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Vine leaf decomposition: Feeding preferences and effects of physico-chemical traits of litter on life-history traits of the woodlice *Armadillidium vulgare* Latreille, 1804

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Abstract

Litter decomposition is a key ecosystem process which is dependent on the litter characteristics and diversity, the decomposer community and activity, and the environmental conditions. We assessed vine leaf decomposition by *Armadillidium vulgare* (Latreille, 1804), a terrestrial isopod widely distributed and naturally present in vineyards. We compared the decomposition of three grape varieties (Chardonnay, Pinot Noir and Sauvignon) with regular laboratory food (*Tilia tomentosa* (Moench, 1785)) for seven consecutive weeks. Seven traits were measured on the four litters tested in order to define their importance concerning (i) litter mass loss by the action of microorganisms and isopods (ii) the trophic traits (consumption and assimilation) and (iii) life-history traits (survival and growth) of *A. vulgare*. Thus, the chemical and physical traits (C/N ratio, tannin and fiber content, thickness) known to influence litter palatability and digestibility for decomposers were determined by standardized methods. In addition, the copper frequently used in viticulture as a fungicide which is potentially responsible for toxic effects on decomposers was measured by ICP-OES after litter mineralization in nitric acid. Our results showed a higher percentage of decomposability by microorganisms in litter with low cellulose content and C/N ratio. Higher isopod consumption and assimilation was found in the litters which is the poorest in tannin, lignin and copper contents. Variation of consumption according to litter was on average 1.5 to 2.7 lower for grape varieties compared to *T. tomentosa* litter. Assimilation was significantly lower with Pinot Noir than the other litters. To conclude, after seven weeks of experimentation, this study showed that if the growth and survival of woodlice were not affected by inter-varietal differences in vine leaf quality, their role in the decomposition process may be strongly modulated

Keywords: grape variety, terrestrial isopod, soil macrofauna, functional trait, consumption rate, vineyard

1. Introduction

Macrodetritivores, such as millipedes and woodlice, play an important role in the decomposition process and can feed on a large variety of litter (Ilieva-Makulec et al., 2006; Slade and Riutta, 2012; Wieser, 1978). The consumption of leaf litter by macrodetritivores accelerates decomposition rate reviewed in David (2014). Currently, most of the studies evaluating the role and feeding preferences of macrodetritivores were done in forest ecosystems, or under controlled conditions, using woody litter (García-Palacios et al., 2015; Slade and Riutta, 2012; Vasconcelos and Laurance, 2005). A lower number of studies were done with grass litter (Coq et al., 2018; Kajak, 1997; Schaefer et al., 2009) or in orchards (Sofa et al., 2020). Surprisingly, while vineyards are widely distributed around the world and cover 7.3 mha of surface area (OIV, 2021), there is no study addressing feeding preferences of macrodetritivores for vine leaf litter. Indeed, most of the studies located in vineyard ecosystems focused on vine leaf decomposition by microbial activities (Brunetto et al., 2018; Probst et al., 2007) or by aquatic macroinvertebrates in adjacent streams (Fernández et al., 2015; Oliveira et al., 2022). To our knowledge, only one study measuring decomposition process related to earthworms and springtails activities has been published (Buchholz et al., 2017) and none on the woodlice.

According to the Intergovernmental Organisation of Vine and Wine OIV (OIV, 2017), ten thousand of grape varieties are listed, but only 33 varieties are cultivated on half of the vine surface. Chardonnay, Sauvignon Blanc and Pinot Noir grape varieties are widespread and gathered 435 000 ha of global production surface (OIV, 2017). In France, these three grape varieties are among top ten of the most commonly cultivated (i.e., 14% of vine surfaces) (OIV, 2017). Fungal diseases are severe threats and are major drivers of pest management programs (Oliva et al., 1999). Synthetic fungicides and organic fungicides (copper and sulfur-based compounds such as Bordeaux mixture) are regularly used as preventive and curative treatment. Grape varieties resistant against downy mildew

(*Plasmopara viticola*) and powdery mildew (*Uncinula necator*), such as Sauvignier gris and Muscaris have been recently cultivated in France. These fungus-resistant grape varieties are more resistant to diseases and need less fungicide applications (Casanova-Gascón et al., 2019; Pedneault and Provost, 2016) and thus contained lower copper concentrations in their leaves.

Vine leaves on the ground are available as a food source to decomposer (microorganisms, soil fauna) at two main periods: during canopy management operations (trimming and leaf removal) and during senescence of vine leaves (Reynolds et al., 1996). During the decomposition, different steps can be achieved by soil organisms such as the fragmentation, mineralization, and the horizontal and vertical transportation of decaying litter, thus their activities contribute to the incorporation of organic matter into soils (Chapin III et al., 2012; Coulis et al., 2016). Microbial communities participate in leaves decomposition through chemical alterations with specific enzymes such as cellulases (Zimmer and Topp, 1998b) or lignin-degrading enzymes (Rahman et al., 2013) and may increase the palatability of litter for detritivores (Bardgett, 2005; Coleman et al., 2017). Due to a generally low assimilation rate, especially for millipedes and woodlice, most of the ingested litter returns to the soil as fecal pellets. Recent studies showed that fecal pellet decomposition was faster than intact litter decomposition, due to increased leaching and available surface for microbial colonization (Coulis et al., 2016; Joly et al., 2020; Joly et al., 2018).

