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Feeding rates of the woodlouse *Armadillidium vulgare* on herb litters produced at two levels of atmospheric CO₂

Received: 1 February 2000 / Accepted: 30 October 2000 / Published online: 19 January 2001
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Abstract The consumption and assimilation rates of the woodlouse *Armadillidium vulgare* were measured on leaf litters from five herb species grown and naturally senesced at 350 and 700 $\mu\text{l l}^{-1}$ CO₂. Each type of litter was tested separately after 12, 30 and 45 days of decomposition at 18°C. The effects of elevated CO₂ differed depending on the plant species. In *Medicago minima* (Fabaceae), the CO₂ treatment had no significant effect on consumption and assimilation. In *Tyrimnus leucographus* (Asteraceae), the CO₂ treatment had no significant effect on consumption, but the elevated CO₂ litter was assimilated at a lower rate than the ambient CO₂ litter after 30 days of decomposition. In the three other species, *Galactites tomentosa* (Asteraceae), *Trifolium angustifolium* (Fabaceae) and *Lolium rigidum* (Poaceae), the elevated CO₂ litter was consumed and/or assimilated at a higher rate than the ambient CO₂ litter. Examination of the nitrogen contents in these three species of litter did not support the hypothesis of compensatory feeding, i.e. an increase in woodlouse consumption to compensate for low nitrogen content of the food. Rather, the results suggest that in herbs that were unpalatable at the start of the experiment (*Galactites*, *Trifolium* and *Lolium*), more of the litter produced at 700 $\mu\text{l l}^{-1}$ CO₂ was consumed than of that produced at 350 $\mu\text{l l}^{-1}$ because inhibitory factors were eliminated faster during decomposition.

Keywords Elevated CO₂ · Herb litter · Saprophages · Palatability · Nitrogen content

Introduction

Changes in plant litter quality (e.g. reduced N concentration, increased C:N ratio) have been reported after atmo-

spheric CO₂ enrichment, but these effects are less pronounced and much more variable among species than for green plant material (reviews by Cotrufo et al. 1998b; Coûteaux et al. 1999). This makes it difficult to predict the effects of elevated CO₂ on litter decomposition at the ecosystem level. Furthermore, very little is known of the influence of changes in litter quality on the soil organisms that control decomposition. This is particularly the case for the saprophagous macrofauna (macroarthropods, gastropods, earthworms), which reach a biomass of several tens of grams live weight per square meter in a wide variety of ecosystems (Dangerfield 1990; Decaëns et al. 1998; David 1999). These organisms are involved in the fragmentation of dead plant material, its incorporation into the soil and mixing with mineral particles and therefore play a major role in the decomposition processes (Anderson 1988; Schaefer 1991a, 1991b). To understand the effects of increased atmospheric CO₂ on litter decomposition, possible changes in the feeding activities of these animals must be taken into account, at least in ecosystems where they are abundant.

The decomposition of dead leaves grown in elevated CO₂ is obviously changed by epigeic macroarthropods, which are mainly responsible for the fragmentation of litter. Coûteaux et al. (1991) showed that, in the absence of macroarthropods, the mineralization of chestnut leaves produced at 700 $\mu\text{l l}^{-1}$ CO₂ was slower than that of leaves produced at 350 $\mu\text{l l}^{-1}$, whereas the opposite occurred in the presence of the woodlouse *Oniscus asellus*. However, the mechanisms involved remain obscure and have been little studied. Recently Hättenschwiler et al. (1999) showed that the woodlouse *Porcellio scaber* consumed more beech leaf material derived from the higher CO₂ level. As these leaves were poorer in nitrogen than leaves grown under ambient CO₂ conditions, these authors suggested that saprophagous arthropods might enhance their consumption when feeding N-depleted litter, in analogy with compensatory feeding reported for herbivorous insects (Bezemer and Jones 1998; Whittaker 1999). On the other hand, Cotrufo et al. (1998a) observed that the woodlouse *O. asellus* consumed less ash-leaf material de-

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rived from the higher CO₂ level, and they assumed that the lower leaf nitrogen content could have a negative effect on consumption by animals. In these two studies, the tests were conducted on litters at one stage of decomposition, comprising only newly fallen leaves.

In the present study, we measured the consumption by the woodlouse *Armadillidium vulgare* (Isopoda: Armadillidiidae) of litter from five herb species produced at two concentrations of CO₂, to attempt to answer the following questions:

1. Does elevated CO₂ increase or decrease the consumption and assimilation of litter by *A. vulgare*?
2. Do the effects of elevated CO₂ on consumption and assimilation change during decomposition? Herb litters, which decompose faster than tree litters, are more suitable for addressing this question.
3. Can the effects observed be interpreted in terms of compensation, particularly with respect to the amounts of nitrogen ingested and assimilated?

