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ELEVATED CO_2 AFFECTS FIELD DECOMPOSITION RATE AND PALATABILITY OF TREE LEAF LITTER: IMPORTANCE OF CHANGES IN SUBSTRATE QUALITY

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Summary—Field decomposition rates of ash (*Fraxinus excelsior* L.) and sycamore (*Acer pseudoplatanus* L.) leaf litters were measured for litters grown at ambient and elevated concentration of atmospheric CO_2 inside solar domes. Litter raised at 600 $\mu l\ l^{-1}$ CO_2 retained significantly more mass at the end of the first year of field decomposition than material raised at 350 $\mu l\ l^{-1}$. This reduction in decomposition could be related to changes in tissue quality resulting from growing the plants at higher CO_2 concentrations, with C-to-N ratios and lignin contents being significantly increased. The elevated CO_2 treatment also affected the rate of consumption of ash leaf litter by *Oniscus asellus* L. (Isopoda: Oniscoidea), with significantly less (−16%) material being consumed for litter derived from the high CO_2 regime. Our results indicate that changes in litter quality, which we may expect under elevated CO_2, may affect litter palatability for soil fauna.

INTRODUCTION

There is considerable debate about the interactions between elevated concentrations of atmospheric CO_2 and the development of terrestrial C stores (IPCC, 1995) and, despite the large amount of information on the effects of elevated CO_2 concentrations on plant productivity and biomass (Wullschleger *et al*., 1995), we lack studies dealing with the responses of soil C stores to elevated CO_2 (Curtis *et al*., 1994). Increasing amounts of C are anticipated as a result of greater litter inputs under elevated CO_2 conditions, which might have altered litter quality, and lower decomposition rates (Cotrufo and Ineson, 1996; Gorissen, 1996).

The concept of "litter quality" is difficult to define since factors regulating decomposability of litter change during the course of decomposition. However, it refers to the relative decomposability of litters, depending, among other things, on nutrient concentrations and on the relation between labile and recalcitrant compounds. In the present context we consider "litter quality" largely in terms of litter chemical composition and recognize N and lignin concentrations of litters as key factors in defining litter quality (Melillo *et al*., 1982).

The overall effect of elevated CO_2 on litter decomposition is still a matter of debate (O'Neill and Norby, 1996), and many interactions have been observed. In fact, there is evidence of an indirect effect of elevated CO_2 on decomposition of leaf litter via changes in litter quality, with decay rates being reduced when CO_2 fumigation treatments decrease litter N concentrations (Cotrufo *et al*., 1994; Kratz *et al*., 1995; Cotrufo and Ineson, 1996). Elevated CO_2 appears not to affect litter decomposition when litter quality remains unchanged (Kemp *et al*., 1994; O'Neill and Norby, 1996). However, there are also studies in which elevated CO_2 have been shown to decrease plant litter quality (i.e. increased C-to-N ratio) but without reductions in litter decay rates (Torbert *et al*., 1995; Henning *et al*., 1996). Other studies, on reygrass, have shown that elevated CO_2 did not change the C-to-N ratio of the root tissue, yet roots generated under elevated CO_2 showed lower decomposition rates than control roots (Gorissen, 1996; Van Ginkel *et al*., 1996). All these studies examined only few of the variables which define "litter quality", and considered the implications that this has for litter decomposition rates (see Cotrufo *et al*., 1997).

The effects of elevated CO_2 on the chemical composition of naturally senesced litter, and subsequent effects on decay rates, have mostly been studied in experiments where small plants have been raised under controlled conditions in growth cabinets or greenhouses (O'Neill and Norby, 1996). However, field studies on natural vegetation are producing evidence that elevated CO_2 have the potential to significantly affect the quality of naturally senesced leaf litter (Drake, 1997).

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Soil fauna play a fundamental role in decomposition processes (Swift *et al.*, 1979) with macrofauna having a major effect during the early stages via fragmentation and gut processing of the litter material. Isopods are considered as primary decomposers; they accelerate the initial stages of decomposition increasing the acceptability to microorganisms and the release of nutrients in their faecal material.