Life-history traits (Drobne, 1997; Roy and Joy, 2009; Zimmer and Topp, 1997) and feeding preferences (Pey et al., 2019; Zhang et al., 2008) of decomposers could depend on litter quality and more precisely to a combination of several physical and chemical traits of litter. The total nutrient content (C, N, P, K, Ca, Mg) is important to satisfy nutrient requirements of detritivores (David and Handa, 2010). Litter with low C/N was preferred by detritivores (Joly et al., 2018; Quadros et al., 2014; Zimmer et al., 2002). Cellulose, hemicellulose and thickness provide information about leaf structure and contribute to indicate litter digestibility (Coûteaux et al., 1995; Zimmer and Topp, 1998a). Secondary metabolites like polyphenols (i.e., phenolics and tannins) and some structural traits (lignin) are plant defenses and thus chemical deterrents to fauna (Coq et al., 2010; Coulis et al., 2009). These

recalcitrant compounds decreased litter ingestion or digestion by fauna (Slade and Riutta, 2012). Physical elements like leaf toughness and thickness may impact mechanical breakdown and thus leaf decomposition speed (Pey et al., 2019; Ristok et al., 2019). Finally, pollutants such as chemicals or metals can involve negative effects on life-history trait and feeding activity of soil organisms (Cortet et al., 1999; Edwards, 2002). In vineyards, the frequent use of fungicides (Cuq et al., 2020; Karimi et al., 2021) is known to increase copper concentration in leaf litter. They may induce potential toxicity (from 500-600 mg Cu/kg in laboratory tests) for detritivores species (Farkas et al., 1996; Loureiro et al., 2006; Zidar et al., 2004) and consequently, reduce the leaf decomposition rates.

In our study, we will focus on the role of woodlice and more specifically on *Armadillidium vulgare* (Crustacea, Isopoda, Oniscidea) in vine leaf litter decomposition of three grape varieties. We have chosen *A. vulgare* because (i) it is a geographically widespread terrestrial isopod species, (ii) its presence is mentioned in vineyards (Hadjicharalampous et al., 2002; Sommaggio et al., 2018) and in our inventories in several French vineyards (Mondet, 2022), (iii) woodlice decomposition ability of litter is well-documented (David and Handa, 2010).

We measured physico-chemical traits of three grape varieties and Isopod breeding food (*T. tomentosa* litter), as well as Isopod physiological traits to address the subsequent questions: are differences in litter quality sufficient to induce [Q1] differences in litter decomposability by microorganisms? [Q2] differences in litter consumption and assimilation by the isopod *A. vulgare*? and [Q3] effects on their growth and survival? We thus expect that [H1] Litter rich in nutrient, thin, and poor in copper, lignin and tannin will be more consumed (higher mass loss) by (a) microorganisms and (b) Isopods than the other; [H2] the assimilation rate (difference between ingestion and excretion) of Isopod will be more related to the C/N and lignin/N ratio than other traits and [H3] Litter with the highest chemical deterrents content will have negative effects on life-history traits of *A. vulgare* (survival and/or growth).

2. Materials and Methods

2.1. Biological Materials

2.1.1. Woodlice culture

Experiments were conducted with the woodlice species *A. vulgare* reared for 40 years (originating from Helsingør, Denmark) under standard laboratory conditions (20°C, natural photoperiod of Poitiers (46.58° N, 0.34° E, Nouvelle-Aquitaine, France)) with *ad libitum* *T. tomentosa* litter, supplemented with fresh carrot slices. Each spring, gravid females were isolated, offspring were sexed, and males and females separated in different plastic boxes (26 × 13 cm) before sexual maturity. For the current study, equal number of virgin males and females, 7-8 months olds and in normal intermoult phase was used (Beauché and Richard, 2013).

2.1.2. Leaves collection

Senescent vine leaves (*Vitis vinifera* Linnaeus, 1753) of several grape varieties were hand-picked in fall 2021 on aerial part of the vine stock by mechanical abscission. Leaves came from two organic vineyards, one is located near Poitiers (46.73° N, 0.38° E, Nouvelle-Aquitaine, France) and the other near Santenay (46.54° N, 4.41° E, Bourgogne, France). Five grape varieties were collected: Pinot Noir (red wine), Sauvignier (rosé or white wines), Chardonnay, Sauvignon Blanc and Muscaris (white wines). Physico-chemical trait measurements on these litters were measured. Among the five litter analysed, the three most dissimilar litter were selected for woodlice feeding preferences (see Supplementary Table S1). *T. tomentosa* litter (i.e. the same species used in the woodlice breeding) were collected at the same time (University Campus of Poitiers) and were used as control for woodlice feeding preferences. After collection, leaves were air-dried at 20°C during several weeks. Only leaves with no macroscopic signs of decomposition were used for the experiments.

