Forage grass litter chemical and physical traits explain feeding performances of 2 two soil macrodetritivores

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2 **two soil macrodetritivores**

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35 **Abstract**

36 Understanding the relationship between litter quality and macrodetritivore feeding

37 performances is of prime importance. Among soil invertebrates, macrodetritivores such

38 as millipedes (*Diplopoda*) and terrestrial isopods (*Crustacea, Isopoda*) could play a

39 significant role in the decomposition process. Furthermore, studies relating herb litter to

40 macrodetritivore performances (consumption, dejection, assimilation) are scarce and

41 rarely used litter traits (especially no physical trait). We thus design a laboratory

42 experiment to answer the following question: what are the pivotal chemical/physical

43 traits informing litter grass quality that shape such macrodetritivore performances? The

44 performances of two common macrodetritivores *Armadillidium vulgare* (Latreille,

45 1804) and *Glomeris marginata* (Villiers, 1789) on heterogeneous litter coming from

46 perennial forage grasses to have a wide spectrum of functional profiles (*Brachypodium*

47 *pinnatum* P. Beauv., *Bromus erectus* Huds., *Festuca rubra* L. and *Holcus lanatus* L.)

48 were assessed. We used litter traits to inform litter quality. We also used some

49 conservative plant traits. *A. vulgare* performances were correlated with nutrient aspects

50 (litter N and P contents) and plant mechanical aspects (leaf dry matter content). *G.*

51 *marginata* performances were correlated with plant fiber contents (cellulose and lignin

52 contents).

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54 **Keywords:** consumption, assimilation, soil macrodetritivore, forage grass litter,

55 functional trait

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59 **Highlights**

60 Millipedes and isopods contribution to soil decomposition is partially understood

61 We assessed some of their feeding performances on heterogeneous grass litter species

62 Litter species have been chosen to represent a wide spectrum of functional profiles

63 *A. vulgare* performances were correlated with nutrient and mechanical aspects

64 *G. marginata* performances were correlated with fiber contents

65

1 Introduction

Soil fauna consists in a huge diversity of life forms mainly represented by invertebrates (Decaëns et al., 2006). At the ecosystem level, they contribute to the delivering of ecosystem services (Barrios, 2007; Kibblewhite et al., 2008) such as climate regulation and the production of agricultural goods. They are highly involved in the soil behaviour by contributing to major soil functions such as organic matter decomposition.

Among soil invertebrates, millipedes (*Diplopoda*) and woodlice (*Crustacea, Isopoda*) play a significant role in the decomposition processes when they are abundant (David and Handa, 2010; Wolters, 2000). Their effects on decomposition can be direct and indirect through litter comminution or by interacting with soil microorganisms (David, 2014). Understanding the relationship between litter quality and macrodetritivore feeding performances is a key step for understanding the effect of these animals on decomposition (Coulis et al., 2013; Joly et al., 2015). However the mechanisms implied are far to be completely understood and predictable. For instance, David et al. (2014) pointed out that not a single litter trait can explain macrodetritivore preference. A combination of traits informing the litter nutritive value (*e.g.* N content, or C-to-N ratio) and the feeding deterrents are determinant. Feeding deterrents could be split into chemical and physical deterrents. Chemical deterrents are compounds that reduce the litter ingestion or digestion (*e.g.* mainly secondary compounds such as tannins, alkaloids, glycosides or structural compounds such as lignin). Physical deterrents limits litter mechanical breaking (*e.g.* litter toughness, litter thickness, silica spicules)(Levins, 1973; Zimmer et al., 2005). Theses mechanical aspects were generally indirectly informed by some chemical traits (*e.g.* cellulose, hemicellulose, lignin contents). However they were scarcely informed by some physical traits (*e.g.* toughness, specific

90   leaf area, water holding capacity) which were supposed to be more or less directly

91   connected to these mechanical aspects (Coulis et al., 2015; Joly et al., 2015; Zimmer et

92   al., 2005).

