

Review Article

Effect of Elevated CO₂, O₃, and UV Radiation on Soils

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In this work, we have attempted to review the current knowledge on the impact of elevated CO₂, O₃, and UV on soils. Elevated CO₂ increases labile and stable soil C pool as well as efficiency of organic pollutants rhizoremediation and phytoextraction of heavy metals. Conversely, both elevated O₃ and UV radiation decrease inputs of assimilates to the rhizosphere being accompanied by inhibitory effects on decomposition processes, rhizoremediation, and heavy metals phytoextraction efficiency. Contrary to elevated CO₂, O₃, or UV-B decreases soil microbial biomass, metabolisable C, and soil N_t content leading to higher C/N of soil organic matter. Elevated UV-B radiation shifts soil microbial community and decreases populations of soil meso- and macrofauna via direct effect rather than by induced changes of litter quality and root exudation as in case of elevated CO₂ or O₃. CO₂ enrichment or increased UV-B is hypothesised to stimulate or inhibit both plant and microbial competitiveness for soluble soil N, respectively, whereas O₃ favours only microbial competitive efficiency. Understanding the consequences of elevated CO₂, O₃, and UV radiation for soils, especially those related to fertility, phytotoxins inputs, elements cycling, plant-microbe interactions, and decontamination of polluted sites, presents a knowledge gap for future research.

1. Introduction

Carbon dioxide, ozone, and ultraviolet radiation are individual climate change factors that have direct biological effects on plant coverage. Elevated CO₂ causes up- and downregulation of genes of primary plant metabolism and N₂ fixation; elevated O₃ significantly diminishes the carbon sink of soil-plant systems [1, 2]. Both rising CO₂ and surface O₃ impact upon plant growth, response of crops to pests and herbivores, and the ability of plants to support decontamination of polluted sites [1]. Decrease in stratospheric O₃ is accompanied by increasing UV radiation of which most attention has been given to UV-B. Elevated UV-B reduces crop yields and tree biomass, plant respiration potential, gas exchange, leaf area, and water-use efficiency and increases the content of amino acids, hormones, and flavonoids [3].

While replacement of current solvents by oxygenates decreases O₃ pollution [4], forest fires increase O₃ concentrations in some countries [5]. Calfapietra et al. [6] also reported formation of O₃ from volatile organic compounds (especially isoprenoids) released from vegetation, which react in the atmosphere with NO_x to produce O₃ under UV radiation.

Many reviews focused on the effects of elevated CO₂, O₃, and UV-B radiation on plant biomass, ecosystems, and human health (e.g., [1, 7]). Nevertheless, only little work has focused upon understanding the consequences for soils. In this paper, we present a review of the current knowledge on the impact of elevated CO₂, O₃, and UV on soils and identify new hypotheses for future research.

2. Effect of Elevated UV Radiation on Soils

2.1. Direct Effect of UV Radiation on Soil Microorganisms. Pigment content, cell oxygen yield, growth, C assimilation, and PSII of cyanobacteria change with increasing UV-B [8]; besides, UV-B also induces synthesis of mycosporine-like amino acids [9]. Soil surface bacteria are more resistant to UV than subsurface bacteria [4]. Nonmotile Gram-positive bacteria isolated from Antarctic soils are tolerant to UV radiation due to synthesis of protective melanins [10]. Also, compost-born thermophilic methanogenic Archaea were proved to be resistant to UV-B, probably due to their attachment to compost material acting as an effective carrier [11]. Growth

of lichens is not affected by UV-B due to increased phenolics content [12].

Direct effects of UV on soils occur through a shift of the fungal community with an increase in competitive abilities of darkly pigmented fungi [13]. Only some of the soil and phylloplane fungal species are sensitive to UV-B [14]. For example, the entomopathogenic fungus *Tolypocladium* sp. is UV-B tolerant [15]. Peatland amoebae are more abundant in ambient than reduced UV-B and diversity of some species increases under ambient UV-B [16].

2.2. Direct Effect of UV Radiation on Soil Meso- and Macrofauna. UV-B pretreatment decreases rotifers, nematodes and mites population size and increases generation time in soils polluted with heavy metals due to reproductive defects; nevertheless, it protects *Caenorhabditis elegans* from disturbed locomotion [16, 17]. Experiments showed that a large increase in nematode density in Antarctic soils (especially microbivorous genus *Plectus*) resulted from blocking UV with a UV-absorbing perspex cloth [18]. No effect of UV-B on the mass of earthworms feeding on litter was found, and some of the species benefited from UV-B [19]. Low mortality of spider mites due to UV-A, UV-B, and UV-C was reported by Suzuki et al. [20], while inactivation of *Ascaris* eggs was significant only in water [21].