2.2. Experimental conditions and microcosms

Plastic boxes (24x18x10 cm) with holes in the lid for air circulation (later called microcosm) were used. At the bottom of each microcosm, 1.5 cm of Paris plaster was added in order to facilitate the maintenance of microcosm humidity. An amount of $10 \pm 0.03\text{g}$ (mean \pm sd) of air-dried leaves

without petiole and fragmented (~3 cm square on average) were placed in each microcosm (4 species x 5 replicates), what was considered as *ad libitum* food. To estimate the initial dry weight of litter in each microcosm, residual leaf water content was measured by drying $10 \pm 0.03\text{g}$ for each litter at 60°C for 48 hours and weighed (4 species x 5 replicates). One day before the start of experiment, air dried leaves were rehydrated by immersing them in water for four hours and then draining them until no water remained to run off the leaves. Woodlice were starved 48 hours before the start of the experiment. Two hundred individuals were divided into groups of ten (5 males and 5 females) in the microcosms. The initial individual mass of the woodlice was 58.5 ± 22 mg. Group biomass (585 ± 9.4 mg) was equilibrated among treatments and boxes.

In parallel, microcosms without woodlice (control) were designed in the same conditions in order to measure litter mass loss due to soil microorganism activity only (4 species x 5 replicates). Three additional replicates of microcosms without woodlice were added to specifically check the maintenance of humidity in the boxes four times a week (which gives 8 microcosms without woodlice per litter). During the whole experiment (49 days), twice a week, each microcosm was moistened with 1.6 ml of water on the plaster to maintain constant the humidity of leaves and the position of each microcosm in the room were randomized. Microcosms were maintained in a room with a controlled 12:12-h light:dark rhythm and a continuous temperature of 20°C . Experiments were carried out in the fall 2021.

2.3. Trait measurements

2.3.1. Leaf litter trait measurements

We determined seven litter traits as follows. Chemical properties of the grape varieties and *T. tomentosa* litter were measured on subsamples. Three replicates of about ten leaves per litter were crushed to a uniform particle size of 1 mm (Cyclotec Sample Mill, Tecator, Höganäs, Sweden). These samples were used to calculate C/N ratio based on total carbon (C) and nitrogen (N) contents of the litter measured with a flash CHN Element Analyzer (Flash 2000, AE 2000 Series NC soils analyser,

Thermo Fisher, Bremen, Germany). Condensed and hydrolysable tannins were estimated with protein precipitable phenolics microplate assay (Coulis et al., 2009; Hagerman, 2002; Hagerman and Butler, 1978). Concentration of structural compounds (lignin, cellulose, hemicellulose) were estimated by sequential neutral detergent/acid detergent digestion by an automated fiber extraction analyzer and are then reported as percent dry weights (Fibretherm FT12, Gerhardt, Burladingen, Germany). Leaf litter thickness was measured with micrometer on re-moistened leaves avoiding leaf veins on four zones five times per leaf according to Vile et al. (2005). Finally, litter copper concentration was measured because the vine leaves came from vineyards treated with Bordeaux mixture. Leaves were mineralized by microwave (Anton-Paar Multiwave Pro, Les Ulis, France) with nitric acid (HNO₃). Then, the samples were analysed for copper content by Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES) (Agilent 5110 VDV, Santa Clara, CA, USA).

2.3.2. Litter mass loss, consumption, assimilation and life-history traits of woodlice

To evaluate vine leaves decomposition, we collected the remaining leaves at the end of the experiment. For microcosms with woodlice, leaves and feces were separated. Both leaves and feces were dried at 60°C and weighed. Several parameters of litter decomposition and feeding preferences were defined and calculated as follows: (i.) Litter mass loss (g) was the difference between initial dry litter mass and the dry remaining mass at the end of the experiment. (ii.) Woodlice litter consumption by woodlice (C_t) was estimated according to the formula of David (1998):

$$C_t = \frac{(M_i - M_i D - M_f)}{\sqrt{1-D}}$$

$$\text{with } D = \frac{M'_i - M'_f}{M'_i}$$

with M_i the initial litter dry mass, M_f the final litter dry mass, D the contribution of microbial-driven decomposition to each litter species mass loss, i.e., the mean proportion of litter mass loss in the absence of woodlice for each species (latter called decomposability), M'_i initial litter dry mass in control microcosms and M'_f the final litter dry mass in control microcosms (David, 1998). This formula

takes into account initial and final litter dry mass of a microcosm with woodlice and its corresponding control without woodlice. (iii.) Litter consumption rate of woodlice was expressed per day and per woodlice mass (fresh body mass) in their respective microcosms. The first week of the experiment, feces production (g) was measured 24 hours after the start of the experiment (collected and weighed out) and after every two days (four times). A last measurement of feces production was realized at the end of the experiment, collecting and weighing. These two measurements were added together to estimate total woodlice feces production per microcosm in 49 days. (iv.) Daily feces production rate (F) was the sum of all dried feces (g) per individual biomass mean (g) per day. (v.) Assimilation rate was calculated as follow: Assimilation = Consumption rate - Feces production rate. (vi.) Finally, assimilation efficiency was determined by dividing the assimilation rate by the consumption rate.