93   In addition, it has been theorize that "apparent" plants (*e.g.* tree or grasses) could often

94   have low nutrient status and either quantitative chemical deterrents (*e.g.* polyphenols) or

95   physical deterrents, whereas "unapparent plants" (*e.g.* small dicotyledonous species)

96   often have a high nutrient status and could rely on rapidly degraded chemical qualitative

97   toxins (*e.g.* alkaloids) (Hassall and Rushton, 1984). Furthermore, among "apparent

98   plants", grasses could rely on physical deterrents against herbivory such as trichomes

99   (Levins, 1973), silicon spicules which could likely persist in litter material (Hassall and

100 Rushton, 1984; Massey et al., 2006; Rushton and Hassall, 1983).

101 The main literature in temperate ecosystems concerns mainly tree or shrub litters but

102 scarcely herb litters. To our knowledge only few studies deal with herb litters (David et

103 al., 2001; Paris, 1963; Rushton and Hassall, 1983; Zimmer et al., 2002). Only few of

104 them used chemical traits. In the work of David et al. (2001) the consumption and

105 assimilation of 5 herb species by *A. vulgare* (2 *Asteraceae*, 2 *Fabaceae*, 1 *Poaceae*) at

106 two atmospheric CO_2 levels were measured for several litter submitted to different

107 decomposition pre-treatments (12, 30, 45 days). In this study, the consumption was

108 overall positively correlated with litter nitrogen content and negatively correlated with

109 the litter C-to-N ratio. However, the N content and C-to-N ratio had no decisive

110 influence on litter consumption in slightly decomposed litter. The authors made the

111 assumption that feeding-deterrent factors could be removed as decomposition

112 progressed, making the litter more palatable. The assimilation was only negatively

113 correlated with the C-to-N ratio at the lowest atmospheric CO_2 level. Furthermore in

114   another study, in salt marshes, performances of three isopods (*Littorophiloscia*

115   *(Halophiloscia) vittata* (Say, 1818), *Porcellionides (Metaponorthus) virgatus* (Budde-

116   Lund, 1885), *Venezillo (Armidillo) parvus* ((Budde-Lund, 1885)) on three litters (2

117   forest litter and 1 grass litter, *Juncus roemerianus* Scheele) are predicted by chemical

118   litter traits such as phenolic concentrations (ferulic acid and tannins) and C-to-N ratios

119   (Zimmer et al., 2002). Futhermore, no study including herb litters used physical traits.

120   This present study would like to contribute to the general comprehension of the

121   interaction between macrodetritivores and herb litters by answering the following

122   question: what are the pivotal grass litter chemical/physical traits that shape

123   macrodetritivore feeding performances? Consequently, we designed a laboratory

124   experiment in which we assess the performances of two common macrodetritivores

125   *Armadillidium vulgare* (Latreille, 1804) and *Glomeris marginata* (Villiers, 1789) on

126   heterogeneous litter coming from perennial forage grasses, as a first step. We used a

127   trait-based approach using both litter and plant chemical and physical traits.

128   **2 Materials and Methods**

129   *2.1 Litter selection, collection and characterization*

130   We selected litter of perennial forage grasses based on Cruz et al.' plant classification

131   (Cruz et al., 2010). This classification was made to dissociate plant species according to

132   their use values in agriculture. It was made from 6 traits which were obtained from the

133   leaves: the leaf dry matter content (LDMC), the specific leaf area (SLA), the length of

134   life duration (LLD) and surface tensile strength (STR); and from the whole plants: the

135   flowering date (FD) and the maximum height (MH). It discriminated several functional

136   groups which state different growth strategies, biomass accumulation strategies,

137   phenology, frequency of use and feeding values for cattle. For our study, we made the

138   hypothesis that litter from species belonging to these different functional groups will be

139   differently consumed by soil macrodetritivores. We selected four species among

140   different functional groups to have a wide spectrum of functional profiles:

141   *Brachypodium pinnatum* P. Beauv., *Bromus erectus* Huds., *Festuca rubra* L. and

142   *Holcus lanatus* L.

143   Litters were collected from an experimental set-up consisting in several small plots

144   (60*40cm) in which a single plant species has been sown in September 2010. A

145   fertilization was performed every year in March or April (75 kgN/ha, 50 kgP/ha and 50

146   kgK/ha). A mowing was performed every year and plots were irrigated. Litter of *H.*

147   *lanatus*, *F. rubra*, *B. erectus* and *B. pinnatum* were collected in October 2015 and

148   February 2016. Only entirely senescent fragments were conserved. Litters were then air-

149   dried during a few days and then conserved in paper envelopes before the beginning of

150   the experiments.