2.3. Release/Degradation of Soil Pollutants by UV Radiation. Elevated UV-B (but not UV-A) directly reduces soil-associated Hg through significant increase of Hg emissions from forest soils [22]. UV-B is also known to increase degradation of pollutants (phenylurea herbicides, p,p'-DDT, 2,4-dichlorophenoxyacetic acid, biphenol, Z or PAHs), while PAHs degradation on soil surfaces, in the presence of nanometer anatase TiO₂, follows pseudo-first-order kinetics [23]. UV photolysis has been suggested as a suitable treatment for extracts of PAHs contaminated soils, where up to 83% removal was achieved [24].

2.4. Measured Effects of UV-B Radiation on Soils. Elevated UV-B does not substantially influence initial chemical composition of leaf litter [25] and has only little effect on total carbon (C_t) and nitrogen (N_t) in soils; on average they decrease by 2 and 9%, respectively (Figure 1). On the other hand, elevated UV-B decreases NH₄⁺-N and NO₃⁻-N by 46 and 14%, respectively (Figure 3), and reduced UV-B (compared to ambient value) decreases dissolved organic carbon (DOC) and phosphorus content in 0–10 mm of peatland in course of vegetation [16]. Pretreatment of air-dried litter with UV followed by rewetting did not change decomposition rate [26], whereas some researchers found inhibitory effect of UV-B on soil organic matter (SOM) decomposition (reduced by 32% on average) with no effect on Q₁₀ (Figure 2). Lower effect later in the season occurs due to increasing crop coverage reducing soil sterilization [27]. Also, N₂O fluxes in soils are reduced by elevated UV-B by ca. 22% with no change of diurnal variation patterns (Figure 2). Elevated UV-B equivalent to 15% O₃ depletion decreases N₂ fixation in tropical leguminous crops due to reduced photosynthesis

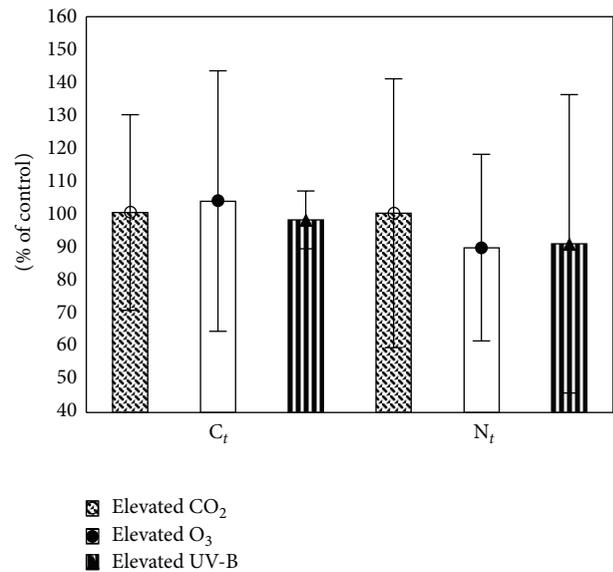


FIGURE 1: Effect of elevated CO₂, O₃, and UV-B on C_t and N_t (recalculated from [30–33]). The values are expressed in % of control = 100% which represent ambient CO₂, O₃, or UV-B (mean ± SD).

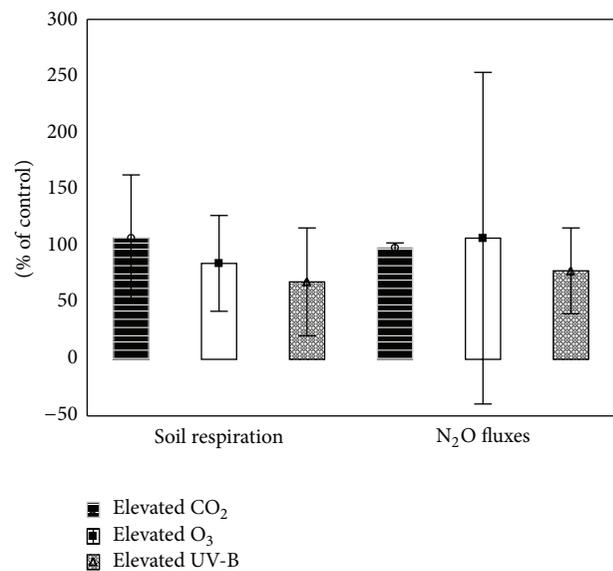


FIGURE 2: Effect of elevated CO₂, O₃, and UV-B on soil respiration and N₂O fluxes (recalculated from [27, 34–40]). The values are expressed in % of control = 100% which represent ambient CO₂, O₃, or UV-B (mean ± SD).