To evaluate the impact of grape varieties and *T. tomentosa* litter consumption on life-history traits of woodlice, we recorded several parameters on woodlice: individual survival, number of moults, individual weight. Survival was checked and moults were counted twice a week during rehumidification of the microcosms. If a woodlice died, it was replaced by another individual of the same sex and biomass to maintain a consumption pressure constant of ten woodlice per box. The ten individuals per microcosms were weighed at the beginning, the middle (25 days after the start) and at the end of the experiment (49 days). Woodlice growth was estimated by the number of moults and mass gain [Day 0-Day 49].

2.4. Data analysis

Normality and homoscedasticity of variance of variables were assessed with Shapiro-Wilk and Levene tests ($\alpha = 0.05$) on the R software v.3.6.3 (R Core Team, 2020). Differences between litter traits were tested using a Kruskal-Wallis test followed by a post-hoc Dunn test. Differences between treatment in litter mass loss (with or without woodlice) were also tested using a Kruskal-Wallis test followed by a post-hoc Dunn test. Consumption and assimilation were tested using a one-way Anova followed by a post-hoc Tukey test. Concerning the differences of *A. vulgare* growth (mass gain, moult)

between treatments, they were tested with a linear mixed-effects model and general linear mixed-effects model (Lmer and Glmer). Survival was tested with a Cox proportional-hazards model (Cox, 1972).

In order to detect relationships between litter traits and woodlice physiological traits, we used a co-inertia analysis in a symmetric way. This technique performs a double inertia analysis of two matrices with maximizing co-variance on axes of co-inertia (Dolédéc and Chessel, 1994). The intensity of covariation between the matrices is described by the RV coefficient (Monte-Carlo test) that varies between 0 and 1 (with 1 as maximum correlation). Co-inertia was performed using the Principal Component Analysis (PCA) ordination method for both matrices (litter and traits) with 999 permutations to assess the significance of the co-structure of the data sets. To perform the Co-inertia analysis, the Ade4 package in R was used.

3. Results

3.1. Litter properties

Significant differences of chemical or physical traits were found between the four plant litter (Table 1). C/N ratio was significantly lower in Sauvignon than the other tested litter ($\chi^2 = 16.579$, $df=5$, $p < 0.01$). Cellulose and hemicellulose content do not differ between the tested litter, while lignin was significantly higher in the Sauvignon litter ($\chi^2 = 13.608$, $df=5$, $p < 0.05$) (Table 1). Lignin/N ratio was higher in Pinot Noir, Sauvignon. Regarding tannin values, Chardonnay and Pinot Noir litter were the richest and Sauvignon the lowest ($\chi^2 = 41.259$, $df=5$, $p < 0.001$) (Table 1). Copper was present in very low quantity in *T. tomentosa* litter (control) and in high quantity to grape varieties tested (Chardonnay, Pinot Noir and Sauvignon). Finally, thickness comparison between litter showed that Pinot Noir litter was thinner than the others (Table 1), the thickest was the Chardonnay ($\chi^2 = 40.883$, $df=5$, $p < 0.001$).

3.2. Litter decomposition and feeding preferences of woodlice

3.2.1. Litter mass loss

Litter mass loss due to microbial activity (without woodlice) was significantly higher for all tested vine litter than *T. tomentosa* litter (Fig.1, $\chi^2 = 29.09$, Df=3, $p < 0.001$), Sauvignon exhibited the greatest mean mass loss of $38.65 \pm 1.71\%$ followed by Chardonnay ($30.98 \pm 0.82\%$), Pinot Noir ($26.38 \pm 2.54\%$) and *T. tomentosa* litter ($21.94 \pm 1.30\%$). In the presence of woodlice, a significant difference in mass loss was found between litter ($\chi^2 = 17.58$, Df=3, $p < 0.001$), with the highest values for Sauvignon litter ($54.79 \pm 1.82\%$), followed by a similar consumption of *T. tomentosa* ($48.95 \pm 1.29\%$) and Chardonnay ($46.44 \pm 1.82\%$). Pinot Noir ($35.82 \pm 1.82\%$) was the least palatable litter. Finally, litter mass loss in presence of woodlice was greater than that measured in the presence of microbial activity only ($\chi^2 = 28.74$, Df=1, $p < 0.001$).

3.2.2. Woodlice consumption of vine litter

T. tomentosa litter was the most consumed by woodlice ($F = 29.2$, Df=3, $p < 0.001$) with 0.084g consumed per day per gram of woodlice. The consumption of Pinot Noir ($0.031 \pm 0.003 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) by woodlice is almost three times lower than the control. Consumption of Chardonnay and Sauvignon was medium (see Supplementary Table S2).

3.2.3. Woodlice feces production and assimilation of vine litter

Daily feces production of woodlice fed with *T. tomentosa* litter ($0.070 \pm 0.004 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) was significantly higher than those fed with Chardonnay ($0.033 \pm 0.005 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$). For Sauvignon and Pinot Noir litter, the feces production was similar ($0.036 \pm 0.006 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$). Woodlice assimilation rate of *T. tomentosa* litter ($0.014 \pm 0.005 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) was similar to Chardonnay ($0.017 \pm 0.003 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) and Sauvignon ($0.022 \pm 0.006 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) litter, but significantly higher than Pinot Noir ($-0.004 \pm 0.008 \text{ g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) ($F = 18.99$, Df=3, $p < 0.001$). Assimilation efficiency was on average 16.74% for *T. tomentosa*, 34.45% for Chardonnay and 37.84% for Sauvignon and -3.9% for Pinot Noir (Supplementary Table S2).