A. vulgare was chosen to measure the consumption of herb litters because this saprophagous species is very common in open vegetation habitats, and because the relationships between its consumption, assimilation and growth have been studied in detail. Paris (1963) and Rushton and Hassall (1983a, 1983b) showed that this woodlouse consumed and assimilated much less litter derived from grasses than from forbs, which are in fact the only herbaceous species that enable it to grow. Rushton and Hassall (1983b) and Hassall and Rushton (1984) also studied changes in palatability and digestibility during the decomposition of various plant species, and discussed the physico-chemical properties that could influence the palatability of litter to *A. vulgare*.

Materials and methods

Materials

Specimens of *A. vulgare* were collected from the grounds of the Centre d'Ecologie Fonctionnelle et Evolutive (CEFE) in Montpellier, southern France, mostly from a Mediterranean old field dominated by grasses, legumes and composites. Individuals more than 30 mg in weight were chosen as these could be considered to be adults (Dangerfield and Hassall 1992). Before being used in feeding tests, the animals were kept in plastic boxes with moist soil and fed on a mixture of herb litters, decomposed tree leaves and sliced carrots. This diet provides nearly optimal conditions for *A. vulgare* (Lawlor 1976).

Leaf litter of *Medicago minima*, *Trifolium angustifolium* (both Fabaceae), *Tyrimus leucographus*, *Galactites tomentosa* (both Asteraceae) and *Lolium rigidum* (Poaceae) was obtained after growing plants in four climate-controlled greenhouses. Two greenhouses were maintained at a CO₂ concentration close to ambient atmospheric levels (350 µl l⁻¹) and two at a concentration twice as high (700 µl l⁻¹). The CO₂ concentrations were increased to 375 and 750 µl l⁻¹ during the three winter months to simulate natural seasonal variations. Air temperature, humidity and watering mimicked open-air conditions with similar variations in the four greenhouses, and the light was about 60% of incident radiation. One-week-old seedlings were planted in October at a density of 700 m⁻² on intact, unfertilized soil monoliths (clay loam, 0.5 m², 27 cm deep), with similar communities of grasses, legumes and

composites in the four greenhouses (details in Nijs et al., in press). Standing dead material was harvested in July, when seeds were mature and the plants senescent (all the species are annuals). Leaves were separated from the rest of the plant and, in order to have enough material, leaves of a given species but from both greenhouses at a given CO₂ level were pooled. Prior to pooling, it was confirmed that litter quality was not significantly affected by individual greenhouses within each CO₂ level. Subsamples of dead leaves from each species were analysed for carbon and nitrogen contents, and partially hierarchical ANOVAs were conducted on the N concentration and C:N ratio of all the litters. The CO₂ treatment effect was significant ($P < 0.01$ for the N concentration and $P < 0.05$ for the C:N ratio) – with a significant CO₂ treatment × species interaction in the case of the N concentration – whereas the effect of the greenhouses nested within the CO₂ treatment was negligible ($P = 0.81$ for the N concentration and $P = 0.83$ for the C:N ratio). The differences in litter quality could be ascribed to the CO₂ treatment and the litters obtained at the two concentrations will be subsequently referred to as the 350- and 700-litters.

Experimental protocol

Dried leaves of each species produced at each CO₂ level were weighed, then soaked overnight (15 h) in water that had been percolated through soil, in order to inoculate the litters with soil microorganisms. The material was drained and left to decompose in plastic pots (5 cm in diameter by 9 cm high) without any substrate. The pots were covered with clingfilm and kept at 18°C in the dark, under ambient CO₂ conditions. At roughly 2-week intervals (12, 30 and 45 days) the litter from three pots per species and per CO₂ level was dried for 3 days at 45°C to stop decomposition. The litter weight loss, as a percentage of the initial dry weight, was determined for each pot. The carbon and nitrogen contents of the material decomposed for 12, 30 and 45 days were determined using a Carlo-Erba CHN analyser, with two measurements for each plant species and each CO₂ level.

Three series of feeding tests were conducted using material decomposed for 12, 30 and 45 days. Samples of dried leaves (≥200 mg) were weighed, soaked overnight and drained, before being placed on moist plaster of Paris, in closed plastic pots 6 cm in diameter and 7 cm high. Two adult woodlice (mean weight 126 ± 4 mg; range 82–222 mg), after fasting for 3 days, were introduced into each pot and allowed to feed for 8 days at 18°C in the dark. The first series of feeding tests had three replicates (three pots per plant species and per CO₂ level) and the following two series four replicates. The animal faeces were collected every day, dried at 45°C to stop their decomposition and stored. At the end of the tests, the remaining litter was dried for 3 days at 45°C and weighed. The woodlice were kept for a further 3 days in the pots without litter to collect their last faecal pellets, then all the stock of faeces produced was weighed dry.

Alongside the feeding tests, controls (i.e. pots of litter without woodlice) were set up, under the same conditions and with the same number of replicates as in the presence of woodlice.