and nodulation including nitrogenase activity; nevertheless, the molecular basis of this phenomenon is not known yet [28]. Altered gene activity due to elevated UV-B was found to enhance rice allelopathic potential (inhibition and stress of neighbouring plants especially at high density in native environment) including autotoxicity via phytotoxins of root exudates and leaf leachates [29] of which identification presents a knowledge gap for future research.

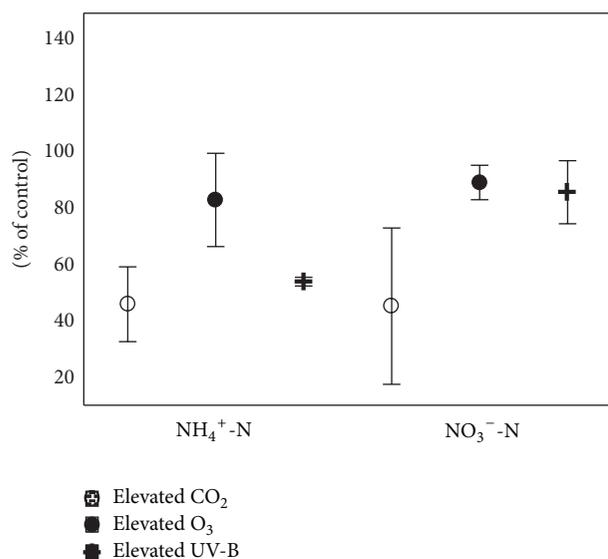


FIGURE 3: Effect of elevated CO₂, O₃, and UV-B on NH₄⁺-N and NO₃⁻-N content in soil (recalculated from [16, 27, 33, 41]). The values are expressed in % of control = 100% which represent ambient CO₂, O₃, or UV-B (mean ± SD).

2.5. Hypotheses on Indirect Effects of UV Radiation on Soils.

Plant coverage ameliorates the impact of elevated UV-B on soil microorganisms; nevertheless, indirect effects via altered quality and reduced quantity of plant biomass are hypothesised to inhibit SOM decomposition and heavy metals bioremediation. These include especially accumulation of phenolics, salicylic acid, tannins, cinnamic acid, and flavonoids [3]. Phenolics are involved in stabilization of aggregates and some of them (e.g., gallic acid) decrease cation exchange capacity (CEC) of soils; on the other hand, hydrolysable tannins (e.g., β -1,2,3,4,6-penta-O-galloyl-D-glucose) increase the CEC [42]. Phenolics and flavonoids are inhibitors of decomposition processes including enzymatic activities (sulphatase, phosphatase, β -glucosidase, xylosidase, chitinase, and dehydrogenase) and are also involved in stabilization of xenobiotics and Fe complexation representing a potential constraint in wetland-based acid mine drainage bioremediation, due to low Fe availability (e.g., [43, 44]). Phenolics are also known to support growth of PCB-degrading bacteria [45].

3. Effect of Elevated CO₂ on Soils

3.1. Alteration of Soil Properties due to Elevated CO₂. Elevated CO₂ delays soil water depletion due to partial plant stomatal closure and alters solarization efficiency and heat fluxes [46, 47]. Furthermore, dilution of plant biomass by carbohydrates and increased plant-derived C inputs including rhizodeposition are hypothesised to increase C_t with no effect on N_t and reduction of mineral nitrogen content in soils [48]. Nevertheless, recalculation of data from a range of studies showed negligible effect of elevated CO₂ on soil C_t and N_t (Figure 1). Effect of elevated CO₂ on soil C_t and N_t is

ecosystem- and type of plants-dependent being increased only in sweetgum or cotton plantations, deserts, *Agrostis capillaris* cover, or seminatural grasslands (Table 1). It may also be affected by the initial soil properties, the type of experiment (laboratory *versus* field), occurrence of N₂-fixing species, and the plant C allocation pattern being affected by plant genotypic variation [34]. For example, the effect of elevated CO₂ on soils may be diminished in base-rich sites [49]. Contrary to cultivated plants, wild genotypes allocate more C into roots resulting in greater rhizodeposition under elevated CO₂ [34, 48].