3.3. Effects of vine litter diet woodlice physiological traits

3.3.1. Woodlice life-history traits

During the 49 days of experiment, a total of 17 woodlice died ($n= 4, 4, 7$ and 2 individuals in *T. tomentosa*, Chardonnay, Pinot Noir, Sauvignon litter respectively). Nevertheless, survival of woodlice was not impacted by the type of litter (Cox proportional-hazards model, $p=0.39$). Mass gain was 6.02 ± 2.25 g for the first of 25 days [Day 0-Day 25] and 19.82 ± 2.50 g during the whole period (seven weeks) ($F=111.84$, $Df=2$, $p<0.001$). We did not find any relationship between woodlice mass gain and litter type consumed ($F=2.15$, $Df=3$, $p=0.09$) or total litter consumed over the time ($F=1.39$, $Df=6$, $p\text{-value} \geq 0.05$). Regarding moults, a total of 39 were recorded for isopods fed with *T. tomentosa*, and 37, 30, and 26 for Isopods fed with Pinot noir, Chardonnay and Sauvignon respectively, but these differences were not significant ($\chi^2=9.57$, $Df=10$, $p=0.48$; Supplementary Table S2)

3.3.2. Relationship between litter and woodlice traits

Co-inertia showed on the first axis (64.9 % of variance) a clear separation of the litter types (Fig. 5). This axis opposed Pinot Noir litter, rich in lignin, tannin and copper to *T. tomentosa* litter rich in hemicellulose and uncontaminated by copper (Fig. 5). At the center, Sauvignon and Chardonnay litter showed more similar properties. These litter traits covariate significantly with woodlice traits ($RV=0.48$, $p=0.001$). Co-inertia showed a higher consumption, assimilation and growth for woodlice feeding on litter poor in tannin, lignin and copper. The second Axis (31.1 % of variance) separated litter (Pinot Noir and *T. tomentosa*) rich in cellulose and poor in nitrogen to litter with a high percentage of decomposability by microorganisms (Chardonnay and Sauvignon) (Fig. 5). The low nitrogen content in Pinot Noir and *T. tomentosa* was associated with a higher number of woodlice moults, while the higher microbial activity was associated with a higher survival rate of woodlice. On this axis, consumption covariates with the percentage of cellulose, hemicellulose and C/N ratio, while individual growth and assimilation seem to be more influenced by their thickness and decomposability (Fig. 5).

4. Discussion

Litter quality and microbial activity

The first objective of our study was to find out if differences in litter quality were sufficient to induce differences in litter decomposability by microorganisms, and if so, which traits were the most involved in vine litter mass loss. In absence of woodlice, our results showed that nitrogen content and C/N ratio are what predominantly drive variations in decomposability of the four litter tested. In contrast, the investment of plant in defense (tannin) or structural (fiber, lignin, thickness) traits were poor predictors of microbial activity. After highlighting inter-varietal differences vine litter traits, our study showed effectively a significantly higher mass loss in rich-N litter and a strong negative correlation between C/N ratio and litter decomposability by microorganisms (Axis 2, Figure 5). This results in higher mass loss for litter of Sauvignon, followed by Chardonnay and Pinot Noir. With only $1.02\% \pm 0.03$ of N, the control litter *T. tomentosa* was the less decomposed. These results are in accordance with the literature showing that rich-N litter are known to enhance microorganisms' growth, facilitated carbon utilization (Chapin III et al., 2012; Frouz et al., 2007), and accelerate litter mass loss (Frouz et al., 2007; Špaldoňová and Frouz, 2019). However, this result only partially validates our first hypothesis (H1a) because we failed to establish a link between decomposability and traits related to structure or defense (Cornelissen et al, 2004; Freschet et al., 2012). Differences in duration of experimentation, range of trait values, and/or environmental conditions (*in situ* vs *in vitro*...) may explain this result.

Woodlice trophic traits established by litter traits and habits

Woodlice consumption rate can be multiplied by two or even four times depending on the type of litter available (Ganault et al., 2022; Pokhylko, 2020). Litter consumption rates obtained in our experiment (from 31 to 84 $\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) are in line with previous findings (from 61 to 89 $\text{mg herb litter}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ and 77 $\text{mg forest litter}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ respectively in Coulis et al. (2015) and David et al. (2001). If the ranking of feeding preferences for grape varieties was similar for woodlice and microorganisms, a different pattern occurred for *T. tomentosa* which was the most consumed species by *A. vulgare*.

This feeding preference could be due to the home-field advantages (HFA) since *T. tomentosa* litter was their rearing food (Reis et al., 2018). However, according to several authors testing this hypothesis with woodlice (Quadros et al., 2014; Reis et al., 2018), HFA was not an important factor determining their feeding preferences. They suggest that some isopod species may prefer plant litter depending on the nutritional content and palatability of the respective litter types, regardless the origin of the plant litter. In our study, significant covariation between woodlice trophic traits and litter physico-chemical traits was found.

