitrogen and stem starch content: A short communication. *J. Arid Environ.* **2013**, *94*, 76–79. [CrossRef]
- 63. Harborne, J.B. Introduction to Ecological Biochemistry; Elsevier Academic Press: London, UK, 1993; ISBN 9780080918587.
- 64. Leather, S.R. Prunus padus L. J. Ecol. 1996, 84, 125-132. [CrossRef]
- 65. Leather, S.R. Insects on bird cherry I. The bird cherry ermine moth, *Yponomeuta evonymellus* (L.) (Lepidoptera: Yponomeutidae). *Entomol. Gaz.* **1986**, *37*, 209–213.
- Łukowski, A.; Giertych, M.J.; Walczak, U.; Baraniak, E.; Karolewski, P. Light conditions affect the performance of *Yponomeuta evonymellus* on its native host *Prunus padus* and the alien *Prunus serotina*. *Bull. Entomol. Res.* 2017, 107, 208–216. [CrossRef] [PubMed]
- Ristok, C.; Leppert, K.N.; Franke, K.; Scherer-Lorenzen, M.; Niklaus, P.A.; Wessjohann, L.A.; Bruelheide, H. Leaf litter diversity positively affects the decomposition of plant polyphenols. *Plant Soil* 2017, 419, 305–317. [CrossRef]
- Bezemer, T.M.; Fountain, M.T.; Barea, J.M.; Christensen, S.; Dekker, S.C.; Duyts, H.; Van Hal, R.; Harvey, J.A.; Hedlund, K.; Maraun, M.; et al. Divergent composition but similar function of soil food webs of individual plants: Plant species and community effects. *Ecology* 2010, *91*, 3027–3036. [CrossRef] [PubMed]
- 69. Madritch, M.D.; Lindroth, R.L. Soil microbial communities adapt to genetic variation in leaf litter inputs. *Oikos* 2011, 120, 1696–1704. [CrossRef]
- Horodecki, P.; Jagodziński, A.M. Tree species effects on litter decomposition in pure stands on afforested post-mining sites. *For. Ecol. Manag.* 2017, 406, 1–11. [CrossRef]
- 71. Ayres, E.; Steltzer, H.; Berg, S.; Wall, D.H. Soil biota accelerate decomposition in high-elevation forests by specializing in the breakdown of litter produced by the plant species above them. *J. Ecol.* **2009**, *97*, 901–912. [CrossRef]
- 72. Ayres, E.; Steltzer, H.; Berg, S.; Wallenstein, M.D.; Simmons, B.L.; Wall, D.H. Tree Species Traits Influence Soil Physical, Chemical, and Biological Properties in High Elevation Forests. *PLoS ONE* **2009**, *4*, e5964. [CrossRef]