Proportion of labile to recalcitrant C fraction changes in response to elevated CO₂ via increased transfer of C into slow-decay C pool and reduces decay of old C; some works describe rhizodeposition-induced decomposition of stable soil C; quality and quantity of the labile C are altered by increased plant litter and root exudation [34, 35]. Elevated CO₂ increases decomposition of metabolisable C only in topsoils with opposite effect in subsoils and no effect on amides degradation [34]. Root biomass and volume of rhizospheric soil including mycorrhizal symbiosis of trees in boreal and temperate zones increase due to elevated CO₂ [34, 48]. In some ecosystems (peatlands), growth of root biomass of low decomposability is induced by elevated CO₂, and in some cases, decomposition of fine roots is faster [50]. Concentrations of both mineral nitrogen forms (NH₄⁺-N and NO₃⁻-N) in soils are significantly reduced (by >50% on average) by elevated CO₂ (Figure 3), probably due to N dilution in foliage and increased plant-microbes competition for N sources [48]. Furthermore, elevated CO₂ may alter the chemistry of groundwater (Ca²⁺, trace metals and other types of cations and anions) [48] and its effect on bulk density or pH of soil is low (Table 1).

3.2. Elevated CO₂ versus Soil Microbial Community and Activity of Enzymes.

Elevated CO₂ (including transient elevation) changes the structure and physiology of soil microbial community in favour of bacteria due to lower soil nitrogen inputs which are accompanied by reduction of the abundance of taxonomic units within the *Firmicutes* as well as the populations of Gram-positive bacteria in rhizosphere soils [54, 55]. Allocation of C to soil microorganisms usually depends on the type of ecosystem [34, 56] and is often accompanied by increased C_{MIC}/C_t ratio. An increase of soil microbial N (N_{MIC}) as a posttreatment response to elevated CO₂ in N-limited ecosystems was found probably due to lower nutrient (nitrogen) competition between microorganisms and plants [57]. Soil respiration increased by 7% on average due to elevated CO₂ (Figure 2) compared to ambient control without change of substrate use efficiency [35] and N₂O fluxes were only slightly changed (1.5% decrease) (Figure 2).

Numbers of archaeal and bacterial 16S rRNA and genes encoding key enzymes of ammonia-oxidation (*amoA*), denitrification (*nirK*, *nirS*, and *nosZ*), and genes of nitrate-reducing bacteria (*narG*, *napA*) are increased or reduced (or not affected) in the rhizosphere by elevated CO₂ depending on inputs of fertilizers (N), soil depth and moisture, type of plant metabolism (C₃ versus C₄), time of sampling during

TABLE 1: Effect of elevated CO₂ on soils according to type of ecosystem.

Type of ecosystem	Soil properties	References
Deciduous and coniferous forests	Increased or decreased C/N	[42]
Poplar cultivation	No effect on C _{ox} , N _t and bulk density, increased humification, increased or reduced export of DOC, increased leaching of refractory C	[35]
Rice-wheat rotation	Decreased available N by up to 50% and available P by 30%	[50]
Oak ecosystem	No effect on total organic carbon (TOC), 30% reduced slow-degradable C, 41% increased C _{MIC} , no effect on pH	[50]
C ₄ plant communities	Decreased N mineralization	[36]
<i>Agrostis capillaris</i>	Increased C _{ox} and decreased C/N	[30]
<i>Lathyrus pratensis</i>	Decreased C _{ox} and increased C/N, decreased soil bacteria and mycorrhizal fungi	[30]
<i>Plantago lanceolata</i>	Increased net N mineralization	[31]
Different ecosystems	Decrease in relative abundance of Acidobacteria Group 1 bacteria, increased fluxes of CO ₂ , NH ₃ , N ₂ O, and CH ₄ with induction of CH ₄ oxidation	[39]
Pine ecosystem	No effect on soil properties	[39]
Sweetgum plantation	Increased C _{ox} , no effect on soil microbial community, enzymatic activity, potential N mineralization and nitrification	[33]
Seminal natural grasslands	Increased C _{ox} and N _t	[51]
Cotton plantation	Increased C _{ox} only under wet moisture regime, no effect on N _t	[52]
Deserts	Increased C _{ox} and N _t under some types of coverage, low effect on soil pH and bulk density, no effect on arbuscular mycorrhizas; no effect on fluxes of CO ₂ , NH ₃ , N ₂ O, and CH ₄	[53]

growing season (start, peak, or senescence), and sampling year [58, 59]. Reduced crenarchaeal sequences and altered abundance of 16S rDNA as well as *amoA* genes of archaeal community or enhanced fungal cellulolytic community gene *cbhl* fragment richness due to elevated CO₂ were found in the rhizosphere of C₃ but not C₄ plants [58]. Abundance of red-like *cbbl* genes of CO₂-fixing bacteria is reduced and diversity of soil purple phototrophic bacteria increased in conditions of elevated CO₂ [58, 59]. N fertilization increases abundance of bacterial *amoA* gene only under ambient CO₂ whereas an opposite effect occurs for thaumarchaeal *amoA* gene [58, 59].