First, we showed that the C/N ratio covaried positively with *A. vulgare* consumption (H1b invalidated) and negatively with assimilation (axis 2, Figure 5). These results can be explained by a compensatory feeding behavior that is expressed by (1) a higher consumption rate of *T. tomentosa* to compensate for its low nitrogen content (2) a higher excretion rate and (3) consequently a lower assimilation rate.

Secondly, consumption and assimilation by *A. vulgare* were both negatively influenced by tannin content, lignin/N ratio and copper concentration, which are particularly high in Pinot Noir litter (Figure 5, H2 validate).

Condensed tannins contribute to leaf toughness (Hagerman and Butler, 1991) and participate to plants' defense against herbivores. After senescence, tannins still present in leaves are known to induce negative effects on the density of hindgut microbiota and hepatopancreatic bacteria of saprophagous arthropods (Zimmer, 1999), with cascading negative effects on their assimilation rate, as demonstrated in Roy and Joy (2009) with the millipede *Anoplodesmus saussurei* (Polydesmida, diplopoda).

Lignin is not digested by detritivore fauna without a prior action of microorganisms (Gillon and David, 2001; Neuhauser et al., 1978). In their meta-analysis, Knorr et al. (2005) distinguished three litter-quality categories (high, intermediate, low) mainly based on lignin concentrations (respectively <10;

10-20; > 20% lignin). Applied to our study, the litter of Sauvignon, Chardonnay and Pinot noir can be considered as poor-quality, while *T. tomentosa* would be classified as intermediate quality ($\approx 13\%$). The most contaminated litter (Pinot noir, with 981 mgCu.kg^{-1}) by copper was also the less consumed. Even if copper is an essential element needed for woodlice respiration, immune response and digestive process with phenol oxidase (Zimmer, 1999, 2002), it may induce detrimental effects on detritivore fauna (Weißenburg and Zimmer, 2003). In a 14 days experiment, Zidar et al. (2003), showed a significant decrease of forest litter consumption by woodlice beyond $1200 \text{ mg Cu.kg}^{-1}$. Negative effects on consumption were found by Farkas et al. (1996) from only $500 \text{ mg Cu.kg}^{-1}$ in a longer experiment (four weeks). Finally, Loureiro et al highlighted both a decrease of consumption and egestion of copper-contaminated forest litter (Loureiro et al., 2006).

For the Isopod *A. vulgare*, copper, lignin/N ratio and tannin, explains an important part of differences of trophic traits between the three grape varieties.

Litter quality and life-history traits

In the current study, mortality (5-17.5%) was similar to that seen in other laboratory experiment, with 10-20 % of woodlice mortality, on a shorter period (28 days) (Loureiro et al., 2006). During the 49 days of the experiment, woodlice growth was regular over time and similar to that observed in our breeding (Mondet, 2022).

Based on literature studies, our last hypothesis was that litter containing the most chemical deterrents will have negative effects on the life-history traits (survival and/or growth) of *A. vulgare*. If numerous authors found a positive effect of nitrogen on detritivore species growth and survival (Lardies et al., 2004; Souty-Grosset and Faberi, 2018), other traits such as tannins (Zimmer and Topp, 2000) and copper (Farkas et al., 1996) may have detrimental effects on life-history traits but contrary to what we expected [H3 invalidate], neither survival, moult number nor mass gain were significantly

influenced by litter quality. The observed mortality may be explained by natural mortality rate, especially during the critical moult period but also to potential stress due to repeated manipulations.

5. Conclusion and perspectives

Our results showed that litter traits are strongly variable between grape varieties. These traits impact the consumption rate and the assimilation of *A. vulgare*. These results bring new insight on litter quality in vineyard and its impact on decomposition process and feeding preferences for detritivore species. Thus, further studies should consider this litter quality which probably has an influence on a broader scale on macrofauna communities with a vineyard context. Furthermore, landscape, management context and other available diet sources will possibly affect the decomposition of litter. More experiments need to be done with more diversity (ie. grape variety, origin, mores detritivore species) during long term experiment and in parallel more natural conditions (ie *in situ* litterbag experiment), in the perspective of improving the fertility of the vineyard soils.

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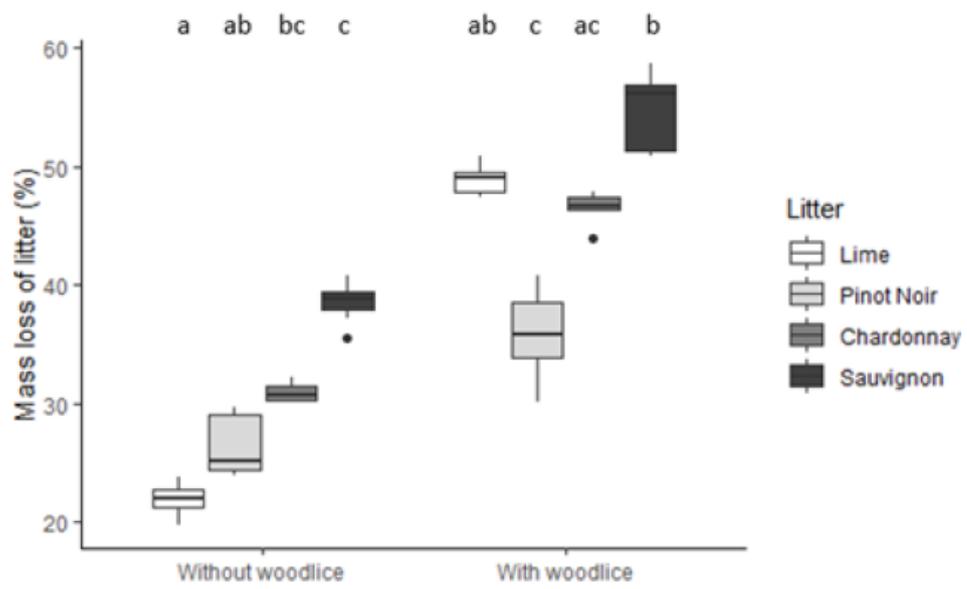