There are few studies on the rate of consumption of litter derived from enriched CO_2 environments by soil animals. Coûteaux *et al.* (1991) studied the effect of faunal communities of different complexities on the decomposition of litter raised under elevated CO_2, in laboratory microcosms, but this study produced somewhat inconclusive results. Chestnut leaf litter raised at elevated CO_2 showed both enhanced and reduced decay rates, when compared to control litter, depending on the complexity of the faunal community to which litters were exposed. Other studies were performed under either laboratory conditions in the absence of soil animals (Cotrufo *et al.*, 1994; Gorissen *et al.*, 1995), or under field conditions, where the specific effects of the fauna could not be observed (Kemp *et al.*, 1994; Cotrufo and Ineson, 1996).

Our objectives were: (1) to evaluate the effect that altered tissue quality, resulting from exposure to elevated CO_2 regimes, had on litter decomposition rates in the field; (2) to assess changes in palatability of litter derived from high CO_2 environment with a feeding trial using the woodlouse *Oniscus asellus* L.

MATERIALS AND METHODS

Two-year-old rooted cuttings of ash (*Fraxinus excelsior* L.) and 2-year-old plants of sycamore (*Acer pseudoplatanus* L.) were grown for one growing season (May–November) in 1 dm^3 pots under two atmospheric concentrations of CO_2: ambient (350 $\mu l\, l^{-1}$) and enriched (ambient + 250 $\mu l\, l^{-1}$) inside solar domes at Lancaster University field station, Lancaster.

Solar domes consisted of large closed-top chamber fumigation systems (20 m^3), as described by Lucas *et al.* (1987), modified for CO_2 exposure (Townend, 1993). CO_2 was supplied from a 5.5 t capacity tank (BOC, U.K.) and was injected, as a gas, into the inlet fans of the enriched treatment at a constant rate, to elevate the air concentration to 250 $\mu l\, l^{-1}$ above ambient. A ventilation system forced the air into the chambers at 2.5 air changes min^{-1}, providing environmental conditions of temperature and relative humidity close to those outside the solar domes (Townend, 1993). Plants were watered daily for the duration of the experiment, with two solar domes being used per treatment.

Senescent leaves were collected as they fell, air-dried at room temperature for several days, and stored separately until used for decomposition experiments, chemical analysis and palatability tests. A full description of chemical analysis is given in Cotrufo *et al.* (1994).

Litter decomposition was studied in the field using litter bags, *ca.* 12 cm × 18 cm, made of a PVC coated fiberglass net with a mesh size of 2 mm. Leaf litter (1 g) was enclosed in each bag, which was identified by a Dymotape label; a total of 20 bags per growth chamber were prepared. In January 1992, the litter bags were exposed in Meathop Wood, Cumbria (Nat. Grid Ref. SD 435795), a mixed-deciduous woodland located on the northern edge of Morecambe Bay, in an oceanic climate. A full description of the site is given in Cotrufo and Ineson (1996). The decomposition study lasted 1 yr, and four collections were made at different intervals during the year of field exposure. At each sampling, five replicate bags per growth chamber were returned to the laboratory, where litter was carefully removed from the bags and oven-dried at 80°C for 48 h, for the determination of weight remaining.

A palatability experiment was performed to assess the relative acceptability to the woodlouse *Oniscus asellus*, a common arthropod saprovore, of ash leaf litter derived from the elevated CO_2 regime. Similar experiments were not performed with sycamore due to insufficient amount of litter. Specimens of *O. asellus* were collected from Meathop Wood and used, a few hours later, for the feeding trial.

The air dried litter was rehydrated by soaking the litter in deionized water. Leaves were then cut into fragments of 1 cm^2, which were weighed before use. One leaf fragment from each growth chamber was placed in a 6 cm diameter Petri dish with the relative position of the four litter fragments within each Petri dish being systematically varied, in order to eliminate bias due to location. At the time of establishment of the feeding trial, 10 litter fragments for each litter type were analyzed for litter water content, by drying fragments in oven at 80°C for 48 h; no statistically significant differences in water content were observed between ambient and elevated CO_2 litters. Litter was maintained moist during the entire experiment by regular spraying of the contents of each Petri dish with deionized water.

Fifteen replicate Petri dishes, each containing one animal, were kept in the dark at constant temperature (15°C) for 3 d; initial controls (10) without animals were also established and kept under identical environmental conditions to the treatments. At the end of the experiment, animals were removed from the Petri dishes which were cleaned free of faecal pellets. The litter fragments, left in the original position within the Petri dishes in order to facilitate

differentiation among them, were then dried in oven at 80°C for 48 h to determine final dry weights.