Measurements of consumption, egestion and assimilation

The consumption in each pot was determined gravimetrically from the difference between initial dry weight (M_i) and final dry weight (M_f) of litter, corrected for losses due to leaching plus decomposition. The mean proportion of weight loss of each litter type was estimated from the controls without woodlice, in the form:

$$D = (M_i - M_f) / M_i \quad (1)$$

where M_i is the initial dry weight of control litter before soaking and M_f is the final dry weight of control litter after soaking plus 8 days of decomposition. The amount of dry litter consumed dur-

ing a 8-day test (mg) was estimated from the following formula (David 1998):

$$C_T = (M_i - M_i D - M_f) / \sqrt{1 - D} \quad (2)$$

The consumption in each pot was then expressed per unit of animal biomass (by dividing by the mean live weight of woodlice at the start and end of the test) and per unit of time (by dividing by the number of days) to obtain the consumption rate C ($\text{mg g}^{-1} \text{day}^{-1}$). The egestion rate F was also expressed in $\text{mg g}^{-1} \text{day}^{-1}$. The difference $A=C-F$ is the assimilation rate ($\text{mg g}^{-1} \text{day}^{-1}$).

Statistical analyses

The effect of the CO_2 treatment on the percentage weight loss, N concentration, C:N ratio, consumption rate and assimilation rate of litter was tested by analysis of variance (ANOVA). For each plant species, a two-way ANOVA (CO_2 treatment and decomposition time) was first conducted on the data from the entire experiment. When the number of measurements was not the same in all the series of tests, ANOVAs with unequal but proportional sample sizes were used (Sokal and Rohlf 1995). When there was a significant interaction between treatment effect and decomposition time, ANOVAs were re-conducted to test the CO_2 treatment effect on data from two successive series of tests or from a single series of tests. All the data in percentages were arcsine transformed before ANOVA. Homogeneity of variances was tested before each analysis by the F_{\max} -test (Sokal and Rohlf 1995). This condition was not met for the assimilation rate of *Galactites*, so the data were cube-root-transformed to make the variances uniform before ANOVA.

The relationships between consumption rate, assimilation rate and N concentration or C:N ratio were analysed by simple linear regression.

Results

Effects of the CO_2 treatment on decomposition and litter quality

The percentage weight loss of each type of litter due to initial leaching and decomposition for 12, 30 and

45 days is shown in Table 1. Two-way ANOVAs for each herb species showed that the 350-litter lost significantly more weight than the 700-litter in *Medicago* ($F_{1,12}=5.4$, $P<0.05$), *Trifolium* ($F_{1,12}=15.4$, $P<0.01$) and *Lolium* ($F_{1,8}=9.5$, $P<0.05$). No significant difference was detected in *Tyrimnus* and *Galactites*. In the latter species, the weight loss was in fact significantly higher in the 700-litter after 12 days of decomposition ($F_{1,4}=14.0$, $P<0.05$), the difference then becoming non-significant.

The N concentration and C:N ratio of each type of litter after 12, 30 and 45 days of decomposition are also shown in Table 1. Two-way ANOVAs for each herb species showed that the CO_2 treatment effect varied from one species to another. In *Lolium* and *Tyrimnus* litters, elevated CO_2 resulted in a significant depletion of nitrogen; the N concentration was significantly higher in the 350-litters than in the 700-litters ($F_{1,6}=225$, $P<0.001$ for *Lolium*; $F_{1,6}=137$, $P<0.001$ for *Tyrimnus*), and the C:N ratio was significantly lower in the 350-litters than in the 700-litters ($F_{1,6}=293$, $P<0.001$ for *Lolium*; $F_{1,6}=17.9$, $P<0.01$ for *Tyrimnus*). In the two legumes, *Medicago* and *Trifolium*, the CO_2 treatment had little effect on the N concentration and C:N ratio, the differences between 350- and 700-litters being non-significant. Finally, in *Galactites* litter, elevated CO_2 resulted in a significant enrichment in nitrogen; the N concentration was significantly higher in the 700-litter than in the 350-litter ($F_{1,6}=578$, $P<0.001$) and the C:N ratio was significantly lower in the 700-litter than in the 350-litter ($F_{1,6}=1019$, $P<0.001$).

Effects of the CO_2 treatment on litter consumption and assimilation

The consumption and assimilation rates of the different types of litter by *A. vulgare* are shown in Fig. 1. The