151   Some litter of each species was crushed using a plant shredder. The crushed material

152   was then oven-dried at 40°C during 72h. Five replicates of twenty milligrams was

153   weighed at the nearest μg to quantify the C and N contents (elemental analyzer, Flash

154   2000 ThermoFisher). Five replicated of 7-10 mg were weighed at the nearest μg to

155   analyze the P content (spectrometric method with ammonium molybdate after a

156   persulfate oxidation). The litter water-holding capacity (WHC) was measured in

157   accordance with following the protocol. Five replicates of 0.6 gram of litter of each

158   species was oven-dried at 40°C during 72h before being weighed at the nearest 0.01 g.

159   Litter was then immerged during 24h in large hermetic plastic boxes (180*120*75 mm)

160   previously filled with 300 mL of deionized water, then gently collected and put on a 1-

161   mm plastic mesh. The mesh was set up as lids of other empty large plastic boxes using

162   elastic bands. This device allows the litter to be drained. After 6 hours of drainage, litter

163   was weighed at the nearest 0.1 mg to assess the moist weight (W_m). Litter was then

164   oven-dried at 60°C during 48h, then put in desiccator until being weighed at the nearest

165   0.1 mg to assess the dried weight (W_d). The water holding capacity was calculated as

166   follows: $WHC = (W_m - W_d)/ W_d$.

167   Means of litter and leaf characteristics used as traits are presented in the Table 1 (Cottier

168   et al., 2001; Cruz et al., 2010). We made the hypothesis that plant traits used in the

169   present study are conservatives from the plant to the litter. Litter C, N, P contents aimed

170   to mainly inform on the main essential macrodetritivore requirements. Leaf dry matter

171   content (LDMC) and litter water holding capacity (WHC) aimed to mainly inform

172   indirectly on mechanical aspects (*e.g.* toughness). Leaf cellulose content (LCC), leaf

173   hemicellulose content (LHC) and leaf lignin content (LLC) informed mainly on

174   digestibility and indirectly on mechanical aspects.

175   *2.2 Macrodetritivores selection and collection*

176   Two common macrodetritivores species were used: the woodlice *Armadillidium vulgare*

177   (Latreille, 1804) and the millipede *Glomeris marginata* (Villiers, 1789).

178   Macrodetritivores were collected from a permanent mown meadow in Benque, France

179   (Haute-Garonne, 43°16'24.3"N 0°55'23.3"E). The meadow is included into the Long-

180   Term Ecological Research site ''Vallées et Coteaux de Gascogne''

181   (LTER_EU_FR_003). They were collected in February and March 2016. Individuals

182   were conserved in plastic boxes filled with soil, plants and litter from the meadow

183   before the beginning of the experiments.

184   *2.3 Experimental design*

185   Hermetic plastic boxes were used as microcosms (120*90*50 mm). Each monospecific

186   combination of litter and macrodetritivore species was made, resulting in 12 treatments

187   plus 4 control treatments (litter without macrodetritivore). A total of 64 microcosms

188   were initiated corresponding to 16 treatments and four replicates. Each box was filled

189   with 0.5 gram of dried litter and one individual. Before the experiment, litters were

190   oven-dried at 40°C during 72h, let in a desiccator before being weighed at the nearest

191   0.1 mg. At the beginning of the experiment, litter was moistened (80% WHC) with

192   deionized water using a propette. Litter and water were then gently homogenized using

193   plastic pliers. Before the experiment, macrodetritivores were subject to a diet of 5h-7h

194   before being weighed. They were then individually weighed at the nearest 0.1 mg. At

195   the beginning of the experiment, individual biomass for a given macrodetritivore

196   species was equilibrated among treatments.

197   Microcosms were then stored at 17 ± 2 °C with a photoperiod (10 light/14h dark) for 7

198   days. At day 2 and 5, cosms were moistened with deionized water if necessary, using a

199   propette, to reach their initial weight. At day 2, 5 and 7, faecal pellets were gently

200   collected and were immediately oven-dried at 40°C for at least 72h, put in a dessicator

201   and weighed at the nearest 0.001 g. At the end of the experiment, remaining litter and

202   animals were weighed following previous described protocols.