Data were processed using the SAS system, version 6.0 (SAS, 1989). For the field decomposition experiment, significant differences between CO_2 treatments for weight remaining were analyzed using Student's t test for each species and sampling (n = 10, 2 growth chambers × 5 litter bags). Mean yearly decomposition rate constants were calculated using the Olson (1963) model, $k = \ln(X_o/X_t)/t_t - t_o$, for each litter type.

Because of the similarity of this experiment and the experiment with birch (*Betula pendula,* Roth; Cotrufo and Ineson, 1996) the data for all three litter types were combined and a linear regression was applied to decomposition rate constants against mean initial N concentrations across all litter types (i.e. ash and sycamore litters from this study and the birch litter derived from the non fertilized treatment, i.e. −N data, from Cotrufo and Ineson, 1996), n = 6.

For the feeding trial, Student's t was applied to test the significant differences between CO_2 treatments for weight remaining of litter fragments incubated in the presence or absence of animals (n = 30 and 20, 2 growth chambers × 15 and 10 replicates, respectively).

RESULTS

Litter derived from the elevated CO_2 atmosphere showed reduced decomposition rates (Fig. 1), with differences being significant in the first stages of decomposition for ash litter. In contrast, decomposition rates for sycamore leaf litter diverged only in the later stages, when litters had lost 40% of their initial weight (Fig. 1).

Figure 2 shows the results derived from this study (ash and sycamore) combined with results from Cotrufo and Ineson (1996) (birch, -N data), and identifies the consistent reductions in decomposition rate found for litters grown under elevated CO_2. The extent of the effect differed between species, being proportionally greater for birch litter, with three times more material remaining from the elevated CO_2 treatment than from the ambient.

The role of tissue quality in this response is demonstrated in Fig. 3, which shows the initial N concentrations of litters from the different CO_2 treatments, together with corresponding yearly decomposition rate constants (Olson, 1963). Litters derived from elevated CO_2 had lower N concentrations and higher lignin-to-N ratios, with associated reductions in decomposition rates (Table 1).

Figure 4 shows the dry weights of litter fragments after they had been incubated for 3 days in the presence or absence (control) of the woodlouse. *O. asellus* clearly preferred litter raised under ambient CO_2 concentration, with the final dry mass of the ambient litter significantly ($P < 0.05$) reduced (−16%) when compared to litter fragments raised at elevated CO_2. In contrast, litter derived from the high CO_2 regime had a final weight similar to those of litters incubated in the absence of animals (Fig. 4).

DISCUSSION

Litter decomposition is mainly influenced by chemical composition and environmental conditions. In our experiment the exposure of ash and sycamore seedlings to elevated CO_2 affected the chemical composition of leaf litter, and decreased the rate of mass loss in the field and the rate of consumption of the ash leaf litter by the woodlice. The reduction in the initial N concentration induced by the high CO_2 treatment appeared to be the most likely factor explaining the observed reduction in leaf litter decomposition rates, since the initial N concentrations of litter material were highly correlated with litter decay constants (Fig. 3). However, changes in the concentrations of secondary plant metabolites, which are likely to occur under elevated CO_2 (Peñuelas *et al*., 1997), could also play an important role in affecting litter palatability and decomposition rates, but no measure of secondary plant metabolites was made in this study.

Litter chemical composition is recognized as a major factor controlling litter decay rates (Swift *et al*., 1979), with N concentration exerting a regulating effect in the early stages of decomposition, whilst lignin concentrations become more important in later stages (Berg *et al*., 1987). Additionally, C-to-N ratios have been shown to be good predictor of decomposition rates both across a great number of plant species (Taylor *et al*., 1979) and within a single species (Cotrufo *et al*., 1995).

Elevated CO_2 induces changes in the chemical composition of plant tissues, particularly N concentration. In a recent review Cotrufo *et al*. (1998) established a general 14% reduction in the N concentration of plant tissues exposed to high CO_2 regimes. Although it had been proposed that senescent materials may not maintain the CO_2 treatment effects found in harvested plant tissues (O'Neill, 1994), these litter quality changes, induced by the elevated CO_2, persisted into senescent material with a mean 11% decrease in N concentration of leaf litter being reported for woody-species (Cotrufo *et al*., 1998). Increasing concentrations of lignin and other polyphenolics have also been reported in plants exposed to high concentrations of atmospheric CO_2 (Cipollini *et al*., 1993; Cotrufo *et al*., 1994) and a 40% increase in tannin concentrations was reported for white oak exposed to doubled CO_2 concentrations (Norby *et al*., 1986).