Table 1 Weight loss, as a percentage of the initial dry weight, nitrogen concentration and carbon:nitrogen ratio of five species of litter grown in ambient or elevated CO_2 (350 vs. 700 $\mu\text{l l}^{-1}$). For

each species and each CO_2 level, the results (means \pm SE) are given after 12, 30 and 45 days of decomposition (*m.d.* missing data)

| | | Weight loss (%) | | Nitrogen (‰) | | C:N ratio | |
|-------------------|---------|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|
| | | 350 $\mu\text{l l}^{-1}$ | 700 $\mu\text{l l}^{-1}$ | 350 $\mu\text{l l}^{-1}$ | 700 $\mu\text{l l}^{-1}$ | 350 $\mu\text{l l}^{-1}$ | 700 $\mu\text{l l}^{-1}$ |
| <i>Medicago</i> | 12 days | 25 \pm 1 | 25 \pm 2 | 15.2 \pm 0.2 | 14.8 \pm 0.2 | 26.4 \pm 0.2 | 27.1 \pm 0.1 |
| | 30 days | 37 \pm 1 | 33 \pm 0 | 17.3 \pm 0.1 | 17.0 \pm 0.1 | 23.5 \pm 0.1 | 23.1 \pm 0.1 |
| | 45 days | 39 \pm 2 | 37 \pm 1 | 19.2 \pm 0.2 | 19.8 \pm 0.1 | 20.1 \pm 0.1 | 19.3 \pm 0.1 |
| <i>Tyrimnus</i> | 12 days | 19 \pm 1 | 18 \pm 1 | 6.0 \pm 0.1 | 5.6 \pm 0.1 | 59.4 \pm 1.7 | 62.4 \pm 0.2 |
| | 30 days | 34 \pm 1 | 33 \pm 1 | 6.8 \pm 0.0 | 6.7 \pm 0.1 | 51.5 \pm 0.0 | 50.7 \pm 0.7 |
| | 45 days | 38 \pm 1 | <i>m.d.</i> | 8.6 \pm 0.1 | 6.4 \pm 0.2 | 39.2 \pm 0.1 | 45.9 \pm 1.0 |
| <i>Galactites</i> | 12 days | 11 \pm 0 | 18 \pm 2 | 5.0 \pm 0.0 | 5.5 \pm 0.0 | 76.1 \pm 0.0 | 69.5 \pm 0.4 |
| | 30 days | 20 \pm 3 | 18 \pm 1 | 5.0 \pm 0.0 | 5.5 \pm 0.0 | 77.4 \pm 0.2 | 67.1 \pm 0.1 |
| | 45 days | 23 \pm 3 | 19 \pm 5 | 5.6 \pm 0.1 | 6.2 \pm 0.1 | 67.8 \pm 0.6 | 55.3 \pm 0.5 |
| <i>Trifolium</i> | 12 days | 17 \pm 2 | 14 \pm 1 | 10.4 \pm 0.1 | 9.8 \pm 0.1 | 40.2 \pm 0.4 | 41.8 \pm 0.1 |
| | 30 days | 40 \pm 2 | 32 \pm 1 | 12.8 \pm 0.1 | 12.5 \pm 0.1 | 32.9 \pm 0.1 | 32.3 \pm 0.4 |
| | 45 days | 44 \pm 2 | 38 \pm 1 | 14.0 \pm 0.2 | 14.0 \pm 0.2 | 28.9 \pm 0.4 | 28.2 \pm 0.4 |
| <i>Lolium</i> | 12 days | 12 \pm 1 | 10 \pm 1 | 5.5 \pm 0.1 | 4.4 \pm 0.1 | 72.9 \pm 0.6 | 88.7 \pm 1.0 |
| | 30 days | <i>m.d.</i> | 17 \pm 0 | 5.4 \pm 0.1 | 4.8 \pm 0.1 | 74.6 \pm 0.8 | 84.0 \pm 0.6 |
| | 45 days | 21 \pm 0 | 17 \pm 1 | 5.5 \pm 0.1 | 4.6 \pm 0.1 | 71.7 \pm 1.2 | 81.5 \pm 0.6 |