203   *2.4 Detritivores performances calculation and statistical analysis*

204   The average individual biomass was expressed as the mean between the initial and final

205   macrodetritivore biomass. Individual consumption rate (mg.day-1.g-1) was assessed

206   using the David's formula based on initial and final litter dry mass of a microcosm and

207   its corresponding controls (David, 1998). Dejection production rate (mg.day-1.g-1) was

208   the summed dry weights of the collected faecal pellets (mg) per average individual

209   biomass (g) and per day. Finally, individual assimilation rate (mg.day-1.g-1) was

210   expressed as the difference between the consumption and the dejection production rates.

211   Analyses of variance (ANOVAs) were performed to test for the effect of litter species,

212   macrodetritivore species and their interaction on detritivore performance (consumption,

213   dejection production and assimilation rates). Normality and homoscedasticity

214   assumptions were tested using Shapiro-Wilk and Bartlett tests respectively, and data

215   transformations were done if necessary. To bury into mechanisms, 48 simple linear

216   regressions were performed, relating each quantitative leaf/litter trait (8 variables) to

217   each detritivore performance variable (3 variables), one for each of the 2

218   macrodetritivores. For these regressions, p-values were deemed significant without

219   (alpha=0.05) and with a Bonferroni correction (alpha=0.05/8=0.00625) given that there

220   are initially 8 different traits and respective tests for a relationship for each of the 6

221   combinations of detritivore performance variable and macrodetritivore. Using the

222   Bonferroni correction decreases the risk to make a type I error (`false positive'; finding

223   a non-existing relationship) but increases the risk to make a type II error (`false

224   negative'; missing an existing relationship).

225

226   **3 Results & Discussion**

227   We observed no mortality during the experiment. *A. vulgare* performance mean values

228   in our experiment were the most of the time higher than observed values on *Poaceae* in

229   existing literature (Table 2). For instance, the consumption rate of *Festuca ovina (L.)*

230   and *Koelaria cristata (L.)* ranged from 0 to 14.07 and from 1.38 to 14.06 mg.day^{-1}.g^{-1}

231   respectively, the egestion rate from 0 to 13.19 and from 1.99 to 12.73 mg.day^{-1}.g^{-1}

232   respectively and finally the assimilation rate from 0 to 0.88 and from -0.16 to 1.33

233   mg.day^{-1}.g^{-1} respectively (Rushton and Hassall, 1983). In another study, the

234   consumption and assimilation rates for *Lolium rigidum* Gaudin (1811) ranged from

235   almost 0 to approximately 20 and from almost 0 to 6 mg.day^{-1}.g^{-1} respectively (David et

236   al., 2001). The low N content and high C-to-N ratio of *L. rigidum* litter could explain

237   this last result. In our study, litter is coming from a well fertilized experimental set-up

238   which contributed to have high litter N contents. This could be invoked to explain

239   theses higher performances values. To our knowledge no data on *G. marginata*

240   performances on herb litter exist.

241   Mean assimilation rates were negative for two treatments *G. marginata* with *B. erectus*

242   and *G. marginata* with *B. pinnatum* (Table 2). This situation have been already met in

243   the literature in the case of studying *A. vulgare* performances on herb litters (David et

244   al., 2001; Rushton and Hassall, 1983). We decided, as these authors did, to conserve

245   these negative values rather than discarding them as it would avoid to evict arbitrarily a

246   part of variability. To our point of view, the main reason of obtaining negative

247   assimilations could be the failure to correctly remove the microorganism part in the

248   calculation of macrodetritivore consumption in these short-term laboratory experiments.

249   In our experiment, consumption was calculated through the David's formula which

250   estimated macrodetritivore consumption from a litter mass loss value in presence and in

251   the absence of macrodetritivore, considering that microorganism effect is conservative.

252   It could thus sometimes underestimate the macrodetritivore consumptions and thus led

253   to negative assimilation values especially in the case of low effective consumption.

254

255   The litter species significantly impacted the consumption, the dejection production and

256   the assimilation rates and contributes to 28.4%, 22.1% and 23.1% to the explained

257   variance respectively (Table 3). The macrodetritivore species only significantly

258   influenced the dejection production rate by contributing to 15.9% to the explained

259   variance. Finally, interaction between litter and macrodetritivore species significantly

260   impacted both the consumption rate and the dejection production rate by contributing to

261   38.2% and 33.7% to the explained variance respectively. These results confirmed that

262   both litter and macrodetritivore species are required to fully understand the

263   macrodetritivore performances.