Elevated CO₂ induces an increase of soil enzymatic activities (protease, xylanase, invertase, phenol oxidase, alkaline phosphatase, and arylsulphatase) in the main rooting zone due to enzyme regulation (synthesis and activity) via enlarged pool of easily available substrates rather than by shifts in microbial abundance [57]. Stimulation of plant root-derived enzymatic activities due to enhanced photosynthesis is also hypothesised under elevated CO₂ [43].

3.3. Effect of Elevated CO₂ on Soil Meso- and Macrofauna. Elevated CO₂ suppresses the role of fauna in litter decomposition due to its dilution by carbohydrates and the effect is ecosystem-dependent being significant especially in tropical forests [60, 61]. Elevated CO₂ modifies the pattern (abundance and diversity) of nematode communities (especially groups of omnivores, saprophagous feeders, and predators), earthworms and enchytraeids, oribatid mites, microarthropods, collembolans, and omnivorous insects as well as the proportion of edaphic groups via changes of plant biomass quality and moisture [61]. Elevated CO₂ has generally been found to have negative impacts on the performance of insect

herbivores whose larvae reach smaller size when feeding on elevated CO₂-grown plants [61]. The hypothesised negative impact of elevated CO₂ on omnivorous bugs via lowering the quality of plants and prey was not proved; on the contrary, the predators may benefit from elevated CO₂ through increased vulnerability of their prey [60, 61].

4. Effect of Ozone on Soils

4.1. Alteration of Soil Properties due to Elevated O₃. Effect of elevated O₃ on soils is poorly understood. O₃ deposition to soil has been expressed by parameters such as aerodynamic resistance (R_a), quasilaminar boundary layer resistance (R_{bO_3}), and soil resistance (R_{soil}) being a function of soil water content with daily variations [62]. Ozonation of humic acids or their components (p-hydroxybenzaldehyde, vanillin, syringaldehyde, vanillic acid, and di-n-butylphthalate) leads to formation of mutagenic compounds and O₃ also induces amino acid racemization [63].

Contrary to elevated UV-B or CO₂ which cause N dilution and increased phenolics in plant biomass, elevated O₃ modifies plant biomass via decrease in both N and phenolics [36, 64]. Elevated O₃ increases C_t and reduces N_t by 4 and 10%, respectively (Figure 1); NH₄⁺-N and NO₃⁻-N are also reduced by 17 and 10%, respectively (Figure 3), including humic acids fraction, C_{MIC}, and pH of soils in different ecosystems (black cherry, milkweed, spring wheat, and beech) [19]. Soil respiration is decreased (by 15% on average) (Figure 2) under O₃ enrichment; the same was found in case of methane emissions from soils of different ecosystems (e.g., temperate lowland peat bogs or rice soils) which are reduced by about 25% [65]. On the other hand,

N_2O fluxes are enhanced (by 7% on average) under O_3 enrichment (Figure 2) as it reacts with N_2O emitted from fertilized soils [37]. Elevated O_3 increases Ca^{2+} , Mg^{2+} , and Mn^{2+} in soil solution and stimulates export of NO_3^- from forest sites [19].