There is growing evidence that these changes in litter quality induced by exposure to elevated CO_2

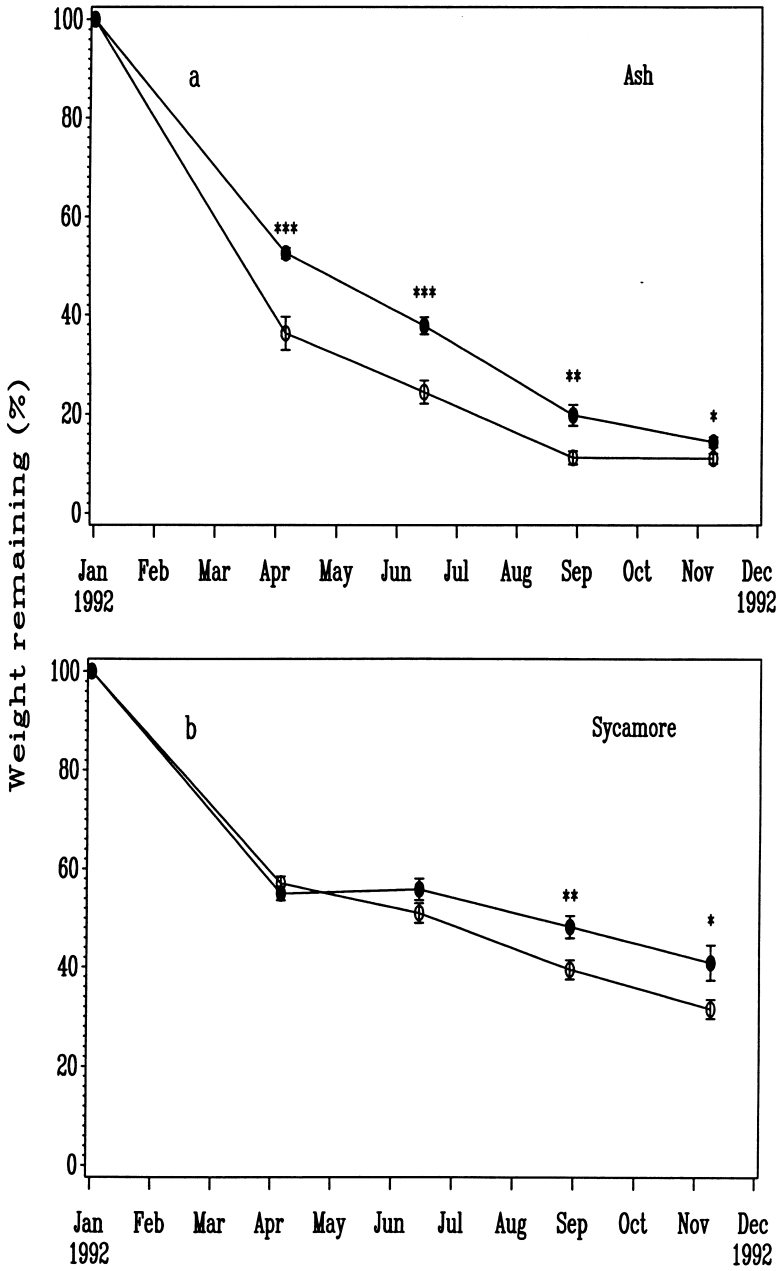

Fig. 1. (a) Ash (*Fraxinus excelsior* L.) and (b) sycamore (*Acer pseudoplatanus* L.) field decomposition rates for litters derived from ambient (350 μl l^{-1}, ○) and elevated (600 μl l^{-1}, ●) CO_2 concentrations. Vertical bars indicate standard errors, $n = 10$. Significance levels after Student's t test are given (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$)

atmospheres may lead to a reduction in litter decomposition rates (Kratz *et al.*, 1995; Cotrufo and Ineson, 1996). However, to date the work has been limited and somewhat equivocal (see O'Neill, 1994 and Cotrufo *et al.*, 1997). Significant reductions in decomposition rates have been observed in simple laboratory systems, yet are difficult to extrapolate to field conditions (Coûteaux *et al.*, 1991; Cotrufo *et al.*, 1994). Of the few reports on field decomposition rates, the majority have used materials which have not shown an effect of elevated CO_2 on litter quality and no significant differences in the rate of decomposition between control and CO_2-enriched litters have been found (Kemp *et al.*, 1994; O'Neill and Norby, 1996) with the exception of Van Ginkel *et al.* (1996) who found reductions in the decay