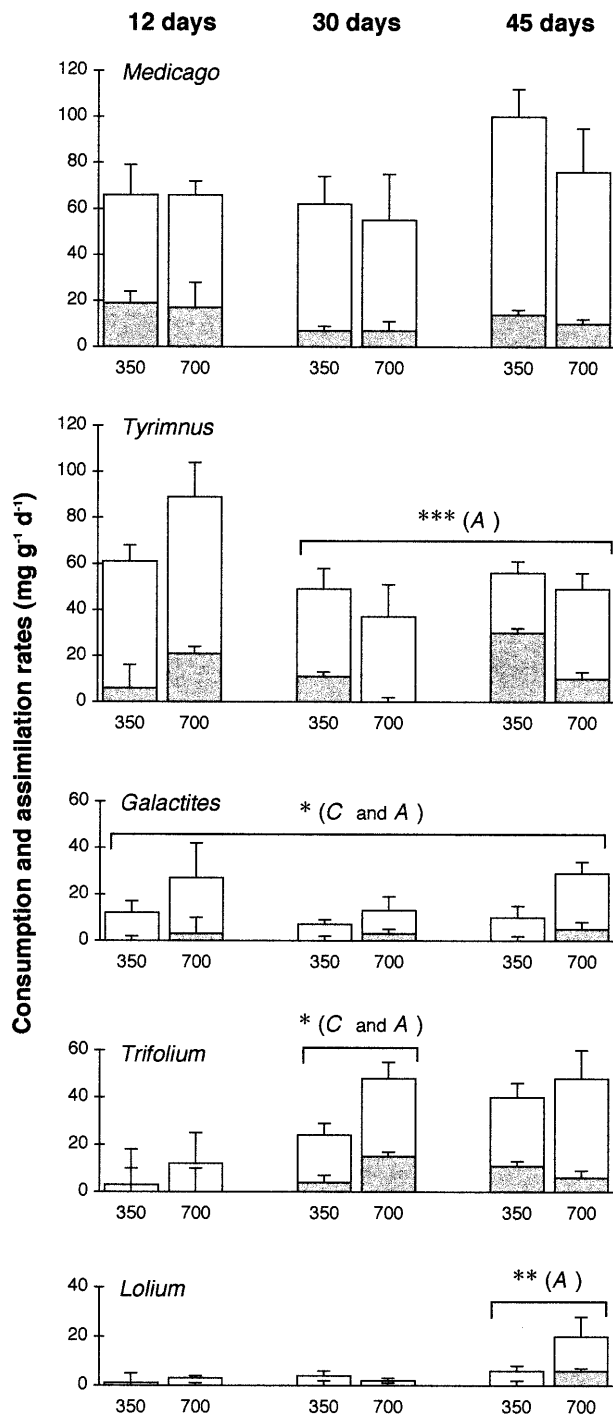


Fig. 1 Consumption rate (total column) and assimilation rate (darker part of column) of litter from five plant species by adult *Armadillidium vulgare* (means \pm SE). The feeding tests were conducted after 12, 30 and 45 days of decomposition, as indicated at the top of the figure. On each occasion, litters derived from ambient (350 μ l l⁻¹) and elevated (700 μ l l⁻¹) CO₂ conditions were compared. Asterisks indicate significant effects of the CO₂ treatment on the consumption rate (C) and assimilation rate (A) (* P <0.05, ** P <0.01, *** P <0.001). The slightly negative values for assimilation rates were equated to zero in this figure

treatment effect differed depending on the plant species, but two groups could be distinguished, the first including *Medicago* and *Tyrimnus*, and the second *Galactites*, *Trifolium* and *Lolium*.

Medicago and *Tyrimnus* were the only two species consumed in large amounts from the start of the experiment (between 61 and 89 mg g⁻¹ day⁻¹ in the first series of tests). The CO₂ treatment had no significant effect on the consumption rate of these species. In both cases, there was a tendency for the 350-litter to be more heavily consumed than the 700-litter after 30 and 45 days of decomposition, but the differences were not significant. The CO₂ treatment also had no significant effect on the assimilation rate of *Medicago*. In contrast, the ANOVA showed (1) that the CO₂ treatment had a significant effect on the assimilation rate of *Tyrimnus*, which was higher with the 350-litter than with the 700-litter ($F_{1,16}=6.3$, P <0.05); and (2) that this effect changed over time, the interaction between CO₂ treatment and decomposition time being significant ($F_{2,16}=10.8$, P <0.01). Examination of the data showed that the assimilation rate of 700-litter only decreased in the last two series of tests. From the 30th day of decomposition, the effect of elevated CO₂ on the assimilation rate of *Tyrimnus* was very highly significant ($F_{1,12}=65.9$, P <0.001), *A. vulgare* assimilating on average 20 \pm 4 mg g⁻¹ day⁻¹ of 350-litter compared to 4 \pm 2 mg g⁻¹ day⁻¹ of 700-litter.

Much less of the three other plant species, *Galactites*, *Trifolium* and *Lolium*, was consumed than of the previous ones at the start of the experiment (Fig. 1). Furthermore, the effects of the CO₂ treatment were the opposite of the effects and trends observed in *Medicago* and *Tyrimnus*. In *Galactites*, the consumption rate was significantly higher with the 700-litter throughout the experiment (23 \pm 5 mg g⁻¹ day⁻¹ compared to 9 \pm 2 mg g⁻¹ day⁻¹ for the 350-litter; $F_{1,16}=6.5$, P <0.05). The assimilation rate of *Galactites* was also significantly higher with the 700-litter throughout the experiment (4 \pm 2 mg g⁻¹ day⁻¹ compared to a slightly negative mean value for the 350-litter; $F_{1,16}=7.6$, P <0.05).

With *Trifolium*, very small amounts were consumed in the first series of tests, but these increased markedly after 30 days of decomposition. However, the consumption rate increased faster with the elevated CO₂ litter. In the second series of tests, it was 48 \pm 7 mg g⁻¹ day⁻¹ for the 700-litter compared to 24 \pm 5 mg g⁻¹ day⁻¹ for the 350-litter, the difference being significant ($F_{1,6}=8.2$, P <0.05). The assimilation rate of *Trifolium* was also significantly higher with the 700-litter in the second series of tests (15 \pm 2 mg g⁻¹ day⁻¹ compared to 4 \pm 3 mg g⁻¹ day⁻¹ for the 350-litter; $F_{1,6}=9.1$, P <0.05). After 45 days of decomposition, consumption and assimilation remained high, but the difference between 350- and 700-litter was reduced and no longer significant.