4.2. Alteration of Soil Microbial Communities and Fauna by Elevated O_3 . Elevated O_3 alters soil microflora structure and physiology with a negative impact on numbers of bacteria and fungi, glutathione content of protozoa, and His⁺ reversion of some bacteria [30]. Especially the numbers of functional microbial genes are lower under O_3 treatment in dependence on plant coverage development and N fertilizers inputs with no effect on *amoA* and *nosZ* genes abundance [66]. Increased terpene inputs (especially α - and β -pinene or 3-carene) as a consequence of elevated O_3 are hypothesised to alter soil microbial community, especially via stimulation of bacteria and inhibition of fungi [67]. Roots of forest trees are also a significant source of monoterpenes in soil and over 75% of ectomycorrhizal fungi or 25% of isolated saprotrophic fungi were inhibited by one of the monoterpenes, affecting the structure of the fungal community [67]. On the other hand, monoterpenes supplied to soil increase degradation of polychlorinated biphenyls (PCB), even without increasing the bacterial biomass [68]. Elevated O_3 strongly decreases the abundance rather than genera richness of soil collembolans compared with ambient atmospheric O_3 , probably due to decreased allocation of carbohydrates to roots. However, in the Bt cotton fields, elevated O_3 did not significantly affect the abundance or diversity of soil collembola suggesting that Bt cotton can buffer the effect of elevated O_3 on soil collembolans via root-derived ways [69]. Contrary to elevated CO_2 and UV radiation, elevated O_3 is hypothesised not to increase phytotoxicity of soils through inputs of plant phenolics [36]; nevertheless, a direct effect via racemization of low-molecular-weight organic compounds (amino acids) is hypothesised [63].

5. Hypotheses on the Effect of Elevated CO_2 , O_3 and UV Radiation on Plant-Microbe Competition for N Sources

Plant communities, especially at low productivity sites with acid soils, are more adapted to organic N uptake; nevertheless, higher proportion of both soil organic as well as mineral N is captured by microorganisms rather than by plants [48]. Management practices including grasslands mowing or grazing or forest stands thinning are thought to reduce plant-microbe competition for N sources, since N-cycling and mineralization rates are increased and are accompanied by lower organic N availability and no effect on kinetics of organic N uptake by microorganisms [48].

O_3 enrichment shifts the N-balance in favour of plants over soil microorganisms, being significant especially in ecosystems with low productivity (grasslands, mountain forests, and tundra communities) where organic N forms the dominant pool [48]. Alterations in plant-microbe competition for N sources may be facilitated by natural fungicides

(phenolics) which is hypothesised to be significant in case of elevated CO_2 and UV, but not O_3 [64]. In this case, dominance of the bacterial fraction of the soil microbial community favours microbial competitiveness over plant roots; however, this advantage may be eliminated by fertilization [48]. Also, it is hypothesised that the maximum N acquisition by plants is regulated by intermediate concentrations of phenolics [64]. Elevated O_3 reduces ascorbic acid in plant biomass; its degradation in soils may act to produce an effective sporocide, which plays a role in mitigation of salinity effects on plant growth [70]. Competition between microbes and plants for N sources is regulated by rhizodeposition in terms of exudation rates and qualitative composition of the exudates, both being altered by elevated UV-B, CO_2 , and O_3 [48]. Nitrifiers are strong competitors for NH_4^+ on fertile sites where competition may be reduced due to increased tannins under elevated UV-B or CO_2 [48].

6. Conclusions

Overall, study of the consequences of elevated CO_2 , O_3 , and UV radiation for soils is significant due to increasing CO_2 concentrations worldwide and also because there is clear evidence that stratospheric O_3 is being depleted which causes increased ground UV radiation. On the other hand, change of air quality due to emissions of hydrocarbons and exhaust gases leads to increasing tropospheric O_3 production. Contrary to elevated CO_2 , O_3 , or UV-B decreases C_{MIC} , metabolisable C, and soil N_i content leading to higher C/N of soil organic matter. Mechanism of the CO_2 or O_3 enrichment effects on soils including elevated UV-B radiation differs considerably. Elevated O_3 or UV-B decreases inputs of assimilates to the rhizosphere and has an inhibitory effect on decomposition processes and rhizoremediation of organic pollutants. UV-B shifts soil microbial community and decreases populations of soil meso- and macrofauna directly rather than via induced changes of litter quality and root exudation as in case of elevated CO_2 or O_3 . Worldwide increasing CO_2 concentrations stimulate rhizoremediation of organic pollutants due to higher root biomass and volume of rhizospheric soil as well as phytoextraction of heavy metals (contrary to elevated O_3 or UV-B) as a result of increased mycorrhizal colonization and plant biomass. Enhanced C inputs and root mycorrhizal colonization as a consequence of elevated CO_2 are hypothesised to stimulate both microbial and plant N acquisition. UV-B is hypothesised to reduce both plant and microbial competitiveness for soluble soil N whereas O_3 enrichment favours microbial competitive efficiency. Since the effects of elevated CO_2 , O_3 , and UV radiation on soils are only little understood, it is essential to conduct further studies to understand their consequences for soil fertility, elements cycling, and decontamination of polluted sites.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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