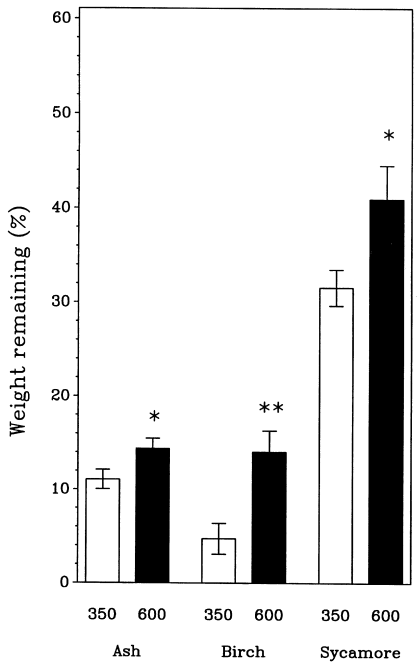

Fig. 2. Weight remaining after one year field incubation of ash, birch and sycamore leaf litters derived from ambient (350) and elevated (600) CO_2 atmospheric concentrations. Vertical bars indicate standard errors, $n = 10$. Significance levels after Student's t test are given ($*p < 0.05$; $**p < 0.01$). Data for the -N birch (*Betula pendula* Roth.) litters from Cotrufo and Ineson, 1996

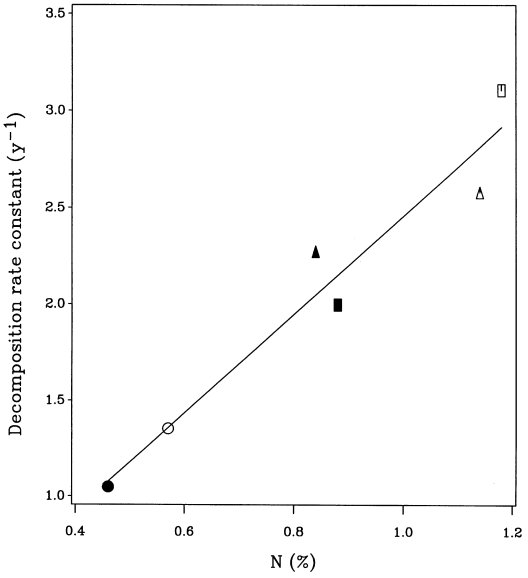

Fig. 3. Yearly decomposition rate constants, after the Olson (1963) model $k = \ln(X_o/X_t)/t_t - t_o)$, against initial leaf litter N concentrations for ash (△), birch (□) and sycamore (○) litters grown at two levels of atmospheric CO_2: 350 μl l^{-1} (open symbols) and 600 μl l^{-1} (closed symbols), $r^2 = 0.94$, $p < 0.001$, $y = 2.558x - 0.10$

rates of reygrass root tissues generated under elevated CO_2, but no changes in their C-to-N ratio.

In the decomposition experiments reported here using tree leaf litters grown under ambient and elevated CO_2 concentrations and decomposed in the field, leaves had been allowed to senesce naturally and were decomposed for a year under field conditions. Additionally, the results reported here confirm those obtained by Cotrufo *et al.* (1994) in laboratory microcosms, and demonstrate that elevated CO_2 also reduces decomposition rates of tree leaf litters under natural field conditions, when litters are also exposed to attack by soil fauna.