Figure 1

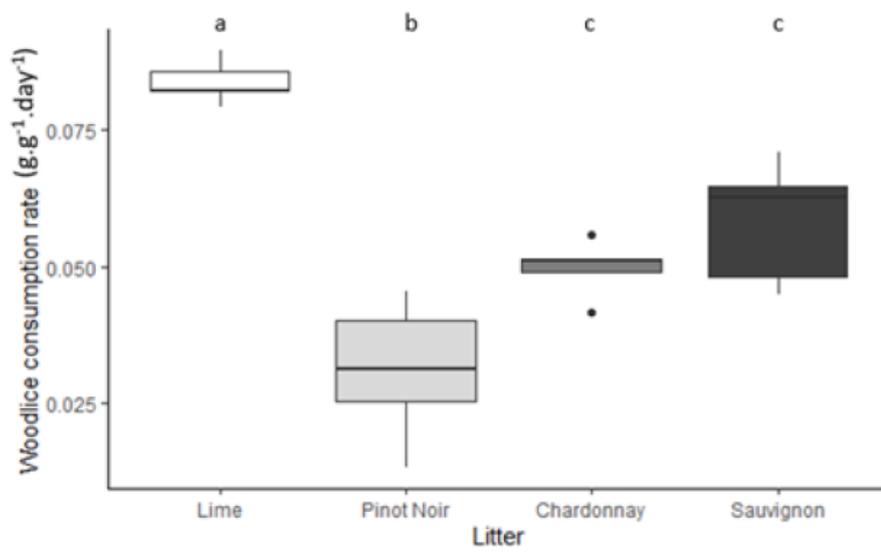


Figure 2

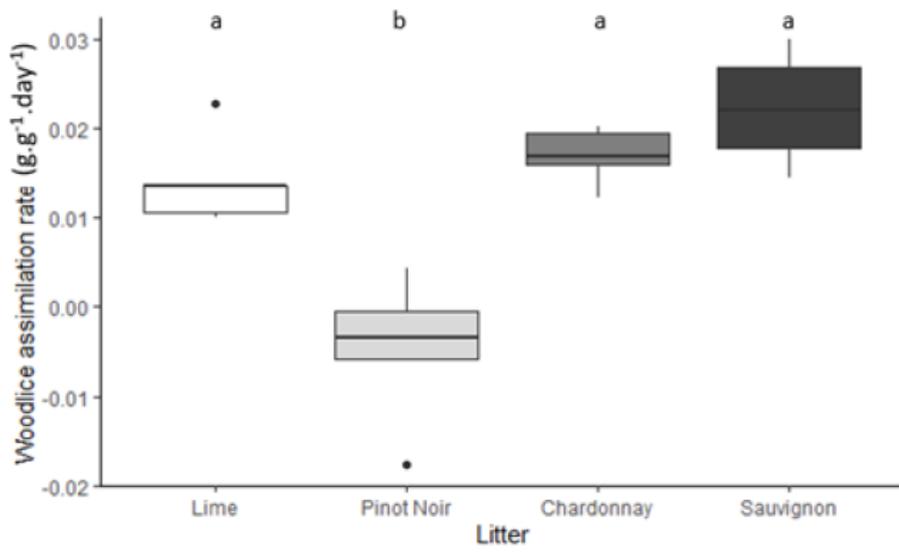