Finally with *Lolium*, the amounts consumed and assimilated were almost zero in the first two series of tests and only started to increase slightly after 45 days of decomposition. In the last series of tests, *A. vulgare*

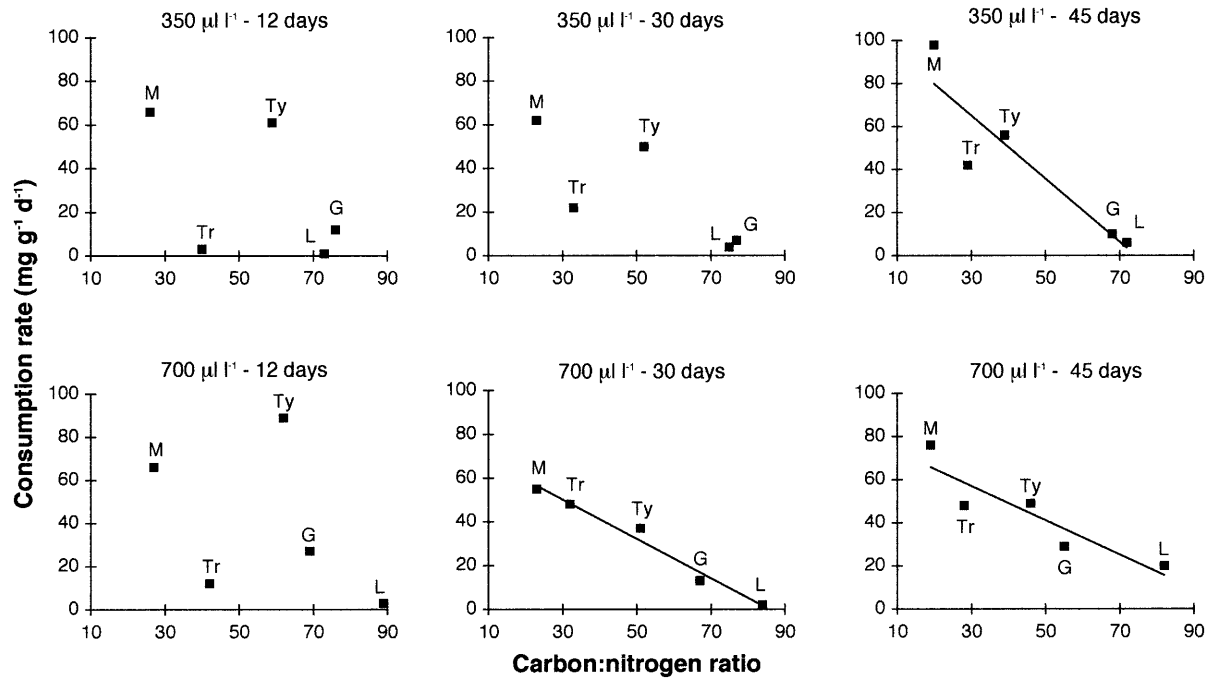


Fig. 2 Relationships between the consumption rate of *A. vulgare* and the C:N ratio of five species of litter (*M Medicago*, *Tr Trifolium*, *Ty Tyrinnus*, *G Galactites*, *L Lolium*). The relationships were calculated after 12, 30 and 45 days of decomposition, for litters derived from ambient (350 $\mu\text{l l}^{-1}$) and elevated (700 $\mu\text{l l}^{-1}$) CO₂ conditions. Only the significant linear relations are illustrated by a regression line. The significance levels are given in the text

showed a tendency to consume the 700-litter at a greater rate than the 350-litter, but the difference was not significant. On the other hand, the assimilation rate was significantly higher with the 700-litter ($6 \pm 1 \text{ mg g}^{-1} \text{ day}^{-1}$ compared to a slightly negative mean value for the 350-litter; $F_{1,6}=22.7$, $P<0.01$).

Relationships between consumption, assimilation and litter quality

Over the entire experiment, there were significant relationships between the consumption rate of *A. vulgare* and the N concentration of the litter types, whether produced at 350 $\mu\text{l l}^{-1}$ CO₂ ($F_{1,13}=13.8$, $P<0.01$, $r^2=0.52$) or at 700 $\mu\text{l l}^{-1}$ CO₂ ($F_{1,13}=6.9$, $P<0.05$, $r^2=0.35$). This shows that, overall, high nitrogen contents had a positive effect on consumption. The inverse relationships between consumption rate and C:N ratio were even more significant, both for the 350-litters ($F_{1,13}=16.1$, $P<0.01$, $r^2=0.55$) and the 700-litters ($F_{1,13}=10.3$, $P<0.01$, $r^2=0.44$). The relationships between assimilation rate and parameters of litter quality were not so strong, as the regression coefficient was significantly different from zero in only one case (assimilation rate vs. C:N ratio of the 350-litters; $F_{1,13}=8.1$, $P<0.05$, $r^2=0.38$).