264

265   For *A. vulgare*, consumption and dejection production rates were similarly positively

266   correlated to litter N and P contents, and negatively to LDMC (Table 4). More than 34%

267   of variance for both feeding performances was explained by each of these traits. *A.*

268   *vulgare* performances seemed to be ruled by chemical litter traits which inform us on

269   litter nutritive value (N and P contents). Furthermore, they also seemed to be ruled by

270   the tissue structure (LDMC). Indeed the LDMC is well-known correlated to the foliar

271   tissue density (Cruz et al., 2010). Finally, LDMC is also well-known correlated with

272   digestibility (Khaled et al., 2006; Pontes et al., 2007). However in our experiment, *A.*

273   *vulgare* performances were not correlated to any plant fiber contents (cellulose,

274   hemicellulose or lignin). As a conclusion for *A. vulgare*, it could have been

275   demonstrated that it was rather the nutritive aspects and some mechanical aspects linked

276   to the LDMC which ruled the feeding performances rather than the chemical deterrent

277   aspects of litter compounds.

278   For *G. marginata*, LLC was negatively correlated to consumption, dejection production

279   and assimilation rates (more than 30% of explained variance). For the consumption and

280   assimilation rates, p-values were significant after the Bonferroni correction. LCC was

281   negatively correlated to consumption and dejection production rates with more than

282   39% of explained variance. Joly *et al.* (2015) found that *G. marginata* consumption was

283   negatively correlated to hemicellulose contents of 26 tree litters. Fiber contents could

284   informed on litter digestibility and indirectly on litter mechanics which could be the

285   main drivers of *G. marginata* performances. However, neither LDMC nor WHC were

286   correlated with *G. marginata* performances suggesting that the litter digestibility could

287   be rather invoked than litter mechanics. In a similar way, Joly et al. (2015) found no

288   correlation between *G. marginata* performances and respectively tree litter surface

289   specific area (SLA) and WHC.

290   These results pointed that the use of grass chemical and physical traits could be relevant

291   to explain macrodetritivore performances. Silica content data or information on

292   trichomes may have contributed to a better general comprehension of the effects of herb

293   litter mechanical aspects on macrodetritivores performances. However, for the studied

294   species, we found only silica data for three of our four species (*B. erectus, F. rubra, H.*

295   *lanatus*) and values are highly variable among studies (Aguirre et al., 2014; Cornelissen

296   and Thompson, 1997; Massey et al., 2006). In addition, if silica content was an effective

297   defence against folivorous insects (Massey et al., 2006), no evidence exist that silica

298   content in litters influence macrodetritivore performances. In addition, no precise

299   trichome data exists for herb species, either on their potential physical deterrent effect or

300   on the potential chemical deterrent effect of the secondary compounds they contain.

301   Much more studies and much more data on these traits could shed light on litter

302   mechanical aspects. Finally, it has been yet demonstrated that litter preferences depend

303   on litter microbes (David, 2014; Ihnen and Zimmer, 2008). Thus, litter phyllosphere

304   traits could be also of great interest.

305　To conclude, the present experiment is a first step to assess trait-based general rules for

306　the interactions between forage grass litter and macrodetritivores. In our study, we only

307　focused on the effect of litter species with a wide spectrum of functional profiles to

308　explain macrodetritivore performances. An interesting perspective to rise general rules

309　about litter-macrodetritivores interactions could be the use of macrodetritivore

310　biomechanical mouthpart traits to be linked with litter mechanical traits such as

311　toughness. Indeed, a biomechanical framework for litter-macrodetritivore interaction

312　can be drawn as it was done in other interaction networks. For instance, a study succeed

313　to explain plant-herbivores interactions (grasshoppers) from relating biomechanical

314　traits of herbivores with plant traits (Ibanez et al., 2013). Such biomechanical traits are

315　poorly studies for soil invertebrates. Another perspective could be the assessment of the

316　matching between chemical element contents (*e.g.* C, N, P) between macrodetritivore

317　and litter. Furthermore, in our study the becoming of fragmented litter or the becoming

318　of faecal pellets were not assessed although there are of prime importance in the

319　decomposition process (Coulis et al., 2013; David, 2014; Joly et al., 2015). Microbial

320　evolution in these processes have to be especially highlighted. Furthermore and finally,

321　from the trait-based results of monospecific treatments, plurispecific combination have

322　to be tested.

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