Figure 3

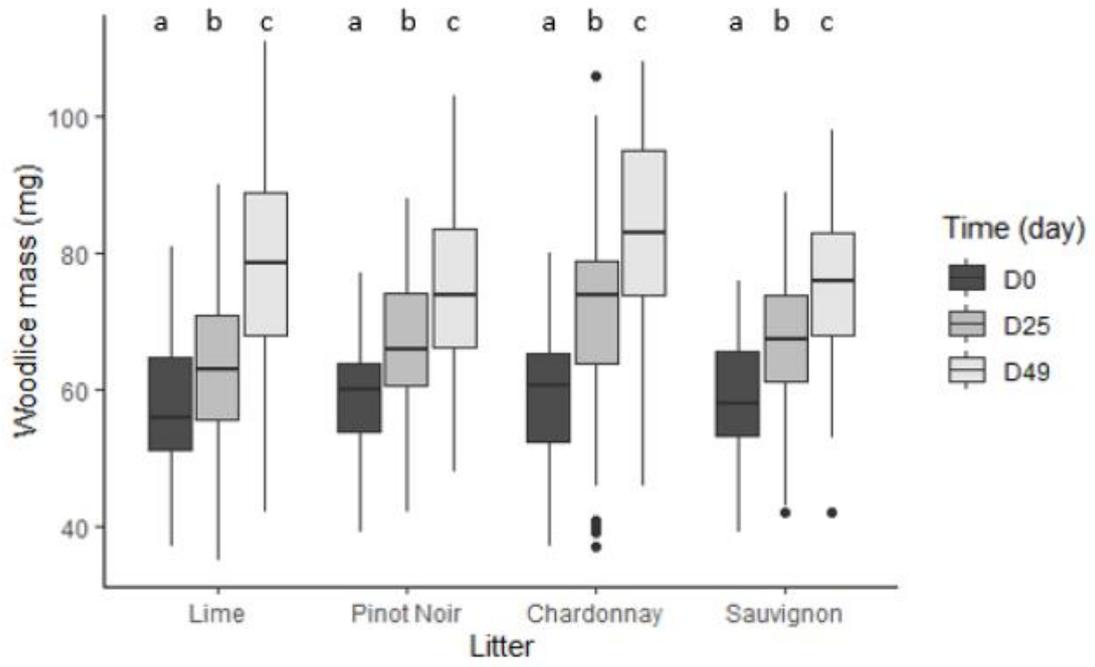


Figure 4

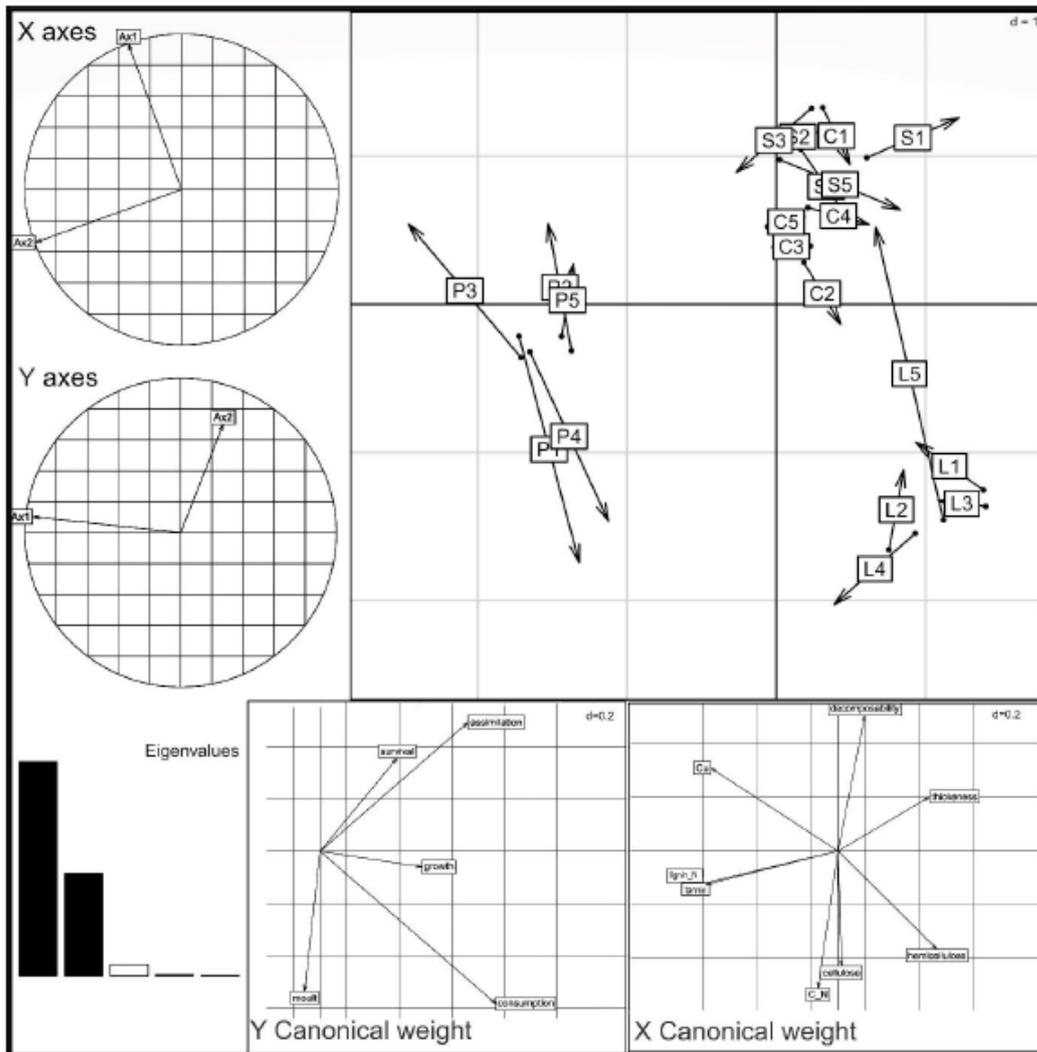


Figure 5