The influence of decomposition on the relationships between consumption rate and litter quality parameters

was determined by testing the linear relations between these variables separately for each series of tests and each CO₂ level (Fig. 2). With the 350-litters, there was no significant relationship between consumption rate and C:N ratio either after 12 or 30 days of decomposition, but the regression coefficient became significantly negative after 45 days of decomposition ($F_{1,3}=12.3$, $P<0.05$, $r^2=0.80$). With the 700-litters, there was no significant relationship between consumption rate and C:N ratio after 12 days of decomposition, but the regression coefficients became significantly negative after 30 and 45 days of decomposition ($F_{1,3}=132.0$, $P<0.01$, $r^2=0.98$ and $F_{1,3}=14.6$, $P<0.05$, $r^2=0.83$, respectively). The relationships between consumption rate and N concentration showed exactly the same pattern, although they were slightly less significant: with the 350-litters, the regression coefficient became significantly positive only after 45 days of decomposition ($F_{1,3}=11.2$, $P<0.05$, $r^2=0.79$), whereas with the 700-litters, the regression coefficient became significantly positive from the 30th day of decomposition ($F_{1,3}=10.6$, $P<0.05$, $r^2=0.78$). Therefore, the initial consumption of litter was not directly related to the leaf nitrogen content, but significant relationships appeared in the course of decomposition, and earlier for the 700-litters than for the 350-litters.

Discussion

Variations in the consumption and assimilation of litters produced in ambient CO₂ conditions

This study confirmed that, with plants grown at 350 $\mu\text{l l}^{-1}$ CO₂, the consumption and assimilation of litter by *A. vulgare* varied greatly from one plant species to another (Rushton and Hassall 1983b). Two types of herb spe-

cies could be distinguished. Forbs such as *Medicago* (Fabaceae) and *Tyrimnus* (Asteraceae) were easily consumed and assimilated from the start of the experiment, while other species were very little consumed and totally indigestible. The latter included not only the grass *Lolium* but also the forbs *Trifolium* (Fabaceae) and *Galactites* (Asteraceae), which shows that the initial palatability of litter is species-specific within a family of plants.

The causes of these differences in litter quality for the saprophagous macrofauna remain poorly known and it is difficult to assess the relative importance of mechanical factors, taste and chemical factors (Schaefer 1991a). High polyphenol contents in fresh litter are often regarded as a major cause of unpalatability, this having been confirmed experimentally in *O. asellus* (Hassall and Rushton 1984). However, Neuhauser and Hartenstein (1978) found no relationship between the rate of consumption of different litters by macroarthropods and the total phenolic content, which suggests that several factors are involved. As has been stated by a number of authors (Cameron and Lapoint 1978; Soma and Saito 1983; Hassall and Rushton 1984), it is obvious that there are both physical factors (e.g. toughness) and chemical factors (e.g. deterrent compounds) which prevent isopods from feeding on certain litters. These factors are removed at various rates during decomposition and it is only then that differences in nutrient status can influence consumption. Our results support such a hypothesis. They showed that N concentration and C:N ratio had no decisive influence on the consumption rate of slightly decomposed material. For example, *Trifolium* was much less consumed than *Tyrimnus* in the first series of tests, despite its much lower C:N ratio. However, with more decomposed material, the rates of litter consumption became inversely correlated with the C:N ratios.

Effects of the CO₂ treatment on litter consumption and assimilation by *A. vulgare*

The effects of elevated CO₂ on the feeding rate of *A. vulgare* varied greatly from one plant species to another. In *Medicago*, there was no significant effect throughout the experiment. In *Tyrimnus*, the 700-litter became much less digestible than the 350-litter after 30 days of decomposition. In the three herb species that were unpalatable and indigestible at the start of the experiment (*Galactites*, *Trifolium* and *Lolium*), the 700-litter was consumed and/or assimilated at greater rates than the 350-litter – although at different times in the decomposition process.

Hättenschwiler et al. (1999) interpreted the higher consumption by woodlice of beech leaves derived from the higher CO₂ level in terms of compensatory feeding, an increased consumption compensating for low contents of essential nutrients such as nitrogen. In the present study, the compensatory feeding hypothesis can be rejected in the two cases where litters produced under elevated CO₂ were significantly more consumed than normal litters (*Galactites* and *Trifolium* after 30 days of de-

composition). In *Galactites*, the 700-litter was significantly richer in nitrogen than the 350-litter. In *Trifolium* after 30 days of decomposition, there was no significant difference in N concentration and C:N ratio between the two types of litter. Therefore, the increased consumption of 700-litters in these two species could hardly be ascribed to lower nitrogen contents. *Lolium* was the only species in which the 700-litter was slightly more consumed and was also significantly poorer in nitrogen than the 350-litter. It is however difficult to interpret this in terms of compensation, since the assimilation rate of this grass (6 mg g⁻¹ day⁻¹, equivalent to about 28 µg g⁻¹ day⁻¹ of nitrogen) seems to be insufficient to ensure the normal growth of *A. vulgare* (Rushton and Hassall 1983a, 1983b).