The food choice of isopods is influenced by the chemical composition of litter, which changes according to the degradation stage of the litter (Van Vensem *et al.*, 1993). Furthermore, according to Hassal and Rushton (1984) isopods prefer litter from plants with relatively low contents of physical and chemical anti-herbivore defenses. Our results showed that the litter derived from the elevated CO_2 treatment was not preferred, since animals only fed on the litter raised at ambient CO_2 regime. The preferred litter showed the highest N concentration and the lowest C-to-N and lignin-to-N ratios confirming the importance of these quality factors in controlling animal food choice (Carefoot, 1984; Gunnarsoon, 1987). The fact that the woodlice showed a clear rapid response, although they had not been accustomed to the litters derived from the solar domes, shows that the palatability test used in this study was a useful tool in providing information on the food preferences of isopods.

The contribution of isopods to litter fragmentation is assumed to be small because of their comparatively small body size and low natural population densities, but their litter consumption rate is reported to be four times greater than that of millipedes (Neuhauser and Hartenstein, 1978). However, their assimilation efficiency is low and much of the material consumed is not decomposed during its passage along the gut, but litter chemical and physical properties may improve during the passage along the gut, stimulating microbial growth (Ineson and Anderson, 1985). In this sense, Coûteaux *et al.* (1991) found a significant animal effect on decomposition of the chestnut litter under elevated CO_2 towards the later stages when a complex faunal community was used. This higher activity of the animal groups was concomitant with the proliferation of white-rot fungi, able to use lignin and aromatic-polymer protein substrates, and which only occurred in the litter produced in a CO_2-enriched environment (Coûteaux *et al.*, 1991).

The responses of soil fauna to elevated CO_2 have received less attention than other components of the soil system, and there is a lack of information about how the populations respond to increasing concentrations of CO_2 in terms of numbers and

Table 1. Litter quality properties and yearly decomposition rate constants (after Olson (1963), $k = \ln(X_o/X_t)/t_t - t_o$) for ash, birch and sycamore leaf litters generated under ambient (350 $\mu l\, l^{-1}$) and enriched (600 $\mu l\, l^{-1}$) CO_2 regimes. Values are means with standard deviation in parentheses

Species	Treatment CO_2 ($\mu l\, l^{-1}$)	N (%)	Lignin (%)	C-to-N ratio	Lignin-to-N ratio	k (yr^{-1})
Ash†	350	1.14 (0.23)	6.1 (0.07)	42 (7.42)	5.4 (1.06)	2.58
	600	0.84 (0.12)	7.4 (1.27)	56 (7.25)	9.1 (2.83)	2.27
Birch‡	350	1.18 (0.18)	17.7 (4.32)	41.8 (6.99)	15.5 (5.14)	3.10
	600	0.88 (0.17)	28.7 (4.80)	57.2 (9.58)	32.4 (9.08)	1.99
Sycamore†	350	0.57 (0.02)	9.1 (1.13)	81 (3.06)	16.2 (2.61)	1.35
	600	0.46 (0.04)	9.8 (0.35)	106 (8.22)	21.5 (0.89)	1.05

†Data for litter chemical composition from Cotrufo *et al.* (1994).
‡Data refer to the -N treatment, from Cotrufo and Ineson (1996).

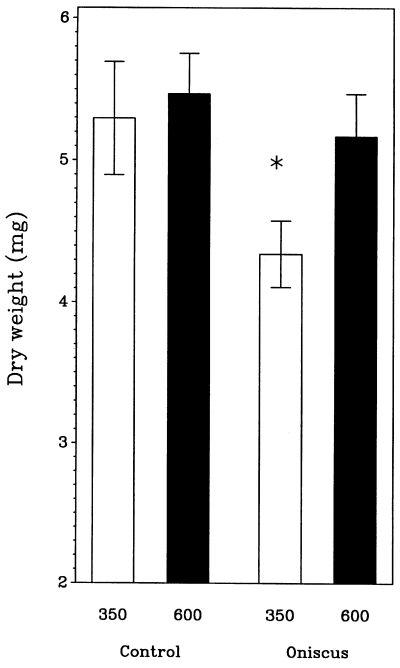

Fig. 4. Dry weights of ash leaf litter fragments, derived from ambient (350) and elevated (600) CO_2, after three days of incubation with (Oniscus, $n = 15$) and without *Oniscus asellus* (Control, $n = 10$). Vertical bars indicate S.E., significance levels after Student's t test are given (*$p < 0.05$)

diversity. Our results indicate that changes in litter quality, induced by elevated CO_2, may affect litter decomposition rates and its palatability for soil fauna and stress the need for more research in this area.

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