Another interpretation would be more compatible with the results obtained. The fact that the three herb species in which the CO₂ treatment led to a higher consumption and/or assimilation of 700-litter were unpalatable at the start of the experiment, suggests that they became palatable faster than the 350-litters merely because inhibitory factors were removed sooner during decomposition. This could result in higher consumption rates on litters produced under elevated CO₂, irrespective of the nitrogen content of the food. This interpretation is supported by the fact that significant relationships between consumption rate and N concentration or C:N ratio appeared earlier with the 700-litters (after 30 days of decomposition) than with the 350-litters (after 45 days of decomposition). As discussed above, the phagostimulant effect of nutrient-rich foods presumably occurred after all deterrent factors had been removed, which must have taken place sooner with the 700-litters. This interpretation could only be demonstrated if the factors that inhibit consumption by woodlice could be precisely identified and quantified in each litter type, which has not yet been done.

However, the view that the CO₂ effect on litter consumption relies on the rate at which unpalatable materials become acceptable for saprophagous macroarthropods – with litters produced under elevated CO₂ improving faster – would explain the contradictory results obtained by Cotrufo et al. (1998a) and Hättenschwiler et al. (1999). Cotrufo et al. (1998a) tested freshly fallen ash leaves, which have been known for a long time to be readily consumed by macroarthropods, especially woodlice (Dunger 1958; Hassall and Rushton 1984; Pearce 1989). In these conditions, *O. asellus* preferred the 350-litter, which had a higher nitrogen content – in keeping with what is observed when there is no physico-chemical deterrent to consumption. In contrast, Hättenschwiler et al. (1999) tested freshly fallen beech leaves, which are among the least palatable tree leaves to the saprophagous macrofauna (Dunger 1958; Hassall and Rushton 1984; Pearce 1989). In this case, *P. scaber* consumed more of the litter produced under elevated CO₂ – despite its lower nitrogen content – as was the case for herb litters with a low initial palatability. Thus, for a total of seven plant species tested, it appears that growth in elevated CO₂ conditions favours consumption by woodlice only when the litter initially exhibits strongly deterrent properties.

At the ecosystem level, the question is whether the higher feeding rate of macroarthropods on certain litter types could counterbalance the overall negative effect on litter weight loss that was observed under elevated CO₂. With species such as *Galactites*, *Trifolium* and *Lolium*, woodlice not only assimilated greater amounts of dead leaves produced at 700 µl l⁻¹ CO₂, but also egested greater amounts of faeces – which may decompose faster than intact leaves if they are deposited in favourable microsites by the fauna (Hassall et al. 1987). This should accelerate the mineralization of these litter components under elevated CO₂. On the other hand, with species such as *Medicago* and *Tyrimnus*, reduced microbial decomposition could not be compensated for by the feeding activities of macroarthropods. Clearly the overall outcome depends on (1) the contribution of different plant species to the litter input and (2) the selection of food by macroarthropods from the plant material available.

Possible changes in the diet of *A. vulgare*

The results of the present study confirmed that elevated CO₂ could have opposite effects on the consumption and assimilation of different litter species at the same stage of decomposition (Cotrufo et al. 1998a; Hättenschwiler et al. 1999). They also showed that the effects of elevated CO₂ changed in the course of decomposition, and that these changes differed from one plant species to another. For example, litter with a high initial palatability, such as *Tyrimnus* litter, lost its digestibility after a few weeks of decomposition when it was produced at 700 µl l⁻¹ CO₂. In contrast, litter types with a low initial palatability became acceptable and digestible more rapidly, as decomposition proceeded, when they were produced at 700 µl l⁻¹ CO₂. This could alter the diet of a generalist saprophage such as *A. vulgare* in an environment where several herb species are available.

Under natural conditions herb litters are produced in summer but, owing to the severe drought occurring in this season in the Mediterranean region, leaching and decomposition only really begin after the first rains in late summer-early autumn. By the end of the dry season *A. vulgare* can feed on slightly decomposed forbs, such as *Medicago* and *Tyrimnus*, while the leaves of *Galactites*, *Trifolium* and *Lolium* can only be consumed much later, after a period of prolonged decomposition. Our results suggest that this succession could be altered under elevated CO₂, *A. vulgare* being forced to give up some litter types of good initial quality and switch to other litters. This possibility would however have to be confirmed by testing the effects of the CO₂ treatment using food mixtures.

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